



## Plant Growth Promotion and Biocontrol by Endophytic and Rhizospheric Microorganisms From the Tropics: A Review and Perspectives

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Currently, the tropics harbor a wide variety of crops to feed the global population. Rapid population expansion and the consequent major demand for food and agriculturebased products generate initiatives for tropical forest deforestation, which contributes to land degradation and the loss of macro and micronative biodiversity of ecosystems. Likewise, the entire dependence on fertilizers and pesticides also contributes to negative impacts on environmental and human health. To guarantee current and future food safety, as well as natural resource preservation, systems for sustainable crops in the tropics have attracted substantial attention worldwide. Therefore, the use of beneficial plant-associated microorganisms is a promising sustainable way to solve issues concerning modern agriculture and the environment. Efficient strains of bacteria and fungi are a rich source of natural products that might improve crop yield in numerous biological ways, such as nitrogen fixation, hormone production, mobilization of insoluble nutrients, and mechanisms related to plant biotic and abiotic stress alleviation. Additionally, these microorganisms also exhibit great potential for the biocontrol of phytopathogens and pest insects. This review addresses research regarding endophytic and rhizospheric microorganisms associated with tropical plants as a sustainable alternative to control diseases and enhance food production to minimize ecological damage in tropical ecosystems.

Keywords: biological control, endophytes, plant-microbial symbiosis, rhizobacteria, sustainable food production, tropical crops

### **INTRODUCTION**

The ever-growing demand for agriculture-based products and food security does not meet the rapid increase in world population (Pawlak and Kołodziejczak, 2020; Fasusi et al., 2021). To overcome this global challenge, in the past few decades, agricultural systems have been adapted to this reality. Within a limited time, the use of chemical fertilizers and agrochemicals is capable of increasing food production and improving crop yield, quality, and shelf life. However, these practices are costly in terms of ecosystem degradation, climate change, soil erosion, and biodiversity loss (Fasusi et al., 2021; Mitter et al., 2021). Reports have reiterated the gradual decrease in soil health in the long

term as an effect of the indiscriminate use of agrochemicals during the past few decades (El-Ghamry et al., 2018; Guha et al., 2020). Furthermore, Berkelmann et al. (2020) showed that the functional potential of soil microbial communities in rainforests is drastically affected by their conversion into managed landuse systems.

Regarding conventional fertilizers (calcium ammonium (CAN). nitrate diammonium phosphate (DAP), monoammonium phosphate (MAP), nitrogen, phosphorus and potassium (NPK), single superphosphate (SSP), triple superphosphate (TSP), and urea, although widely used, it has been reported that in subhumid zones, low nutrient use efficiency is a consequence of using large amounts of these agronutrients (Rop et al., 2018; Lawrencia et al., 2021). According to the International Fertilizer Industry Association (2021) database (https://www.ifastat.org/databases/plant nutrition), between 2016 and 2018, Brazil exported 529.2 thousand tons and consumed on average 15,000,000 tons of N, P2O5, and K2O derivatives. Additionally, diseases caused by phytopathogenic fungi represent a severe threat to the production of several crops worldwide (Brauer et al., 2019; Cullen et al., 2019; Omomowo and Babalola, 2019).

Plant-associated microbes are a well-known source of natural secondary metabolites, as well as a vast and unexplored source of unique chemical structures of phytochemical compounds, biofertilizers, and growth promoters, which can be considered natural and sustainable approaches to minimize the use of agrochemicals. The involvement of these microbiological tools in the development of agriculture and biotechnological processes is evident since issues concerning sustainable agriculture vs. practices entirely dependent on agrodefensives and synthetic fertilizers might cause negative impacts on the environment and human health (Brauer et al., 2019; Cullen et al., 2019; Omomowo and Babalola, 2019).

Endophytes can establish a mutualistic interaction with the host plant by exchanging nutrients and protection; they produce antibiotics and other substances that can protect the plant against stress conditions such as attacks by herbivores and pests and plant pathogens. These microorganisms live in intimate interactions with the host plant without causing any apparent disease symptoms (Azevedo et al., 2000; Pacifico et al., 2019). In contrast, rhizospheric space is a narrow soil zone that surrounds the roots and possesses a dynamic and highly diversified microbial community (bacteria, fungi, arbuscular mycorrhizae, oomycetes, viruses, and archeas) that is attracted by plant exudates and nutrients and capable of directly and indirectly modulating plant growth, nutrition, and health (**Figure 1**) (Philippot et al., 2013).

Tropical ecosystems are major reservoirs of biological diversity on our planet, and with the recent availability of rigorous methods for characterizing microbial communities, the tremendous diversity of microorganisms in tropical environments is now also evident. Microorganisms compose a large proportion of biological diversity on Earth and have fundamental roles in the structure and function of ecosystems around the globe (Azevedo and Quecine, 2017). In this scenario, this review provides insights into the roles of microorganisms in a range of tropical environments, including agricultural fields, mangroves, savannahs, and Atlantic forests, and provides a glimpse into the microbial communities present in a range of tropical environments to explore the many potential applications of tropical microorganisms to agricultural productivity.

### CLASSIFICATION AND INTERACTIONS OF PLANT-ASSOCIATED MICROBES ON THEIR HOSTS

Endophytes were originally described in 1866 by de Bary, who observed and outlined possible distinctions between plant pathogens (Gouda et al., 2016). Such microorganisms might be found from roots to aerial plant structures, living a part of or all their life cycle within their host plants without causing apparent damage or disease (Liu et al., 2017). Endophytic microorganisms typically colonize internal plant tissues through the vascular system, apoplasts, and outer cell layers, where the pathways of penetration might be wounds or emergency areas of lateral roots and rootlets in germination (Liu et al., 2017).

Furthermore, endophytes constitute an important source of a plethora of natural compounds (alkaloids, phenolic acids, quinones, steroids, saponins, tannins, and terpenoids), which play a critical role in plant resistance to phytopathogenic infections (Fadiji and Babalola, 2020; Morelli et al., 2020). However, bacterial secondary metabolism is also mediated by *quorum sensing* (QS), which allows the production of multiple substances, where cell density creates a complex signaling system that transcribes specific genes for their interaction with their hosts (Krzyzek, 2019). Moreover, plants have been reported to possess quorum quenching (QQ) molecules, which can directly influence quorum sensing and respond to QS molecules, promoting direct plant growth (Kandel et al., 2017).

Likewise, the biodisponibilization of phytonutrients in the rhizosphere is regulated by quorum communication of the soil microbial community (Philippot et al., 2013). In summary, soil harbors a competitive and diversified microbiome (Onaka, 2017). The crucial influence of nutrients, exudates, border cells, and mucilage released by the plant in its root environment can significantly affect its rhizospheric microbial colonization (Hassan et al., 2019). Therefore, the role of rhizomicrobes in plant health is crucial (Omotayo and Babalola, 2020).

Plant growth-promoting rhizobacteria and endophytes have diverse beneficial effects on host plants through different mechanisms; these microorganisms are generally referred to as plant growth-promoting microbes (PGPMs). In return, the roots of the plant release exudates containing nutrients and compounds that can be used by PGPM for their development (Lopes et al., 2021). The inoculation of PGPM into crops is considered an environmentally friendly alternative to chemical fertilization (Lopes et al., 2021).

Innumerable interactions between plants and the soil microcommunity, such as PGPM, occur by indirect and direct mechanisms (Hassan et al., 2019). Indirectly, competition for nutrients in the rhizosphere might suppress potential pathogens (Khatoon et al., 2020). However, direct mechanisms include the ability to biosynthesize phytohormones that promote root



**FIGURE 1** The rhizosphere is a dynamic and complex habitat of innumerable microbes and invertebrates that are attracted by nutrients, exudates, border cells, and mucilage released by plant roots. Thus, symbiotic PGPR indirectly/directly regulates the composition and biomass of the plant microcommunity in natural ecosystems. Indirect mechanisms might occur during competition for nutrients, where PGPR suppresses the effects of pathogens by the production of antibiotics, siderophores, and lytic enzymes, whereas nitrogen fixation, phosphate biodisponibilization, and phytohormone production directly affect plant growth.

and shoot growth (e.g., indole-3-acetic acid and cytokinin), solubilization of phosphate, zinc, potassium, and fixation of atmospheric nitrogen (Batista et al., 2018; Khatoon et al., 2020). **Figure 1** Plant and scheme summarize the influence of endophytes and rhizosymbiotic microbes on the plant.

Many plant species currently cultivated and used in agriculture originate or were domesticated in the tropics (Gepts, 2008). Geographic localization, mean annual temperature, and mean precipitation favor high levels of biodiversity in tropical ecosystems (Andresen et al., 2018). Plants residing in tropical regions constitute a promising source of a great diversity of bacteria and fungi with beneficial potential to be explored as biological controllers of pathogens and plant growth promoters in a more sustainable and ecofriendly way (Harman et al., 2020; Umokoro, 2020).

According to Azevedo et al. (2000), the first reports on the isolation of microorganisms associated with tropical hosts in South America date back to the 1980's (Petrini and Dreifuss, 1981; Dreyfuss and Petrini, 1984). Since then, the number of studies focused on the isolation and exploration of endophytic and rhizospheric microorganisms inhabiting plants from different tropical ecoregions has increased worldwide (Azevedo and Quecine, 2017). Some studies related to this theme are discussed in further detail below.

### THE IMPACT OF BENEFICIAL MICROBES ON PLANT GROWTH-PROMOTING OF TROPICAL CROPS

### Beneficial Microbes as Biocontrol and Growth-Promotion Agents for *Paullinia cupana*

*Paullinia cupana* var. *sorbilis* (Mart.) Ducke (Sapindaceae), or guarana, is a typical tropical plant originally from the Amazon rainforest, whose genetic basis is present mainly in the Maués state of Amazonas (Henman, 1982). Brazil is a unique country as a commercial-scale producer of guarana, and soft drinks and other products commercialized as syrup, powder, extract, dietary supplements, cosmetics, and pharmaceuticals serve both domestic and foreign markets (Kuri, 2008; Hamerski et al., 2013).

In recent decades, anthracnose has been limited to the production and expansion of guarana in the Amazon State (Atroch and Nascimento Filho, 2018), and currently, Bahia State leads production (Meneghetti et al., 2021). Since guarana has great social and economic importance for Brazil and methods to control anthracnose are not effective (Tavares et al., 2005), research groups have joined efforts to find the microbiota associated with *P. cupana* var. *sorbilis* as a solution for reducing the incidence of the disease and increasing production.

In a study carried out by Bogas et al. (2015), the authors verified differences in the structure of the endophytic bacterial communities associated with *P. cupana* leaves collected from Santa Helena farm, Maués. Plants with symptoms of anthracnose showed significantly higher diversity, density, and number of operational taxonomic units than asymptomatic plants. The *Firmicutes* phylum, represented mainly by the *Bacillus* genus,

was significantly more isolated from asymptomatic plants. In 16S rRNA gene clone library analysis, *Proteobacteria* was the phylum significantly more present in asymptomatic plants. The *Pseudomonas* genus was observed in both treatments but at the highest frequency in asymptomatic plants. Based on other studies, the authors suggested that the presence of *Colletotrichum* sp. seems to be important to cause shifts in the *P. cupana* microbial communities, and the *Bacillus* and *Pseudomonas* genera could confer protection to asymptomatic plants against infection by phytopathogens.

In a similar study, Bonatelli et al. (2019) evaluated endophytic bacterial communities of leaves of *P. cupana* collected from Santa Helena farm, Maués. In general, the culture-dependent approach revealed a predominance of *Acinetobacter*, *Enterobacter*, and *Serratia* genera in symptomatic leaves and *Erwinia*, *Pantoea*, *Pseudomonas*, and *Stenotrophomonas* genera in asymptomatic leaves. The *Bacillus* genus was accessed similarly in both treatments. Using pyrosequencing, *Proteobacteria* was the most abundant phylum. *Acinetobacter*, *Pseudomonas*, and *Klebsiella* were the most abundant genera in symptomatic leaves. *In vitro* assays showed that especially *Bacillus* sp. EpD2-5 isolated from asymptomatic leaves inhibited the growth of *Colletotrichum* sp., which was attributed to lytic enzymes and siderophores produced by the bacteria evaluated.

Liotti et al. (2018) isolated endophytic bacteria from seed, leaf, and root tissues collected from two *P. cupana* genotypes in Embrapa (Brazilian Agricultural Research Company) experimental farms located in Manaus and Maués, Brazil. The colonization rate, richness, diversity, and species composition varied across the plant organs and geographic location. The main phyla identified were *Proteobacteria*, *Actinobacteria*, and *Firmicutes*. Some strains induced *Sorghum bicolor* growth and antagonistic traits against *Colletotrichum guaranicola and Fusarium decencellulare*.

Batista et al. (2018) evaluated the diversity and plant growthpromoting potential of bacteria isolated from rhizosphere samples collected from asymptomatic and symptomatic guarana plants from Santa Helena farm, Maués. Proteobacteria and Firmicutes were the dominant phyla, and Burkholderia and Bacillus were the most abundant genera found in the rhizosphere samples evaluated. The multitrait PGP strains Bacillus sp. RZ2MS9 and Burkholderia ambifaria RZ2MS16 expressively promoted corn and soybean growth under greenhouse conditions. The strains RZ2MS9 and RZ2MS16 increased the root dry weight in corn and significantly increased the dry weights in both corn and soybean. The data suggested that the RZ2MS9 and RZ2MS16 strains have the potential to be explored as inoculants within a broad range of hosts, which could be related to biological nitrogen fixation and auxin, phosphate, and siderophore production. The agronomic potential of Bacillus sp. the RZ2MS9 strain (Batista et al., 2018) was evaluated in other studies. Andrade et al. (2020) verified an increase in the seed germination and dry mass of seedlings of DKB390 and 30A37PW(R) maize hybrids treated with rhizobacteria, as well as an increase in the seed speed of the 30A37PW(R) hybrid treated with bacteria-free filtrate. Almeida et al. (2021) showed a synergistic effect on maize root and shoot dry weight coinoculated with *Bacillus* sp. RZ2MS9 and the commercial inoculant *Azospirillum brasilense* Ab-V5.

Additionally, studies have demonstrated the importance of the fungal community associated with guarana plants. Silva et al. (2018) isolated and identified endophytic fungi from roots and seeds of *P. cupana* susceptible and tolerant to anthracnose cultivated in Embrapa experimental farms in the cities of Manaus and Maués. The plant geographic location, clonal type, and organ influenced the structure of the endophytic fungal community of *P. cupana*, which harbors species that synthesize lytic enzymes (i.e., *Fusarium oxysporum, Mycoleptodiscus terrestres, Trichoderma harzianum*) and indole-3 acid acetic acid (i.e., *F. oxysporum, Fusarium solani, T. harzianum, Trichoderma asperellum*) *in vitro*, opening possibilities to propose their applications to plant growth and protection.

In a more recent study, Casas et al. (2021) demonstrated the reduction of lesions caused by *Colletotrichum fructicola* in guarana seedlings (cultivar BRS-Maués) after treatment with a conidial suspension of the endophyte *Colletotrichum siamense* isolated from healthy leaves of guarana plants at the Santa Helena farm. The endophyte promoted total protein and pathogenesis-related protein (PRP) synthesis at different times after *C. fructicola* inoculation. This study seems to be the first about resistance induction in guarana plants for the control of phytopathogens.

### Beneficial Microbes as Biocontrol and Growth-Promotion Agents for *Jatropha curcas*

Jatropha curcas L. (Euphorbiaceae), is native to Central America and distributed worldwide in tropical regions. Genetically close to the castor plant (*Ricinus communis* L), *J. curcas* is a rapidly growing plant that is capable of adapting to a wide range of environmental stress conditions, including nutrientlimited soils and low to high rainfall seasons, and might take advantage of anthropic/unproductive areas (Kumar et al., 2016). Moreover, *J. curcas* is recommended for cultivation for soil health improvement, climate change mitigation, carbon sequestration, and socioeconomic development, and in the past few decades, *J. curcas* has been shown to be a biodiesel source (Islam et al., 2014). In Brazil, *J. curcas* is also reported as an alternative supply of vegetable oil from its seeds (Laviola et al., 2015).

Studies concerning the biotechnological and agricultural potential of bacterial microbiota associated with *J. curcas* represent an alternative that might contribute to research aiming to increase productivity and establish this crop. Mohanty et al. (2017) hypothesize that its ability to adapt to environmental stresses could be due to its endophytes (Madhaiyan et al., 2013a).

Sousa and Silva (2012) discuss the differential growth promotion in *J. curcas* by different endophytic strains of *Bacillus. In vitro* studies were performed to test the phosphate solubilization and indole-3-acetic acid (IAA) production of these strains. The best-performing endophytic strain was identified as *B. megaterium* (BP4D), which exhibited the highest phosphate solubilization level and IAA production level. *In vivo* and under greenhouse conditions, the capacity to promote plant growth was observed in certain vegetative parameters, such as mass and the length of the roots, by the BP4D strain.

Jha and Saraf (2012) described a novel *Enterobacter cancerogenus* strain, MSA2, as a plant growth-promoting (PGP) bacterium isolated from the *J. curcas* rhizosphere. MSA2 was then used as an inoculant in *J. curcas* vegetatives under greenhouse conditions. *J. curcas* culture showed an increase in almost all vegetative characteristics of the plant in comparison with the uninoculated control, as well as increased root length and root dry weight.

Madhaiyan et al. (2013b) reported a novel N-fixing endophyte, *Enterobacter* sp. R4-368, which was able to colonize root and stem tissues and significantly promoted early plant growth and seed productivity of *J. curcas* in sterilized and non-sterilized soils. In addition, Madhaiyan et al. (2013c) announced the complete genome sequence of R4-368. Draft genome sequence analysis showed the discovery of a complete set of genes for nitrogen fixation and synthesis and efflux of volatile compounds, auxins, and siderophores. Some authors consider *Enterobacter* strains to be elite plant growth-promoting bacteria (Ramesh et al., 2014; Ikeda et al., 2020).

Madhaiyan et al. (2015) presented a detailed study regarding the role of a novel leaf-colonizing diazotroph, *Methylobacterium radiotolerans* L2-4, on *J. curcas* biomass and seed production. Foliar spray of L2-4 improved plant height, leaf number, chlorophyll content, and stem volume. At the same time, Madhaiyan et al. (2014) reported the draft genome sequence of L2-4, which exhibits several genes involved in metabolic pathways involved in PGP.

Mohanty et al. (2017) characterized the endophytic bacteria of *J. curcas* and their PGP effects on maize (*Zea mays* L.). The main genera found were *Brevibacillus, Paenibacillus, Rhizobium*, and *Sphingomonas*. All isolates were positive for phosphate and IAA production. Inoculation of the endophytic strains on maize seeds significantly increased the shoot and root length of seedlings compared with the shoot and root length of non-inoculated seedlings. Similarly, Machado (2019) described inoculation in *Z. mays* seeds of the bacterial strains EPM-41A, EPM-54, and EPM-92 - *Bacillus* sp.; EPM-63B - *Citrobacter* sp., EPM-34 *Curtobacterium* sp.; EPM-4 and EPM-63 *Klebsiella* sp.; and EPM-2 *Serratia* sp. where the treatment with EPM2- *Serratia* sp. exhibited significantly higher values for all growth parameters.

There is a great incentive for the commercial cultivation of *J. curcas* in Brazil as a renewable raw material for biodiesel production. However, the great expansion of cultivated areas has been accompanied by the occurrence of new pathogens and the appearance of diseases called descending dryness and stem base rot, caused by species of the *Lasiodiplodia* fungus, causing losses in productivity and mortality of 80% of physic nut plants (Machado et al., 2014). Thus, chemical control alone does not provide protection or curative treatment. The adoption of a sequence of prophylactic care has been recommended in the past few decades (Silva et al., 2015).

Recently, Machado et al. (2020) identified bacterial strains belonging to the genera Arthrobacter, Bacillus, Citrobacter, Curtobacterium, Enterococcus, Klebsiella, Leucobacter, Lysinibacillus, Microbacterium, Rhodococcus, and Serratia endophytically associated with *J. curcas.* Additionally, a total of 37 strains were screened *in vitro* for PGP, where 56.75% of evaluated bacteria could fix nitrogen, 62% of the isolates were able to synthesize the phytohormone IAA in the presence of the tryptophan precursor, and 32% of the evaluated isolates had the capacity to solubilize insoluble inorganic phosphate. Additionally, these strains were evaluated *in vitro* against the phytopathogenic fungi *Lasidioplodia subglobosa, L. euphorbicola,* and *L. pseudotheobromae*, where 35% exhibited antagonism to the three tested phytopathogens, whereas the *Bacillus* genus showed higher antagonistic activity than the other strains.

## Beneficial Microbes as Biocontrol and Growth-Promotion Agents for *Citrus* spp.

The *Citrus* genus (Rutaceae family) comprises one of the fruit crops of major economic, social and cultural importance worldwide. Originating from southeastern Asia, where *Citrus* domestication probably started, the crop is well-adapted to tropical and subtropical climate zones (Talón et al., 2020). Brazil, followed by China, India, Mexico, and the United States, is among the largest citrus producers in the world (FAOSTAT, 2019). Global production of citrus fruits was estimated to increase by 4 percent to 98 million tons in 2020/2021 (United States Department of Agriculture, 2021). However, diseases caused by pests and pathogens limit citrus production, leading to considerable damage to orchards and economic losses in the sector.

Among the most important citrus diseases caused by bacteria are huanglongbing (HLB), citrus variegated chlorosis (CVC), and citrus canker (CCK) (Mendonça et al., 2017). Although integrated management maintains citrus disease incidence at lower levels, there is no effective cure or treatment. While CVC incidence has remained lower in 2020 than in 2019, the CCK incidence increased by 15% (Fundecitrus, 2020).

Citrus plants treated with beneficial microorganisms can have important metabolic responses to infection by *Candidatus* Liberibacter spp. (Munir et al., 2021). This phloem-limited bacterium is transmitted to citrus trees by *Diaphorina citri* (Hemiptera: Liviidae) (Ammar et al., 2011) and causes HLB, a disease currently considered the most destructive affecting the citrus industry worldwide (Wang et al., 2017).

Bacillus species have been isolated from healthy/asymptomatic citrus plants at high frequency, which suggests their role in HLB resistance (Munir et al., 2020a). Munir et al. (2020b) showed that primary and secondary metabolites were activated in HLB-affected plants in response to inoculation with the endophyte Bacillus subtilis L1-21. Tang et al. (2018) demonstrated the potential of Bacillus amyloliquefaciens GJ1 isolated from healthy leaves of Citrus sinensis (L.) Osbeck as a novel biocontrol agent in Candidatus Liberibacter asiaticusinfected plants. Different genes and proteins involved in detoxification mechanisms were upregulated by endophytic bacteria, suggesting a use for HLB biocontrol to improve plant health. Recently, Nan et al. (2021) demonstrated that B. amyloliquefaciens GJ1 improved the immunity of C. Liberibacter *asiaticus*-infected citrus by increasing photosynthesis and enhancing the expression of defense-related genes.

Another strategy for HLB management is the discovery of microorganisms to control *D. citri*. Dorta et al. (2018) showed that *Bacillus thuringiensis* (Bt) strains translocated from roots to shoots in citrus seedlings and caused mortality of *D. citri* nymphals. The mortality was 42–77% and 66–90% at 2 and 5 days, respectively, after inoculation in citrus plants of the recombinant Bt strains harboring a single *cry* or *cty* gene.

The endophytic microbial community associated with citrus plants can be used as a biocontrol agent of the xylem-limited bacteria *Xylella fastidiosa*, the causal agent of CVC, one of the diseases that caused the most damage to the Brazilian citrus industry in the 2000's (Azevedo et al., 2016).

Lacava et al. (2004) showed that *X. fastidiosa* growth was reduced by endophytic *Methylobacterium mesophylicum* SR1.6/6 *in vitro*. Later, in experiments of co-inoculation using *Catharanthus roseus* as a model plant, Lacava et al. (2006) showed that the population of *M. mesophylicum* SR1.6/6 was lower in the presence of *X. fastidiosa*, suggesting that these bacteria interact inside xylem vessels competing for space and nutrients. Since *M. mesophilicum* SR 1.6/6 was isolated from CVC-free citrus plants at high frequency (Araújo et al., 2002), this endophyte could contribute to preventing the disease in the host plants (Lacava et al., 2006; Azevedo et al., 2016). Plant exudates and N-acyl-homoserine lactones regulate specific gene expression in *M. mesophilicum* SR 1.6/6 (Dourado et al., 2013), and co-cultivation of this endophyte and *X. fastidiosa* leads to specific adaptive responses of the phytopathogen (Dourado et al., 2015).

X. fastidiosa synthesizes exopolysaccharides (EPSs) or fastidian gum, which are essential for biofilm formation, and occlusion of the sap flow in the xylem, which leads to CVC symptoms (Simpson et al., 2000). Based on the premise of symbiotic control (Miller, 2007), Ferreira Filho et al. (2012) modified Methylobacterium extorques AR1.6/2 isolated from citrus (Araújo et al., 2002) to express endoglucanase A (EglA), which was cloned from a citrus endophytic Bacillus pumilus able to degrade xanthan gum (Lima et al., 2005). Using scanning electron microscopy, the bacterial strain (AREglA) and X. fastidiosa were observed to possibly coinhabit the xylem vessels of C. roseus, and AREglA may decrease biofilm formation. AREglA also stimulated the production of the resistance protein catalase in the inoculated plants. The results suggested the potential use of AR1.6/2 and other bacteria isolated from citrus for the symbiotic control of X. fastidiosa in its niche.

Bogas et al. (2016) demonstrated for the first time the potential of *Methylobacterium* sp. to promote the growth of *Citrus limonia* and *Citrus sunki* seedlings under commercial nursery conditions. *M. mesophylicum* SR 1.6/6, *M extorquens* AR 1.6/2 and *M. extorquens* AR 1.6/11 isolated from citrus (Araújo et al., 2002) significantly increased the height and/or biomass of roots and shoots at the end of rootstock production. The pathway of indole-e-acetic acid (IAA) biosynthesis identified in the *M. mesophylicum* SR 1.6/6 genome suggested that its mechanism was involved in citrus growth promotion. These effects seem to be dependent on specific interactions between *Methylobacterium* and citrus rootstock varieties and on the inoculation method. In general, *Methylobacterium* sp. can accelerate citrus growth, contributing to reducing the costs and the time that plants remain in the nursery.

Endophytes are also promising for the biocontrol of *Xanthomonas citri* subsp. *citri* (*Xcc*), the causal agent of CCK (Brunings and Gabriel, 2003). This disease affects all commercially important citrus species and varieties in many tropical and subtropical citrus-producing areas worldwide (Sharma and Sharma, 2009).

Liu et al. (2021) showed that the differences in bacterial endophytic communities and their abundance in citrus cultivars may be related to host CCK resistance or susceptibility. *Firmicutes* were significantly more abundant in resistant Satsuma mandarin leaves than in susceptible Newhall Navel Orange leaves. However, the abundance of this phylum was lower in all summer samples, with this number being much lower in resistant Satsuma mandarin, suggesting that this season would be the period with the highest citrus canker disease risk. At the genus level, *Bacillus subtilis* with antagonistic potential against *Xcc* was the main species present in all samples but was more abundant in the susceptible Newhall navel oranges. *Pseudomonas*, which also has antagonistic potential, was present in higher abundance in summer samples, particularly in resistant Satsuma mandarin samples.

In a study carried out by Daungful et al. (2019), the endophytes *Bacillus amyloliquefaciens* LE109 and *B. subtilis* LE24, both isolated from healthy *Citrus aurantifolia*, and *Bacillus tequilensis* PO80 isolated from healthy *Citrus maxima*, significantly inhibited the growth of *Xcc in vitro*. Lime plants did not display symptoms of CCK after inoculation with cell suspensions of *Xcc* and LE109 or LE24 or with crude bioactive compounds obtained from these endophytes. The study suggested that endophytes could compete with the pathogen for nutrients and produce metabolites that inhibited the growth of *Xcc* on lime plants.

## MICROBIAL DIVERSITY OF BRAZILIAN BIOMES

### Plant Growth Promotion of Endophytes From Tropical Mangrove Forests

Mangroves are typical tropical ecosystems situated between the land and the sea. These biological communities are frequently found in tropical and subtropical areas and occupy  $\sim$ 18.1 million hectares of the planet. These ecosystems demand high nutrient availability at the start of the trophic chain, which confers high importance on the activities of microorganisms, such as bacteria and fungi, that are responsible for the processes of degradation and formation of essential compounds and most of the carbon flow in the sediments of mangrove forests (Holguin et al., 2001). The adaptation of microbial species to mangrove conditions indicates a potential source of biotechnological resources to be explored, including the discovery of new microorganisms that produce compounds that can be used for agriculture (Dias et al., 2009). In this scenario, endophytes are of agronomic interest because these organisms can enhance plant growth and

improve plant nutrition through diverse mechanisms, such as phosphorus solubilization and nitrogen fixation (Castro et al., 2014; Sebastianes et al., 2017).

In this context, Gayathri and Muralikrishnan (2013) collected root, stem, and leaf samples from mangrove plants at Chidambaram, Tamil Nadu, India. The authors obtained 24 isolates. All isolates were evaluated for plant growth-promoting activity using a PGPR activity test to detect the phosphate solubilization and biological nitrogen fixation activities of endophytic bacteria.

Deivanai et al. (2014) examined the compatible association of bacterial endophytes from *Rhizophora apiculata* of the Merbok brackish river in Semeling, Kedah, Malaysia, in colonizing rice tissues and discussed the likelihood of utilizing the symbiotic association of these endophyte isolates to increase the fitness of rice seedlings. The inoculation of rice seeds with endophytic strains of *Bacillus cereus*, *B. amyloliquefaciens*, and *Pantoea ananatis* significantly increased the root and shoot length, suggesting that endophytic bacteria from mangrove trees can increase the fitness of rice seedlings under controlled conditions.

Brazilian mangroves are primarily made up of three tree species, Rhizophora mangle, Laguncularia racemosa, and Avicennia sp. (Dias et al., 2009), from which several diverse endophytic bacteria have been isolated (Castro et al., 2014). In this scenario, Castro et al. (2014) performed a diversity analysis on endophytic bacteria obtained from the branches of Brazilian mangrove forests. Bacillus was the most frequently isolated genus, comprising 42% of the species isolated. However, other common endophytic genera, such as Curtobacterium, Enterobacter, and Pantoea, were also identified. Additionally, in Brazil, Castro et al. (2018) evaluated a large number of endophytic bacterial strains from three different plant species, namely, R. mangle, L. racemosa, and Avicennia sp., to examine phosphate solubilization. All 115 strains examined produced a halo during the phosphate solubilization test in vitro. The endophytic strain MCR1.48 (Enterobacter sp.), which has a high P solubilization index, was selected for in vivo assays in Acacia polyphylla. These authors selected the commonly used reforestation tree A. polyphylla, which has few published studies involving inoculation by bacteria of agronomic interest and used for the reforestation of degraded areas in Brazil (Rao et al., 2007). Inoculation with Enterobacter sp. strain MCR1.48 increased the dry mass of A. polyphylla shoots and roots, suggesting that the presence of the endophyte generates important benefits that promote the growth and fitness of this plant.

The biological control method using endophytic fungi capable of inhibiting phytopathogens seems to be a more ecofriendly and sustainable tool in agricultural management than using agrochemicals that negatively impact the environment, humans, and other organisms (Tewari et al., 2019). In this regard, Moreira et al. (2020) evaluated the antagonistic potential of *Diaphorte* sp. FS-94(4) strain isolated from *Avicennia nitida*, Brazilian mangrove forests (Sebastianes et al., 2013) against the phytopathogens *Colletotrichum* sp., *Fusarium oxysporum*, *Phytophthora sojae*, and *Rhizopus microspores*. The antagonism index (AI) ranged from 20 to 62%. The endophyte produced *in vitro* cellulase, suggesting that this enzyme is involved in suppressing phytopathogens by breaking down the cell wall.

### The Agronomic Potential of Microorganisms From Tropical Savannah

The Brazilian tropical savannah, known as the Cerrado, has  $\sim$ 6,000 vascular plant species, featuring the highest floral biodiversity among the world's savannahs. The Cerrado also has a high diversity of microorganisms (Lacava and de Sousa, 2016; de Sousa et al., 2017; Lisboa et al., 2021). Much of the biodiversity of this microbiome is not yet known, which makes it one of the 25 most important terrestrial biodiversity hotspots on the planet (Oliveira-Filho and Ratter, 2002; Bogas et al., 2020). Among the diverse trees in the Brazilian savannah, the research groups have considered two species: Stryphnodendron adstringens (Mart.) Coville (Fabaceae) (Figure 2A) and Solanum lycocarpum Saint-Hill (Solanaceae) (Figure 2B). S. adstringens trees have the potential for medicinal applications. Its bark and fruit contain anti-inflammatory (Lima et al., 1998), antiviral (Felipe et al., 2006), and antimicrobial properties (Almeida et al., 2017). S. lycocarpum produces secondary metabolites that exhibit antioxidant, antibacterial, cytotoxic, and antiinflammatory properties (da Costa et al., 2015).

Recently, Lisboa et al. (2021) reported that bacterial strains were isolated from rhizosphere samples of S. lycocarpum and were tested in vitro for direct mechanisms of plant growth promotion, such as phosphate solubilization. Among the 131 strains evaluated, the calcium phosphate solubilizing capacity trials showed that 45.8% of the strains exhibited a positive reaction. Some bacterial strains identified as Bacillus sp., Burkholderia sp., and Microbacterium sp. showed high solubilization potential. In this same study, the rhizobacteria strains were evaluated in visual agar plate assays against phytopathogenic fungi. A total of 50% of the straisn showed antagonist activity against Sclerotinia sclerotiorium, Moniliophthora perniciosa, Fusarium sp., Sphaceloma sp., Ceratocystis paradoxa, Alternaria alternata, Colletotrichum sp., Phytophthora sojae and Rhizopus microsporus. According to the authors, this research is the first report on the characterization, identification, and isolation of rhizospheric bacteria from S. *lycocarpum* in Brazil.

Torres (2018) reported the isolation and identification of 66 endophytic fungi from leaves of *S. adstringens* and *S. lycocarpum* collected in the savannah area of São Paulo State, Brazil (**Figures 2C,D**). The endophytic strains were evaluated *in vitro* for their antagonistic potential against the phytopathogens *Colletotrichum* sp., *Fusarium oxysporum*, and *Lasiodiplodia subglobosa*. The results showed that endophytic strains exhibited antagonistic activity against the phytopathogens tested. Additionally, Torres (2018) reported the ability of an endophytic fungal strain isolated from Brazilian savannah species (Bogas et al., 2020) to solubilize inorganic phosphate. The author observed the potential to solubilize inorganic phosphate with a mean phosphate solubilization index ranging from 1.46 to 1.93 and 1.19 to 2.61 by endophytic strains.

In a similar study, Sharma and Roy (2015) reported that fungal endophytes were isolated from the root, stem, and leaves of the plant *Amaranthus spinosus*, another species occurring in the savannah biome, and stated that endophytic fungal isolates of the plant *A. spiunosus* showed a positive test for phosphate solubilization. The phosphate solubilization efficiency was found to be highest for the fungal genus *Aspergillus* isolated from the stem of the plant.

Finally, Noriler et al. (2018) assessed the fungal community associated with *Stryphnodendron adstringens* leaves and petioles collected in the savannah area of Mato Grosso do Sul State, Brazil. The authors verified the antimicrobial activity of crude extracts produced by the endophytes and suggested that *Diaporthe* cf. *heveae* LGMF 1631 strain may represent an alternative to be used in the biocontrol of the phytopathogens *Phyllosticta citricarpa* and *Colletotrichum abscissum*.

# Agronomic Potential of Archaea in Tropical Crops

Archaea constitute a group of microorganisms initially found only in environments with extremes conditions of pH, temperature salinity, pressure among other factors (Rampelotto, 2013). In the last few decades, archaea also are considered a substancial component of complex microbiomes, including plant-associated microbiomes in the above and belowground (Moissl-Eichinger et al., 2017).

Although the ecological role of archaea and its interaction with their host plants still remain unclear, the metagenomic data set have been essential to reveal archaeal groups living in the rhizosphere and endosphere that could be used to plant improvement. Data obtained by Taffner et al. (2018) provided evidences of the importance of archaea to promote plant growth through carbon and nitrogen cycling and auxin biosynthesis. In addition, the results suggested the potential role of these microorganism in plant protection against abiotic stress. Other metagenomic studies have revealed the importance of archaea in the ammonia oxidation in the soils (Bartossek et al., 2012; Clark et al., 2021).

Some studies have explored metagenomic data set for investigate archaea diversity and community structure in tropical agroecosystems. Fadiji et al. (2020) verified for the first time that organic fertilizer boosts the abundance and diversity of endophytic archaea in roots of maize as compared with chemical fertilizers. The phyla Crenarchaeota, Euryarchaeota, and Thaumarchaeota were identified in the samples with higher abundance collected from the organic fertilizer site. The results suggested a better understanding of the endophytic archaea roles in the maize to reduce the dependence on chemical fertilizers and improve the sustainable practices. Xu et al. (2018) performed the metagenomic sequencing of the rhizosphere and bulk soil samples to define citrus microbiome, and verified a low relative abundance of archaea phyla, such as Crenarchaeota and Euryarchaeota. Despite, the results provided relevant information to explore the potential of the citrus microbiome for sustainable production and improve health plant. Dubey (2016) used metagenomic to analyzed the rhizosphere of bioenergy crop J. curcas adapted to grow under salt stress and high temperature conditions. The results showed high abundances of uncultured archaea Crenarchaeota and Euryarchaeota and suggested their role in the adaptation of J. curcas to stress conditions.



FIGURE 2 | Examples of endemic Brazilian tropical savannah trees (22°01′03″S, 47° 53′27″W). (A) *Stryphnodendron adstringens* (Mart.) Coville (Fabaceae); (B) *Solanum lycocarpum* Saint-Hill (Solanaceae). Fungal morphological groups retrieved in the culture media isolation procedure. Endophytic fungi (morphological groups) isolated from leaves of *S. adstringens* (C) and *S. lycocarpum* (D).



proliferatum (**D**), and Alternaria alternata (**E**).

Despite the archaeal potential to improve plant's adaptation and health, only few studies have demonstrated its direct effects during symbiosis with their hosts. Recently, Song et al. (2019) showed that soil archaea *Nitrosocosmicus oleophilus* MY3 promote growth of model plant *Arabidopsis thaliana* by colonizing its roots and releases volatile compounds that elicit systemic resistance (ISR) against the necrotrophic bacterium *Pectobacterium carotovorum* subsp. *carotovorum* SCC1 and biotrophic bacterium *Pseudomonas syringae* pv. tomato DC3000 via the salicylic acid-independent signaling pathway. However, the literature about symbiotic relationship among tropical crops and archaea is scarce.

The knowledge about the dynamics of archaeal communities, and they physiological and molecular mechanisms to mediate plant growth and stress tolerance are one of challenges to overcome in archaea application in sustainable agriculture (Naitam and Kaushik, 2021).

## Burkholderiales Are Bio-Tools Specialized in Agrobiology

*Burkholderia* spp. is a gram-negative  $\beta$ -proteobacterium that might be found in several habitats, ranging from human pathogens to plants, as endophytes (Esmaeel et al., 2018; Furlan et al., 2019; Kunakom and Eustáquio, 2019; Mullins et al.,

2019). *Burkholderia* consists of an emergent genus in terms of biotechnological applications and the diversity of natural products with potential therapeutic relevance and plant growth-promoting properties.

The metabolic arsenal of Burkholderia species is evident. Their large genomes encode numerous natural products. Several compounds have been reported from Burkholderiales, such as siderophores and lipopeptides, non-ribosomal peptides, and polyketides. The specialized holometabolite pyrrolnitrin plays an important role in plant protection against a wide range of soil- and seed-borne phytopathogens. Pyrrolnitrin was originally isolated from Pseudomonas pyrrocinia and produced by several strains of B. cepacia (Pawar et al., 2019). In B. cepacia strains, the biosynthesis of pyrrolnitrin involves mechanisms of quorumsensing (QS) signaling molecules known as N-acyl-homoserinelactones (Jenul et al., 2018). According to Keum et al. (2009), nutrients, such as glucose, are capable of decreasing pyrrolnitrin production to the detriment of increasing cell density. However, the full potential of the Burkholderia genus has gained notoriety with recent advances in genomic tools (Kunakom and Eustáquio, 2019).

According to the systematic review of Kunakom and Eustáquio (2019), free-living *Burkholderia* species are skilled producers of hydrolytic enzymes that can degrade natural

and synthetic pollutants. Moreover, several studies have been reported the isolation of Burkholderiales from tropical regions which showed promising results on biological control of economic important phytopathogens and in PGP.

Tropical crops such as Banana (*Musa* spp.) holds a worldwide production of 116.8 million tons in 2019 (FAOSTAT, 2021) but is severely affected by fungal diseases mainly caused by *Mycosphaerella fijiensis* (black leaf streak disease) and *Fusarium oxysporum* f.sp. *cubense* (Fusarium wilt), which are responsible for significant losses in annual production (Nakkeeran et al., 2021; Soares et al., 2021). Xu et al. (2020) isolated a rhizosphere-borne *Burkholderia* sp. HQB-1 from healthy plants collected in a pathogen-infected banana orchard is capable of potently inhibiting *Botrytis cinerea*, *Colletotrichum gloeosporioides*, *Curvularia fallax*, and *F. oxysporum* through phenazine-1-carboxylic acid.

A *Burkholderia fungorum* strain UFLA 04-226, isolated from root nodules of *Macroptilium atropurpureum* (da Silva et al., 2012), showed common bean plant (*Phaseolus vulgaris*) growth promotion properties in the presence of nitrogen fertilizer. Additionally, another *Burkholderia* strain UFLA 04-155 was capable of increasing the dry weight of the nodules and shoots, increasing P, Mg, Cu, Fe, K, Ca, S, and Zn in leaves, and inducing nodule formation by the indigenous rhizobial community (de Oliveira-Longatti et al., 2015).

Ganoderma boninense (basal stem rot disease) is a serious threat to the oil palm (*Elaeis guineensis*) cultivars. *G. boninense* might cause the death of the palm by the destruction of the basal tissues, causing significant economic losses (Tan et al., 2021). Palm oil is a valuable raw material used in the manufacturing of several products (e.g., biodiesel, cosmetics, detergents, food, and plastics) and therefore constitutes an important economic activity in Indonesia and Malaysia (Siddiqui et al., 2021). In Nadhrah et al. (2016), an endophyte-oil palm-associated *Burkholderia* GanoEB2, when associated with a bioorganic powder (real strong bioorganic fertilizer) composed of N<sub>2</sub>, P, K, Mg, B, Fe, Zn, and trace elements combined with plantbased organic matter, resulted in a reduction of 18.2% of disease incidence, 26.6% of the severity of foliar symptoms, and 27.7% of disease severity foliar index.

Several studies report the successful association between beneficial Burkholderia spp. and sugarcane (Saccharum spp.) crops. According to Luvizotto et al. (2010), Burkholderiales are often found in association with this cultivar, which confers a wide range of physiological activities. In this same publication, a study regarding the bacterial diversity harbored by this plant was also reported. In addition, phylogenetic analysis based on the sequencing of 16S rRNA and the housekeeping gene gyrB revealed that most of the isolates belong to the Burkholderia cepacia complex (Bcc). Sugarcane is native to regions ranging from warm temperate to tropical climates of south and southeast Asia, where Brazil holds the largest global production, followed by India (Bordonal et al., 2018; El Chami et al., 2020). However, fungal diseases, such as those affected by red rot (Colletotrichum falcatum), seedling rot (Pythium spp.), sett rot (Ceratocystis paradoxa), sugarcane smut (Sporisorium scitamineum), and wilt (Fusarium sacchari) are responsible for substantial losses in production (Viswanathan and Malathi, 2019). Cui et al. (2020) reported that the isolation of a toxoflavin produced by *B. gladioli* strain CGB10 endophytically isolated from sugarcane leaves showed strong inhibitory activity against *S. scitamineum*. Studies have shown the antifungal potential of such molecules. Li et al. (2019) also reported the antifungal activity of such a compound. *Burkholderia gladioli* HDXY-02 isolated from the medicinal plant *Lycoris aurea* exhibited broad-spectrum activity against plant (*Fusarium graminearum, Magnaporthe oryzae*, and *Rhizoctonia solani*) and human (*Aspergillus fumigatus, A. nidulans, Candida albicans*, and *Cryptococcus neoformans*) fungal pathogens.

*Polygala paniculata* is a folk medicinal plant in Brazilian coast which is known for the abundant presence of methyl salicylate in its roots. Moreover, Polygalaceae have reported several pharmacological effects, including anti-inflammatory, anxiolytic, trypanocidal, antinociceptive, and antimicrobial effects, as well as other specialized molecules, such as alkaloids, flavonoids, terpenes, lignins, and coumarins. In Brazil, these plants are widely used for the treatment of lesions and sprains (Lapa et al., 2009). As promising and still unexplored niche-harboring microbes, the literature reports a novel *Burkholderia cepacia* strain endophytically associated with these plants. Showing novel alleles of *gyrB*, *lepA*, and *phaC*, *B. cepacia* ST 1870 (strain COPS) revealed broad-spectrum and potent activity toward the phytopathogenic fungi *Moniliophthora perniciosa* and *Sclerotinia sclerotirium* (**Figure 3**) (Cruz et al., 2021).

### **FUTURE PERSPECTIVES**

## Nanotechnology, Green Chemistry, and Agriculture

Both endophytic and rhizospheric microorganisms have attracted attention based on their potential use in sustainable agriculture, since they represent a key strategy for integrated managment practices to improve plant growth and control pests and diseases (Le Cocq et al., 2016; Kumar et al., 2018). Adopt sustainable farming practices is of great importance to enhance crop production while concurrently addressing food security needs for the growing global population (Arora, 2018).

As mentioned before, chemical compounds or methods offer disadvantages to the environment and human health (Brauer et al., 2019; Cullen et al., 2019; Omomowo and Babalola, 2019). Nanoparticles (NPs) are biotechnologically attractive for their biological effects on pathogenic microbes and plant growth promotion (Ibrahim et al., 2019). In this way, the plantassociated microbes are attaing the new horizons and have been employed in the green synthesis of NPs for use in the agriculture sector (Mishra et al., 2017; Ali et al., 2020). A recent example is the synthesis of silver nanoparticles (Ag-NPs) by Bacillus siamensis endophytically isolated from the medicinal health plant Coriandrum sativum. Ag-NPs strongly inhibited bacterial growth, biofilm formation, and swimming motility of the rice phytopathogen Xanthomonas oryzae pv. oryzae and Acidovorax oryzae and promoted a significant increase in root length, shoot length, fresh weight, and dry weight of rice seedlings (Ibrahim et al., 2019). Furthermore, green synthesized Ag-NPs by the garlic (*Allium sativum*) endophyte *Pseudomonas poae* showed strong inhibition of the wheat pathogen *Fusarium graminearum* in terms of mycelium growth, spore germination, length of the germ tubes, and mycotoxin production (Ibrahim et al., 2020).

Despite the promising potential of endophytic and rhizospheric microorganisms for the synthesis of NPs, some challenges still need to be overcome for its efficient application in the plant breeding. The physicochemical properties (e.g., size, shape) and synthesis parameters (e.g., biomass quantity, temperature, pH) should be optimized for green NPs formulations development in large-scale. In addition, the physicochemical properties (e.g., size, shape) and synthesis parameters (e.g., biomass quantity, temperature, pH) should be optimized for green NPs formulations development in largescale. In addition, is essential know the specificity and toxicity of NPs for target and no-target organisms and environment (Raj et al., 2021).

Therefore, basic and applied researches using both endophytic and rhizospheric microorganisms, comminated or not with new technologies, have essential role in ensuring development, productivity and protection of tropical crops and food security in the imminent future.

### CONCLUSIONS

The use of microbes and their products is a reality on drug development and agricultural processes which is constantly increasing since the past few decades. The search for interesting natural biological activity has been the basis for the development

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of various biotechnological and agricultural applications. Therefore, plant-symbiont microbes constitute a rich and unexplored source of natural secondary metabolites. The microbial world and endophytes and rhizobacteria, in particular, exhibit vast genetic and metabolic biodiversity that has not yet been thoroughly explored. According to Azevedo and Quecine (2017), most studies on endophytes have been carried out using hosts from temperate countries, while data from tropical regions remain scarce. Consequently, the exploitation of the tropical microbiome is critically important since there is ever increasing demand for eco-friendly practices in agriculture which can effectively improve production and neutralize imminent biological threats. Herein, we highlighted the role of these microbes considering fundamental properties of application of biotechnology in strategic areas of agri-business. The available literature has revealed that tropical plants harbor a great diversity of microorganisms which remain unknown.

### **AUTHOR CONTRIBUTIONS**

PL designed the project. PL, AB, and FC wrote the manuscript and edited the manuscript. All authors contributed to the article and approved the submitted version.

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