



# Life Inside Plants: Insights into the Lifestyle, Diversity, and Metabolites of Endophytic Bacteria Involved in Plant Defense Against Phytopathogens

B. N. Aloo , E. R. Mbega, B. A. Makumba, and J. B. Tumuhairwe

## Abstract

One of the pressing issues in agriculture today is low crop yields due to plant diseases and pathogens. Chemical pesticides have generously been applied as remedies to improve the situation, but continue to be shunned globally due to their long-term environmental impacts. Endophytes are microbes that live symbiotically in plant tissues and are continually being associated with the suppression of phytopathogens and plant health. Thus, they present an environmentally-friendly option in plant defense against phytopathogens. However, their diversity, lifestyle, and roles in plant defense against phytopathogens are still not well-understood. This chapter explores the lifestyle of endophytic bacteria and discusses their diversity and metabolites involved in plant defense against phosphagens. The chapter further examines the future prospects and evaluates the emerging gaps relative to their use in plant defense against phytopathogens. Such knowledge is critical in fully exploiting their potential in sustainable agriculture.

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B. N. Aloo (✉)

Department of Biological Sciences, University of Eldoret, Eldoret, Kenya

E. R. Mbega

Department of Sustainable Agriculture and Biodiversity Conservation, Nelson Mandela African Institution of Science and Technology, Arusha, Tanzania

B. A. Makumba

Department of Biological Sciences, Moi University, Eldoret, Kenya

J. B. Tumuhairwe

Department of Agricultural Production, College of Agricultural and Environmental Sciences, Makerere University, Kampala, Uganda

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## 4.1 Introduction

There are efforts worldwide to increase agricultural production to meet the increasing demand for food for the equally-increasing global population (FAO 2017). However, these efforts are still hampered by yield losses from crop pests and diseases (2016). Recent estimates indicate that at least 20–40% of these losses are due to plant pathogens alone which account for annual global losses of approximately \$40 billion (Ab Rahman et al. 2018). Conventional and contemporary agriculture largely depends on chemical pesticides to manage plant pests and diseases (Sivasakthi et al. 2014). While these chemicals are hugely important in minimizing the losses, their indiscriminate use continues to elicit a lot of debate concerning pathogen resistance (Borel 2017), soil/water pollution (Zhang et al. 2011), and effects on nontarget organisms (Muñoz-Leoz et al. 2013; Shao and Zhang 2017; Ankit et al. 2020). As such, alternatives to these chemicals are widely advocated for (Waghunde et al. 2017; Verma et al. 2019). One such option is the exploitation of plant-microbe interactions which offer an efficient, affordable, and environmentally-friendly alternative to synthetic pesticides for phytopathogen control (Tewari et al. 2019).

The exploitation of symbiotic association of microbes with plants has currently become an important tool in plant bio-protection (Gaiero et al. 2013; Gupta et al. 2015). Some of the most studied plant-associated microbes are planted growth-promoting rhizobacteria (PGPR) (Glick 2012; Verma et al. 2019). Endophytes are a subset of PGPR that live endosymbiotically in plants (Gond et al. 2015), without negatively affecting their hosts (Hardoim et al. 2015). Endophytic rhizobacteria reside in many plants as part of their normal microbiome as dictated by biotic and abiotic factors like soil conditions, biogeography, and plant species, among other factors (Gaiero et al. 2013). Within the host microenvironments, endophytes have direct access to nutrients, face less competition from other rhizospheric microbes, and receive protection from environmental stresses (Dutta et al. 2014). Due to the intimate interactions endophytes form with their host plants, they are thought to be more crucial for plant defense against phytopathogens compared to their external counterparts (Tewari et al. 2019).

At the moment, microbial endophytic communities are the center of focus for scientists who aim to unravel and clarify their connection to plant health (Vurukonda et al. 2018). The potential of endophytic bacteria for plant defense against phytopathogens through the production of antibiotics and other antimicrobial metabolites has been researched extensively (Shehata et al. 2016; Sandhya et al. 2017; Vurukonda et al. 2018; Tewari et al. 2019; Singh et al. 2020; Morales-Cedeño et al. 2021). Despite the voluminous literature on the plant protection abilities of endophytic bacteria, our understanding of endophytic lifestyle, diversity, and

mechanisms involved in plant defense are still limited, hindering their utilization and applications in plant disease management. This chapter discusses the endophytic lifestyle in detail and assesses the diversity of endophytic bacteria involved in plant defense against phytopathogens. In the last sections of the chapter, the secondary metabolites of endophytic bacteria that together contribute to plant defense against phytopathogens are critically examined. Finally, the chapter provides a direction on the future of endophytic bacteria in plant defense against phytopathogens in view of enhancing our understanding and prospects of the complex plant-endophyte relationship and plant disease management.

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## 4.2 Endophytic Lifestyle

The term “endophyte” originates from two Greek words; “*endon*” and “*phyton*,” which denote “within” and “plant” respectively (Waghunde et al. 2017). Endophytic bacterial communities can be obligate, facultative, or passive depending on their modes of interaction with host plants (Gaiero et al. 2013). Obligate endophytes are those that can survive solely within plants and are, therefore, viable but nonculturable, with important implications on their identification and study of their diversity and community structures (Gaiero et al. 2013; Kumar et al. 2021). On the other hand, passive or opportunistic endophytes can live partly as epiphytes outside the plant and gain entry into plants when conditions allow while facultative endophytes can alternate between living in and without plants (Waghunde et al. 2017).

Endophytic bacteria are a subset of rhizobacteria that acquire the ability to invade plant roots and live endosymbiotically in plant root tissues (Compant et al. 2005, 2010; Kumar et al. 2016). Endophytic bacterial communities are generally dominated by Proteobacteria, followed by Actinobacteria, Firmicutes, and Bacteroidetes in more or less equal proportions (Liu et al. 2017). In terms of genera, the most abundant plant endophytic bacteria are *Bacillus* and *Streptomyces* (Reinhold-Hurek and Hurek 2011). Endophytic bacteria often penetrate and colonize the root epidermis at the sites of the emergence of lateral root emergence, in root cracks, and below the root hair zones (Compant et al. 2005) and can establish themselves in plant tissues both intercellularly and intracellularly (Zakria et al. 2007). After the initial colonization, some endophytes can migrate to other plant parts through the vascular tissues and spread systemically inside the plant (Compant et al. 2005; Zakria et al. 2007). Although rhizospheric bacteria can also enter and colonize plant roots as endophytes (Santoyo et al. 2016), plant root endospheres are dominated by only a few rhizobacterial groups, which evidences the robust selection of rhizobacteria from soil to plants (Liu et al. 2017).

The rhizosphere is a highly competitive environment for microorganisms in terms of space and acquisition of nutrients (Raaijmakers et al. 2002), and particular traits are needed for plant colonization and the endophytic lifestyle (Afzal et al. 2019; Morales-Cedeño et al. 2021). Plant root colonization generally requires potential endophytes to reach the root surfaces chemotactically, outcompete other

rhizospheric microbes, enter the root passively or actively using cell-wall-degrading enzymes (Elbeltagy et al. 2000) and resist the plant host immune responses through the expression of pathogen-resistance genes (Bais et al. 2006; Rosenblueth and Martinez-Romero 2006; Compant et al. 2010; Singh et al. 2017). In this regard, motility and production of polysaccharides for attachment to plant root surfaces are some of the relevant traits that facilitate plant root colonization (Santoyo et al. 2016). Chemotaxis-induced rhizobacterial motility is especially important for successful root colonization and endophytism (Jiménez et al. 2003). Additionally, transport proteins for the uptake of plant nutrients, secretion systems involved in the endophytic lifestyle, and detoxification mechanisms for protection against plant-induced oxidative stresses during infection have all been identified as determinants of successful endophytism (Sessitsch et al. 2012; Ali et al. 2014).

The coordinated invasion of plant roots by microbes involves numerous reciprocal signaling pathways between plants and endophytes (Rosenblueth and Martinez-Romero 2006). It is hypothesized that endophytic bacteria possess unique genes that make them fit for endophytic lifestyle (Ali et al. 2014). Although no definitive assemblage of genes has been acknowledged to be responsible for endophytic lifestyle, it is proposed that endophytic bacteria may have different genomic characteristics from external rhizobacteria that enable the colonization of internal plant tissues (Santoyo et al. 2016). Some genomic evaluations of endophytes have established the presence of genes related to endophytic colonization of plant tissues (Taghavi et al. 2010; Kaneko et al. 2010; Gold et al. 2014; Lopes et al. 2017; Chlebek et al. 2020; Singh et al. 2021). Genome comparisons have also revealed the important capabilities of endophytic bacteria. For instance, a genome comparison of endophytic and external rhizospheric *Burkholderia* spp. recently identified the existence of genes encoding proteins associated with secretion and detoxification systems, degradation of plant cell walls, and maintenance of redox potential, among other hypothetical genes in the endophytic strains (Ali et al. 2014).

The composition and structure of plant-endophytic bacteria are dependent on various factors such as plant health, part, nutritional state and stage of growth, type of soil, altitude, and temperature, among others (Hardoim et al. 2008). Whether living in plant tissues is advantageous to bacterial endophytes, relative to the freely-living rhizobacteria is not properly understood (Rosenblueth and Martinez-Romero 2004). Nevertheless, endophytes may be better plant-defense agents over their external counterparts in the rhizosphere due to the direct contact with the plant root tissues which offer an opportunity to exert their beneficial effects more directly (Santoyo et al. 2016). According to Afzal et al. (2019), living endosymbiotically and being in direct contact with plant tissues enables endophytes to readily exert direct beneficial effects to their plant hosts in exchange for a consistent supply of nutrients. It is also propounded that endophytes can be more efficient than their external rhizobacterial counterparts because they are protected from abiotic stresses in the rhizosphere (Hardoim et al. 2015).

### 4.3 Diversity of Endophytic Bacteria Involved in Plant Defense Against Phytopathogens

Various endophytic bacteria contribute to the defense of plants against phytopathogens (Singh et al. 2020; Morales-Cedeño et al. 2021), for instance, the production of lytic enzymes and antibiotics and the elicitation of plant defense mechanisms against their pathogens (Pérez-Montañó et al. 2014). Recently, Santoyo et al. (2016), the diversity of bacterial endophytes involved in the suppression of phytopathogens were listed as *Arthrobacter*, *Burkholderia*, *Bacillus*, *Enterobacter*, *Microbacterium*, *Methylobacterium*, *Sphingomonas*, *Micrococcus*, *Pantoea*, *Rhanella*, *Phyllobacterium*, *Pseudomonas*, *Paenibacillus*, *Rhodanobacter*, and *Stenotrophomonas*. *Bacillus* and *Streptomyces* are, however, the most abundant (Reinhold-Hurek and Hurek 2011).

Bacilli are some of the most important bacteria for plant disease suppression due to their antimicrobial metabolites (Aloo et al. 2019b; Riaz et al. 2021). Fairly, recent investigations have shown the in vitro and in vivo antagonistic activities of endophytic *B. methylotrophicus*, *B. amyloliquefaciens*, and *B. subtilis* against the rice-blast-causing *Xanthomonas oryzae* pv. *oryzae* (El-shakh et al. 2015). *Bacillus subtilis* endophytic in *Brassica campestris* also recently exhibited strong antagonistic activities against *X. oryzae* pv. *oryzae* (Cheng et al. 2016). Similarly, tomato-endophytic *B. amyloliquefaciens* (Nawangsih et al. 2011), and chilli-endophytic *B. pseudomycooides*, *B. thuringiensis*, *B. mycooides* (Yanti et al. 2018) have previously been shown to suppress bacterial wilt disease-causing pathogens. More recently, rice-endophytic *B. cereus* and *B. mojavensis* (Etesami and Alikhani 2017) and several other rice-endophytic bacilli (Khaskeli et al. 2020) have also shown antagonistic abilities against several rice phytopathogens like *Magnaporthe oryzae*, *F. moniliforme*, *F. graminearum*, and *Rhizoctonia solani*. Many other studies have confirmed the antagonistic properties of endophytic Bacilli against different pathogens like *F. Circinatum* causing pitch canker in Pinus (Soria et al. 2012), *R. solani* causing damping-off in cotton (Selim et al. 2017), *X. citri* subsp. *citri* causing citrus canker in citrus (*Citrus aurantiifolia*) (Daungfu et al. 2019), *Bortyris cinerea* causing the gray mold disease in many crops (Kefi et al. 2015), *Colletotrichum lindemuthianum* causing in beans (Gholami et al. 2013), and *Fusarium* causing head blight in wheat plants (Chen et al. 2018).

Owing to their powerful antagonistic activities and production of various antifungal metabolites (Colombo et al. 2019), endophytic *Streptomyces* have also extensively been studied for the biocontrol of plant fungal pathogens. For instance, bean-endophytic *S. cyaneofuscatus*, *S. flavofuscus*, *S. parvus*, *S. acrimycini* have previously been shown to control the Anthracnose disease in the plant caused by *C. lindemuthianum* (Gholami et al. 2013). Similarly, rice-endophytic *Streptomyces* spp. have also shown effectiveness against its leaf-blight causing *X. oryza*. (Hastuti et al. 2012). The suppression of *R. solanacearum* by *Streptomyces* spp. has also been established (Achari and Ramesh 2014). Recently, Colombo et al. (2019) identified an endophytic *Streptomyces* that can reduce the symptoms of *Fusarium* head blight in wheat. Likewise, Tan et al. (2011) also demonstrated the biocontrol ability of

tomato-endophytic *S. virginiae* against its wilt-causing *R. solanacearum*. Several other endophytic *Streptomyces* have been implicated in the suppression of plant pathogens (Dias et al. 2017; Vurukonda et al. 2018; Anusha et al. 2019; Zhu et al. 2020).

*Pseudomonas* spp. are some of the most beneficial rhizobacteria because of their potential as biocontrol agents (Haas and Défago 2005). Endophytic Pseudomonads seem to be widely associated with the control of phytopathogens as evidenced by several studies (Table 4.1). Fluorescent pseudomonads have specially gathered a lot of attention as biocontrol agents because of their metabolic versatility (Raaijmakers and Mazzola 2012), and adaptability to different environmental conditions, and efficient colonization of plant roots (Ma et al. 2016). Cognizant of this, these rhizobacteria hold immense potential with regard to promoting plant defense against phytopathogens.

Leguminous plants are widely associated with endophytic rhizobial species that are largely known for biological nitrogen (N) fixation (Das et al. 2017; Volpiano et al. 2019). Interestingly, different rhizobia have also been linked to the suppression of plant pathogens (Chakraborty and Purkayastha 1984; Akhtar and Siddiqui 2008; Yuttavanichakul et al. 2012; Aeron et al. 2017; Volpiano et al. 2018; Jack et al. 2019). Osdaghi et al. (2011) also established inhibitory properties of *Rhizobium leguminosarum* strain against *X. axonopodis* causing bacterial blight in the common bean. These reports provide preliminary evidence of the effects of rhizobia on plant pathogens (Volpiano et al. 2019). Besides, non-rhizobial endophytic associations with legumes have also been implicated in the control of phytopathogens.

For instance, chickpea (*Cicer arietinum*)-endophytic *B. cereus*, *B. thuringiensis*, *Achromobacter xylosoxidans*, and *B. subtilis* recently showed the ability to suppress *F. solani* causing the rot disease in the plant (Egamberdieva et al. 2017). Similarly, faba bean (*Vicia faba*) and chickpea-endophytic *Rahnella aquatilis* B16C, *P. yamanorum* B12, and *P. fluorescens* B8P have recently been shown to have antifungal properties against *F. solani* in vitro and in vivo (Bahroun et al. 2018). Non-rhizobial endophytic bacilli of chickpea such as *B. cereus*, *B. subtilis*, *B. thuringiensis* were recently demonstrated to inhibit *F. solani* causing the root rot disease in the plant (Egamberdieva et al. 2017). These studies show that non-rhizobial legume endophytes are also important in plant-pathogen/disease suppression.

Several other studies have implicated different endophytic bacterial genera in phytopathogen antagonism. For instance, tomato-endophytic *Staphylococcus epidermidis* have previously been shown to significantly lower the incidence of bacterial wilt disease of the plant caused by *R. solanacearum* (Nawangsih et al. 2011). Up to 96% in vitro suppression of the wilt-causing *F. oxysporum* by endophytic *Stenotrophomonas maltophilia*, *Azotobacter chroococum* and *Serratia marcescens* of *Solanum sodomaceum* and *S. bonariense* has recently been established (Abdallah et al. 2020). Endophytic *Enterobacter* of eggplants, cucumbers, and groundnuts (Ramesh et al. 2009), *Enterobacter* sp., and *Agrobacterium* sp. of Solanaceous (Achari and Ramesh 2014) have also been shown to reduce bacterial wilt caused by *R. solanacearum*. Other endophytic

**Table 4.1** Examples of Pseudomonads endophytic in different plants and effective against various phytopathogens

Host plant	Species	Pathogen	Disease	Reference
Black gram ( <i>Vigna mungo</i> L.)	<i>P. aeruginosa</i>	<i>Pythium aphanidermatum</i> , <i>R. solani</i>	Rhizome rot, Leaf Blight	Vinayarani and Prakash (2018)
Black pepper ( <i>Piper nigrum</i> L.)	<i>P. fluorescens</i> BKZ63	<i>Sclerotinia sclerotiorum</i> K229], <i>F. solani</i> W70, <i>F. avenaceum</i>	Wilt, Stem rot	Chlebek et al. (2020)
Cauliflower ( <i>Brassica</i> <i>oleracea</i> )	<i>P. fluorescens</i>	<i>X. campestris</i> pv. <i>campestris</i>	Black rot	Singh et al. (2010)
Chickpea ( <i>Cicer</i> <i>arietinum</i> )	<i>P. fluorescens</i>	<i>F. oxysporum</i>	Wilt	Mohammed et al. (2019)
Chilli pepper ( <i>Capsicum</i> <i>frutescens</i> )	<i>P. cepacea</i>	<i>Ralstonia solanacearum</i>	Wilt	Istifadaha et al. (2017)
Cocoa ( <i>Theobroma</i> <i>cacao</i> )	<i>P. fluorescens</i>	<i>Macrophomina phaseolina</i>	Dry rot	Karthikeyan et al. (2005)
Cotton ( <i>Gossypium</i> spp.)	<i>P. fluorescens</i> PICF7	<i>Verticillium dhaliae</i>	Wilt	Martínez-García et al. (2015)
Eggplant ( <i>Solanum</i> <i>melongena</i> )	<i>P. protogenes</i> MP12	<i>Phaeoaniella chlamydospora</i> , <i>Phaeoacremonium aleophilum</i> <i>R. solanacearum</i>	Tracheomycosis	Andreoli et al. (2019)
Faba bean ( <i>Vicia faba</i> )	<i>P. yananorum</i> , <i>P. frederikbergensis</i> , <i>P. fragi</i> , <i>P. putida</i> , <i>P. brenneri</i> , <i>P. fluorescens</i> , <i>P. rhodestiae</i> <i>P. fluorescens</i> EB69	<i>F. solani</i>	Wilt	Ramesh and Phadke (2012)
		<i>F. oxysporum</i>	Wilt	Bahroun et al. (2018)
			Wilt	Mohammed et al. (2019)

(continued)

Table 4.1 (continued)

Host plant	Species	Pathogen	Disease	Reference
Ginseng ( <i>Panax ginseng</i> )	<i>P. stutzeri</i> E25	<i>B. cinerea</i>	Grey mold	Rojas-Solis et al. (2018)
Grapevine ( <i>Vitis vinifera</i> )	<i>P. aeruginosa</i> , <i>P. putida</i>	<i>Phytophthora capsici</i>	Foot rot	Aravind et al. (2009)
Maize ( <i>Zea mays</i> )	<i>P. aeruginosa</i> , <i>P. montielii</i> , <i>P. putida</i> , <i>P. thriervvalensis</i> , <i>P. lini</i> , <i>P. fulva</i>	<i>F. graminearum</i>	Gibberella ear rot	Mousa et al. (2015)
Oilseed Rape ( <i>Brassica napus</i> L.)	<i>P. putida</i> BP25	<i>Magnaporthe oryzae</i>	Rice blast	Patel et al. (2020)
Olive ( <i>Olea europaea</i> )	<i>P. aeruginosa</i> BRp3	<i>X. oryzae</i> pv. <i>oryzae</i>	Leaf Blight	Yasmin et al. (2017)
Pea ( <i>Pisum sativum</i> )	<i>Pseudomonas</i> spp.	<i>V. dhaliae</i>	Wilt	Erdogan and Benlioglu (2010)
Pine ( <i>Pinus sylvestris</i> )	<i>P. fulva</i>	<i>F. oxysporum</i> , <i>R. solani</i>	Damping-off	Pokojska-Burdziej et al. (2004)
Rice ( <i>Oryza sativa</i> )	<i>P. yunnanum</i> B12, <i>P. fluorescens</i> B8P	<i>F. solani</i>	Root rot	Bahroun et al. (2018)
	<i>P. putida</i> BP25	<i>Magnaporthe oryzae</i>	Blast	Ashajyothi et al. (2020)
	<i>P. fluorescens</i> 63-68	<i>F. oxysporum</i> f. sp. <i>pisii</i> , <i>P. ultimum</i>	Wilt	Ardebili et al. (2011)
	<i>P. fluorescens</i> EB67	<i>R. solanacearum</i>	Wilt	Ramesh et al. (2009)
Sunflower ( <i>Helianthus annuus</i> )	<i>P. montielii</i> , <i>O. fluorescens</i> , <i>P. lini</i> , <i>P. indica</i> .	<i>V. dhaliae</i>	Wilt	Cabanás et al. (2018)



Sweet Pepper ( <i>Capsicum annuum</i> )	<i>P. fluorescens</i>	<i>X. euvesicatoria</i>	Bacterial spot	Akkopru et al. (2018)
Tomatillos ( <i>Physalis ixocarpa</i> )	<i>P. putida</i> BP25	<i>R. solani</i> , <i>P. capsica</i> , <i>P. myriophyllum</i> , <i>C. gloeosporioides</i> , <i>Gibberella moniliformis</i> , <i>Athelia rolfsii</i> , <i>Magnaporthe oryzae</i>	Various diseases	Agisha et al. (2019)
Tomato ( <i>Solanum lycopersicum</i> )	<i>P. fluorescens</i>	<i>R. solanacearum</i>	Wilt	Vanitha and Umesha (2011)
	<i>P. montelii</i> , <i>P. aeruginosa</i>	<i>M. phaseolina</i> , <i>F. solani</i> , <i>R. solani</i> , <i>F. oxysporum</i>	Root rot	Moin et al. (2020)
	<i>P. aeruginosa</i> AS1	<i>P. palmivora</i>	Black pod	Alsultan et al. (2019)
	<i>Pseudomonas</i> sp. p21	<i>Aspergillus niger</i>	Not mentioned	Ma et al. (2017)
	<i>P. fluorescens</i>	<i>X. euvesicatoria</i>	Bacterial spot	Akkopru et al. (2018)
	<i>P. mossellii</i> FS67, <i>P. fluorescence</i> FS167, <i>P. brassicacearum</i> FS184	<i>R. solanacearum</i>	Bacterial wilt	Safdarpour and Khodakaramian (2018)
Tumeric ( <i>Curcuma longa</i> L.)	<i>P. aeruginosa</i> H40	<i>R. solani</i>	Damping-off	Selim et al. (2017)

bacterial genera that have been shown to facilitate plant defense against phytopathogens include Pinus-endophytic *Burkholderia* spp. against *F. circinatum* causing pitch canker in the plant (Soria et al. 2012), cotton-endophytic *Stenotrophomonas maltophilia* against *R. solani* causing damping-off in the plant (Selim et al. 2017), maize-endophytic *Paenibacillus polymyxa* and *Citrobacter* sp. against *F. graminearum* causing gibberella ear rot in the plant (Mousa et al. 2015), rubber-endophytic *S. marcescens* against the wilt-causing *Fusarium* in banana (Tan et al. 2015), tomato-endophytic *Brevibacterium halotolerans* against *Botrytis cinerea* causing the gray mold disease in various crops (Kefi et al. 2015), black-pepper-endophytic *Enterobacter* and *Serratia* against *Phytophthora* blight in the plant (Irabor and Mmbaga 2017), cucumber (*Cucumis sativus* L.)-endophytic *Ochrobactum pseduintermedium* and *Pantoea agglomerans* against *P. syringae* pv. *lachrymans* causing the angular leaf spot disease in the plant (Akbaba and Ozaktan 2018), and corn-endophytic *Burkholderia gladioli* against *Sclerotinia homoeocarpa* of bentgrass (Shehata et al. 2016).

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#### 4.4 Endophytic Metabolites Involved in Plant Defense Against Phytopathogens

The biocontrol activities of many plant-endophytic strains are largely mediated by their secondary metabolites such as lytic enzymes, antibiotics, volatile organic compounds (VOCs), and siderophores (Gunatilaka 2006). According to Jain and Pandey (2016), these secondary metabolites are important defense mechanisms for plant defense against phytopathogens. Herein, we discuss the various metabolites through which endophytic bacteria are known to suppress plant pathogens/diseases.

##### 4.4.1 Antibiotics

The defense of plants against phytopathogens is widely associated with the synthesis of antibiotics (Liu et al. 2017; Khedher et al. 2021). Some of the best-studied antibiotics are lipopeptides such as surfactin, fengycin, iturin, and bacillomycin (Cai et al. 2013). Various studies have established the activities of endophytic lipopeptides against plant pathogens. For instance, the inhibitory activities of lipopeptides of *Bacillus* spp. isolated from Indian popcorn and yellow dent corn have previously been demonstrated against *F. moniliforme* (Gond et al. 2015). Endophytic bacilli like *B. amyloliquefaciens* and *B. subtilis* that produce lipopeptide antibiotics against different phytopathogens have also been investigated (Gond et al. 2015; Jayakumar et al. 2019). Similarly, lipopeptides like iturin-A, bacillomycin-D, surfactin, and fengycin-D of endophytic *B. methylotrophicus*, *B. velezensis*, *B. amyloliquefaciens*, and *B. mojavensis* isolated from *Citrus reticulata*, *C. sinensis*, *C. limon*, *Laurus nobilis*, and *Medicago truncatula* have also been investigated against *Phoma tracheiphila* (Kalai-Grami et al. 2014). In maize, there is evidence that endophytic bacteria can protect their hosts by secreting antifungal lipopeptides

that induce the up-regulation of pathogenesis-related genes (Gond et al. 2015). The association between rhizobacterial lipopeptides and plant resistance against phytopathogens has also been established in *B. subtilis* against *R. solani* in rice (Chandler et al. 2015), and *P. fluorescens* against *P. aphanidermatum* in turmeric (Prabhukarthikeyan et al. 2018).

Several studies have confirmed the genomic capacity of antibiotic production in plant-endophytic bacteria with the potential to defend plants against different phytopathogens (Loper and Gross 2007; Chen et al. 2009; Qin et al. 2015; Li et al. 2020). According to Stein (2005), between 4 and 5% of *B. subtilis* genome is dedicated to the synthesis of antibiotics. Fairly recently, lipopeptides were also established in the genomes of endophytic Bacilli associated with wild Solanaceous plants with antagonistic potential against *F. oxysporum* f. sp. *lycopersici* (Abdallah et al. 2017). The antagonistic potential of cotton-endophytic *Bacillus* spp. against *Verticillium* wilt has also been linked to the existence of genes encoding for bacillomycin, surfactin, and fengycin antibiotics (Hasan et al. 2020). In another recent study, molecular studies also revealed the occurrence of biosynthetic genes encoding for lipopeptides in common-bean-endophytic *B. amyloliquefaciens*, *B. halotolerans*, *B. velezensis*, *Agrobacterium fabrum*, and *P. lini* with antifungal activities against *Fusarium* sp., *Alternaria* sp., and *Macrophomina* sp. causing root rot disease in the plant (Sendi et al. 2020).

Endophytic *Streptomyces* spp. are similarly widely recognized for their potential to defend plants against phytopathogens through the production of antibiotics (Jones and Elliot 2017). Snake-vine (*Kennedia nigriscans*)-endophytic *Streptomyces* sp. NRRL-30562 was previously documented to produce munumbicins which are active against different plant phytopathogenic fungi and bacteria (Castillo et al. 2002). Fairly recently, antibiotic-producing legume-endophytic *S. caeruleatus* was also showed antagonism against the soybean pathogen, *X. campestris* (Mingma et al. 2014). Several other studies have demonstrated phytopathogen control mediated by antibiotic-producing plant root-endophytic *Streptomyces* (Xu et al. 2017; Chandrakar and Gupta 2019; Marian et al. 2020).

Fluorescent pseudomonads have also attracted a lot of interest as plant protection agents (Olorunleke et al. 2015), particularly, through the production of antibiotics (Mazurier et al. 2009; Shankar et al. 2017; Prabhukarthikeyan et al. 2018; Andreolli et al. 2019). Generally, the synthesis of antibiotics by *Pseudomonas* spp. and other rhizobacteria involve a multienzyme complex known as the non-ribosomal peptide synthetase that contains domains for selecting, loading, and synthesizing amino acids, and secreting the antibiotics (Strieker et al. 2010; Dunlap et al. 2013). The genomic biosynthesis of antibiotics has also been attributed to the presence of polyketide synthases, especially in endophytic bacilli (Cai et al. 2016; Harwood et al. 2018).

Antibiotics are probably some of the most studied rhizobacterial metabolites (Liu et al. 2017). The production of antibiotics by plant-endophytic bacteria especially holds immense potential in plant defense against phytopathogens because of the intimate interaction of endophytes and their plant hosts (Lopes et al. 2017; Tewari et al. 2019), which can allow for more efficient and direct antibiosis on

phytopathogens. Besides, some antibiotics have a broad spectrum of activity and can be effective against several phytopathogens.

#### 4.4.2 Lytic Enzymes

Most bacteria produce enzymes that can lyse polymeric compounds such as proteins, chitin, glucans, lipids, and cellulose which are the principal components of phytopathogenic fungal cell walls (Lee et al. 2013; Villarreal-Delgado et al. 2018). Among the most studied rhizobacterial lytic enzymes are cellulases,  $\beta$ -1,3-glucanases, chitinases, and proteases (Mota et al. 2017). Table 4.2 displays some lytic enzymes of endophytic bacteria that have been associated with plant defense against various phytopathogens. Chitinases are the largest group of plant defense-related enzymes (Jalil et al. 2015), involved in the inhibition of phytopathogenic fungi through the hydrolysis of the glycosidic bonds of the chitin components of their cell walls (Lopes et al. 2017). Generally, the synthesis of lytic enzymes involved in the hydrolysis of pathogen cell-walls has been reported in different endophytic *Pantoea*, *Micrococcus*, *Pseudomonas*, *Burkholderia*, *Chryseobacterium*, *Stenotrophomonas*, *Brevundimonas*, *Bacillus*, *Alcaligenes*, *Microbacterium*, *Serratia*, *Enterobacter*, *Curtobacterium*, and *Acinetobacter* (Kalai-Grami et al. 2014; Rania et al. 2016; Vurukonda et al. 2018).

Lytic enzymes are normal metabolites of endophytic bacteria to aid entry into plant roots during plant colonization (Compant et al. 2005; Taghavi et al. 2010; Sessitsch et al. 2012; Liu et al. 2017). However, these enzymes also lyse the cell walls of phytopathogens which possess similar cell wall materials to plants, and the link between endophytic lytic enzymes and the suppression of plant pathogens must not be overlooked.

#### 4.4.3 Siderophores

Siderophores are microorganic bacterial metabolites which are produced mostly under iron (Fe)-deficient conditions to bind Fe (Goswami et al. 2016; Ghosh et al. 2020). These micromolecules have for years gathered attention due to their potential to control phytopathogens through the formation of siderophore-Fe complexes that limit Fe availability in the rhizosphere (Martinez-Viveros et al. 2010; Khedher et al. 2021).

Although plant pathogens can also produce siderophores, it is advanced that rhizobacterial siderophores have a much greater Fe affinity than those of pathogens which consequently inhibit the proliferation of pathogens in the rhizosphere (Compant et al. 2005; Jain and Pandey 2016; David et al. 2018). Consequently, siderophore production is an important aspect of phytopathogen antagonism and plant disease management (Khedher et al. 2021).

The production of different types of siderophores has been established in various endophytic bacteria. During the analysis of secondary metabolites of rice-endophytic

**Table 4.2** Lytic enzymes produced by various endophytic bacteria against phytopathogens in various experiments

Enzyme	Endophyte	Hot plant	Pathogen	Reference(s)
Amylase	<i>P. fluorescens</i>	<i>Atractylodes lancea</i>	<i>Athelia rolfsii</i>	Zhou et al. (2014)
Cellulase	<i>P. fluorescens</i>	<i>Atractylodes lancea</i>	<i>Athelia rolfsii</i>	Zhou et al. (2014)
Cellulase	<i>Acinetobacter</i> sp., <i>P. aeruginosa</i> , <i>Enterobacter</i> sp.	Tumeric ( <i>C. longa</i> L.)	<i>P. aphanidermatum</i> , <i>R. solani</i>	Vinayarani and Prakash (2018)
Chitinase	<i>Streptomyces</i> spp.	Citrus, Soybean	<i>P. parasitica</i> , <i>Guignardia citricarpa</i> <i>R. solani</i> , <i>C. sublineolum</i> , <i>Pythium</i> sp. <i>F. oxysporum</i> , <i>Lactuca sativa</i>	Quecine et al. (2008)
	<i>B. tequilensis</i> SV104, <i>A. faecalis</i> subsp. <i>faecalis</i> S8, <i>Stenotrophomonas</i> S33, <i>B. cereus</i> S42, <i>S. maltophilia</i> S37, <i>B. mojavensis</i> S40, <i>Pseudomonas</i> sp. S85, <i>Serratia</i> sp. C4	Tomato ( <i>S. lycopersicum</i> )	<i>F. oxysporum</i>	Abdallah et al. (2016)
	<i>Brachy bacterium</i> , <i>Bacillus</i> , <i>Burkholderia</i> , <i>Caballeronia</i> , <i>Kitasatospora</i> , <i>Lechevalieria</i> , <i>Leifsonia</i> , <i>Luteibacter</i> , <i>Lysinibacillus</i> , <i>Mycolicibacterium</i> , <i>Nakamurella</i> , <i>Paracoccus</i> , <i>Sinomonas</i> , <i>Sphingobium</i>	<i>Coffea canephora</i> , <i>C. tiberica</i>	<i>F. oxysporum</i> , <i>Radopholus duriophilus</i> , <i>Pratylenchus coffeae</i>	Duong et al. (2021)
	<i>Rhizobia</i>	Fenugreek ( <i>Trigonella foenumgraecum</i> )	<i>F. oxysporum</i>	Kumar et al. (2011)
	<i>S. marcescens</i> ITBB B5-1	Banana ( <i>Musca</i> spp.)	<i>F. oxysporum</i> f. sp. <i>cubense</i>	Tan et al. (2015)
	<i>Stenotrophomonas maltophilia</i> , <i>B. subtilis</i> , <i>Azotobacter chroococcum</i> , <i>S. marcescens</i>	<i>Solanum sodomaeanum</i> , <i>S. bonariense</i>	<i>F. oxysporum</i>	Abdallah et al. (2020)
	<i>Serratia</i> spp.	Tomato ( <i>S. lycopersicum</i> )	<i>F. oxysporum</i>	Niranjana and Hariprasad (2012)

(continued)

Table 4.2 (continued)

Enzyme	Endophyte	Host plant	Pathogen	Reference(s)
Esterase	<i>B. amyloliquefaciens</i> , <i>B. halotolerans</i> , <i>B. velezensis</i> , <i>Agrobacterium fabrum</i> , <i>P. lini</i>	Common bean ( <i>Phaseolus vulgaris</i> )	<i>Fusarium</i> sp., <i>Macrophomina</i> sp., <i>Alternaria</i> sp.	Sendi et al. (2020)
	<i>Bacillus</i> spp.	Maize ( <i>Zea mays</i> )	<i>F. moniliforme</i>	Bressan and Figueiredo (2010)
	<i>Rhizobium</i> sp.	<i>Cicer arietinum</i>	<i>F. oxysporum</i> , <i>M. phaseolina</i> , and <i>S. sclerotiorum</i>	Smitha and Singh (2014)
	<i>Streptomyces</i> spp.	Tomato ( <i>S. lycopersicum</i> )	<i>F. oxysporum</i>	Abbasi et al. (2019)
	<i>Streptomyces</i> spp.	Rice ( <i>Oryza sativa</i> )	<i>X. oryzae</i> pv. <i>oryzae</i>	Hasnuti et al. (2012)
	<i>Brachybacterium</i> , <i>Bacillus</i> , <i>Burkholderia</i> , <i>Caballeronia</i> , <i>Kitasatospora</i> , <i>Lechevalieria</i> , <i>Leifsonia</i> , <i>Luteibacter</i> , <i>Lysinibacillus</i> , <i>Mycolicibacterium</i> , <i>Nakamurella</i> , <i>Paracoccus</i> , <i>Sinomonas</i> , <i>Sphingobium</i>	<i>C. canephora</i> , <i>C. tiberica</i>	<i>F. oxysporum</i> , <i>Radopholus duriphilus</i> , <i>Pratylenchus coffeae</i>	Duong et al. (2021)
	<i>Brachybacterium</i> , <i>Bacillus</i> , <i>Burkholderia</i> , <i>Caballeronia</i> , <i>Kitasatospora</i> , <i>Lechevalieria</i> , <i>Leifsonia</i> , <i>Luteibacter</i> , <i>Lysinibacillus</i> , <i>Mycolicibacterium</i> , <i>Nakamurella</i> , <i>Paracoccus</i> , <i>Sinomonas</i> , <i>Sphingobium</i>	<i>C. canephora</i> , <i>C. tiberica</i>	<i>F. oxysporum</i> , <i>Radopholus duriphilus</i> , <i>Pratylenchus coffeae</i>	Duong et al. (2021)
	<i>Brachybacterium</i> , <i>Bacillus</i> , <i>Burkholderia</i> , <i>Caballeronia</i> , <i>Kitasatospora</i> , <i>Lechevalieria</i> , <i>Leifsonia</i> , <i>Luteibacter</i> , <i>Lysinibacillus</i> , <i>Mycolicibacterium</i> , <i>Nakamurella</i> , <i>Paracoccus</i> , <i>Sinomonas</i> , <i>Sphingobium</i>	<i>C. canephora</i> , <i>C. tiberica</i>	<i>F. oxysporum</i> , <i>Radopholus duriphilus</i> , <i>Pratylenchus coffeae</i>	Duong et al. (2021)
	<i>Bacillus</i> , <i>Ficitibacillus</i> , <i>Lysinibacillus</i> , <i>Paenibacillus</i> , <i>Cupriavidus</i> , <i>Microbacterium</i>	Rice ( <i>O. sativa</i> )	<i>F. moniliforme</i> , <i>Magnaporthe oryzae</i> , <i>F. graminearum</i> , <i>R. solani</i>	Khaskeli et al. (2020)

Pectinase	<i>B. tequilensis</i> SV104, <i>A. faecalis</i> subsp. <i>faecalis</i> S8, <i>Stenotrophomonas</i> S33, <i>B. cereus</i> S42, <i>S. maltophilia</i> S37, <i>B. mojavensis</i> S40, <i>Pseudomonas</i> sp. S85, <i>Serratia</i> sp. C4 <i>P. fluorescens</i>	Tomato ( <i>S. lycopersicum</i> )	<i>F. oxysporum</i>	Abdallah et al. (2016)	
				<i>Atractylodes lancea</i>	Zhou et al. (2014)
				<i>Solanum sodomaicum</i> , <i>S. bonariense</i>	Abdallah et al. (2020)
				Tomato ( <i>S. lycopersicum</i> )	Abdallah et al. (2016)
Protease	<i>B. tequilensis</i> SV104, <i>A. faecalis</i> subsp. <i>faecalis</i> S8, <i>Stenotrophomonas</i> S33, <i>Serratia</i> sp. C4, <i>B. cereus</i> S42, <i>S. maltophilia</i> S37, <i>B. mojavensis</i> S40, <i>Pseudomonas</i> sp. S85 <i>Acinetobacter</i> sp., <i>P. aeruginosa</i> , <i>Enterobacter</i> sp. <i>Streptomyces</i>	Turmeric ( <i>C. longa</i> )	<i>R. solani</i> , <i>P. aphanidermatum</i>	Vinayarani and Prakash (2018)	
				Tomato ( <i>S. lycopersicum</i> )	Abbasi et al. (2019)
				Rice ( <i>O. sativa</i> )	Khaskelli et al. (2020)
				<i>Solanum sodomaicum</i> , <i>S. bonariense</i>	Abdallah et al. (2020)
Xylanase	<i>P. fluorescens</i> <i>P. fluorescens</i> <i>B. amyloliquefaciens</i> , <i>B. halotolerans</i> , <i>B. velezensis</i> , <i>Agrobacterium fabrum</i> , <i>P. lini</i>	Common bean ( <i>P. vulgaris</i> )	<i>Fusarium</i> sp., <i>Macrophomina</i> sp., <i>Alternaria</i> sp.	(continued)	
				<i>Atractylodes lancea</i>	Zhou et al. (2014)
				Olive ( <i>Olea europaea</i> )	Cabanás et al. (2018)
					Sendi et al. (2020)

(continued)

**Table 4.2** (continued)

Enzyme	Endophyte	Host plant	Pathogen	Reference(s)
$\beta$ -1,3-glucanases	<i>P. fluorescens</i>	Olive ( <i>Olea europaea</i> )	<i>V. dahliae</i>	Cabanás et al. (2018)
	<i>Rhizobia</i>	Fenugreek ( <i>Trigonella foenumgraecum</i> )	<i>F. oxysporum</i>	Kumar et al. (2011)
	<i>Serratia</i> spp.	Tomato ( <i>S. lycopersicum</i> )	<i>F. oxysporum</i>	Niranjana and Hariprasad (2012)
	<i>S. marcescens</i> ITBB B5-1	Banana ( <i>Musca</i> spp.)	<i>F. oxysporum</i> f. sp. <i>cubense</i>	Tan et al. (2015)



*P. aeruginosa* BRp3 active against the blight-causing *X. oryzae*, mass-spectrometric analyses detected the presence of phenazine, pyochelin, and pyocyanin types of siderophores (Yasmin et al. 2017). In an earlier study, the production of hydroxamate and carboxylate siderophores *Phyllanthus amarus* endophytic *P. fluorescens* ENPF1 with antagonistic properties against stem blight pathogen *Corynespora casiiicola* was established (Mathiyazhagan et al. 2004). The production of different siderophores has also been established in Rhizobia capable of in vitro and in vivo inhibition of fungal pathogens (Srinivasan 2017; Singh et al. 2018). Rice-endophytic siderophore-producing *Streptomyces* spp. with antagonistic abilities against *X. oryzae* causing bacterial leaf blight on the plant have also been documented (Hastuti et al. 2012).

Recently, various endophytic *B. niabensis*, *B. subtilis*, *B. mojavensis* with antagonistic properties against the banana wilt-causing pathogen were shown to produce various types of siderophores in dual cultures (Kesaulya et al. 2017). In a separate study, the production of siderophores by endophytic *Pseudomonas*, *Acinetobacter*, *Enterobacter*, and *Bacillus* was significantly and positively correlated with the inhibition of *P. sojae* (Zhao et al. 2018). In a more recent study, *B. amyloliquefaciens*, *B. halotolerans*, *B. velezensis*, *Agrobacterium fabrum*, and *P. lini* endophytic in common bean and displaying antifungal activities against the root-rot-causing *Fusarium* sp., *Macrophomina* sp., and *Alternaria* sp. were shown to produce siderophores (Sendi et al. 2020). In yet another study, the in vitro and in planta antagonistic properties of *Acinetobacter* sp., *P. aeruginosa*, and *Enterobacter* sp. endophytic in turmeric (*C. longa* L. against *P. aphanidermatum* and *R. solani* causing leaf blight and rhizome rot respectively were associated with the production of siderophores (Vinayarani and Prakash 2018).

Siderophore biosynthesis, uptake, and transport are generally regulated by Fe-sensitive *Fur* proteins, sigma factors (*RpoS*, *PvdS*, and *FpvI*), global regulators (*GasS* and *GasA*), quorum-sensitive autoinducers, and several site-specific recombinases (Ravel and Cornelis 2003; Compant et al. 2005; Ollinger et al. 2006). Although siderophores are common metabolites of all rhizobacteria, endophytic siderophores may especially be more important in eliciting plant defense against phytopathogens because of the intimate associations endophytes have with their plant hosts (Lopes et al. 2017). Siderophores are also associated with induced systemic resistance of plants against phytopathogens (Nagarajkumar et al. 2004; Djavaheri et al. 2012). Besides the suppression of plant pathogens, rhizobacterial siderophores can also increase Fe supply to plants (Goswami et al. 2016; Aloo et al. 2019b). Although the siderophore-mediated defense of plants against phytopathogens may be restricted to the sites of production and may be inefficient in tackling plant pathogens away from the sites of production, siderophore production and siderophore-producing rhizobacteria are a classic example of how rhizobacteria can suppress plant pathogens and should not be overlooked (Aloo et al. 2019a).

#### 4.4.4 Volatile Organic Compounds

Volatile organic compounds (VOCs) are microorganic compounds of low polarity and high vapor pressure produced by microorganisms through different metabolic pathways as part of their natural metabolism (Vespermann et al. 2007). Rhizobacterial VOCs are not only important in the direct defense against phytopathogens (Ryu et al. 2004) but can also improve root growth nutrient acquisition and enhance plant health under abiotic stress (Khan et al. 2017).

Various studies have demonstrated the relationship between endophytic bacterial VOCs and phytopathogen control. For instance, diffusible VOCs of endophytic *Stenotrophomonas maltophilia*, *Azotobacter chroococcum* S11, *S. marcescens* S14, and *Bacillus* sp. SV81 obtained from *Solanum bonariense*, and *S. sodomaeum* are some of the compounds that were recently implicated in the in vitro control of *F. oxysporum* causing the wilt disease in Solanaceae plants (Abdallah et al. 2020). In a separate study, two endophytic bacteria identified as *Stenotrophomonas maltophilia* CR71 and *P. stutzeri* E25 from *Physalis ixocarpa* antagonism against *B. cinerea* in dual cultures was attributed to the production of volatile dimethyl disulphide (Rojas-Solís et al. 2018). Similarly, various VOCs of *P. putida* BP25 endophytic in black pepper have the potential to suppress *R. pseudosolanacearum*, *P. myriotylum*, *Athelia rolfsii*, *R. solani*, *P. capsica*, *C. gloeosporioides*, *Gibberella moniliformis*, *Radopholus similis*, and *Magnaporthe oryzae* (Agisha et al. 2019). The antifungal activities of various VOCs of black pepper-endophytic *P. putida* BP25 against the rice-blast-causing *Magnaporthe oryzae* have also been established (Patel et al. 2020). In a separate study, that evaluated various endophytic *Pseudomonas* spp. for the in vitro suppression of sunflower fungal infections caused by *F. solani*, *M. phaseolina*, *R. solani*, and *F. oxysporum*, most of them were found to produce volatile antifungal metabolites (Moin et al. 2020).

Rhizobacterial VOCs can largely be classified as alcohols, hydrocarbons, ketones, acids, ethers, esters, and sulfur-containing compounds (Lee et al. 2012; Audrain et al. 2015). In rice, the effects of endophytic *S. platensis* F-1 VOCs on the control of *Botrytis cinerea*, *R. solani*, and *S. sclerotinium* causing fruit rot of strawberry, leaf/seedling blight of rice, and leaf blight of oilseed rape respectively were previously investigated and grouped into alcohols, esters, acids, alkanes, ketones, and alkenes (Wan et al. 2008). In a more recent study by Sheoran et al. (2015), the VOCs produced by black-pepper-endophytic *P. putida* BP25 against *P. capsici*, *Giberella moniliformis*, *P. myriotylum*, *R. solani*, *C. gloeosporioides*, *Athelia rolfsii*, and the nematode, *Radopholus similis* were identified as heneicosane, tetratetracontane, and pyrazine derivatives.

Hydrogen cyanide (HCN) is a volatile organic compound with antagonistic properties against many soil-borne pathogens (Martinez-Viveros et al. 2010; Khedher et al. 2021). According to Mushtaq et al. (2021), HCN suppresses plant pathogens by interfering with the supply of energy to their cells through the inhibition of electron transport chains that ultimately results in cell death. The compound is synthesized from glycine via an oxidative reaction catalyzed by a membrane-bound

flavoenzyme known as HCN synthase (Blumer and Haas 2000; Nandi et al. 2017). The biosynthesis of HCN involves the *hcnABC* operon/gene cluster (Devi et al. 2013; Mousa and Raizada 2015), whose presence has been established in several rhizobacteria such as *Streptomyces* (Subramaniam et al. 2020), *B. amyloliquefaciens* (Bruto et al. 2014), *P. fluorescens* Pf-5 (Paulsen et al. 2005), and *P. aeruginosa* P-18 (Singh et al. 2021).

Rhizobacterial VOCs are sometimes associated with induced systemic resistance of plants to various pathogens. For instance, the resistance of oilseed rape (*B. napus* L.) to various fungal pathogens was recently associated with its endophytic *P. fluorescens* BRZ63, whose genome evaluations confirmed the existence of genes related to the biosynthesis of VOCs like acetoin and 2,3-butanediol (Chlebek et al. 2020). 2,3-butanediol is also one of the main VOCs that were produced by corn-endophytic *Enterobacter aerogenes* that induced the plant's resistance to *Setosphaeria turcica* responsible for its Northern corn leaf blight (D'Alessandro et al. 2014).

Volatile organic compounds are classical and complex rhizobacterial metabolites of importance in phytopathogen control. Unlike other metabolites whose actions may be restricted to the production points, VOCs are unique and can be more effective at phytopathogen control because they can diffuse over long distances and protect the plant from phytopathogens above- and below ground, at sites distant from the point of production (Kai et al. 2009; Santoro et al. 2011; Yuan et al. 2012). Besides, rhizobacterial VOCs are a nonspecific type of plant defense and can be effective against multiple phytopathogens.

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## 4.5 Emerging Gaps and Perspectives

Interest in endophytic bacteria is quickly expanding because of the potential they hold as alternatives to synthetic pesticides (Latha et al. 2019). However, the study of these organisms is complicated partly due to their intimacy with plant roots (Tewari et al. 2019). Although culture-independent techniques and modern molecular tools are now common and have provided an avenue for comprehensive studies of endophytic bacterial communities (Gaiero et al. 2013), researchers maintain that some endophytes are still unculturable and can only be investigated independent of cultures (Schloss and Handelsman 2005). Although culture-independent methods are also challenging because pure cultures of endophytes cannot be obtained for field application using these methodologies (Tewari et al. 2019), their application opens up a new avenue of advancing research on the environmental factors that shape endophytic bacterial communities. Notwithstanding, culture-dependent techniques are still indispensable because they enable the identification of rhizobacterial physiological properties and the prediction of their metabolic potentials and functions (Liu et al. 2017). The current consensus is to complement culture-dependent with culture-independent techniques because of the inherent biases of each (Hardoim et al. 2008; Reinhold-Hurek and Hurek 2011). Metagenomic approaches and other culture-independent methods might in the future reveal more information on endophytes

that are yet to be known. Other new technologies may also be explored to study unculturable endophytes (Thomas et al. 2008; Stewart and Brown 2012).

Genome analyses between rhizobacterial endophytes and other rhizospheric PGPR are slowly beginning to expose the potential genes involved in the endophytic lifestyle and phytopathogen control (Taghavi et al. 2010; Kaneko et al. 2010; Lopes et al. 2017; Chlebek et al. 2020; Singh et al. 2021), but the experimental-involvement in endophytic colonization has only been shown for a few of these genes (Santoyo et al. 2016). According to Monteiro et al. (2012), these genes can help to determine the phenotypic differences between phytopathogens and endophytic bacteria. It is also unclear whether certain bacteria can live interchangeably as phytopathogens or endophytes, and future studies may eventually clarify these overlapping lifestyles (Gaiero et al. 2013). With the extensive availability of modern biotechnological tools, it is expected that many studies will be conducted on the diversity of endophytic bacteria involved in phytopathogen control to broaden our understanding of their molecular basis of plant protection. Hopefully, such information will also facilitate their use in the field to control plant pathogens and promote agricultural sustainability.

Nanotechnology as a new approach can be used together with rhizobacteria technology to better the prevention of crop diseases. Of late, researchers have shifted focus to the development of novel/modern non-target, biodegradable, and environmentally-friendly nano-formulations (Kaur et al. 2012; Adetunji and Neera 2017; Pestovsky and Martinez-Antonio 2017; Miastkowska et al. 2020), that may be more effective than ordinary formulations in controlling plant pathogens (Ladner et al. 2008; Tewari et al. 2019). Several endophytic bacteria can synthesize metallic and oxide nanoparticles for the successful defense of plants against phytopathogens and the diseases they cause (Singh et al. 2020). For instance, copper nanoparticles produced by *S. capillispiralis* isolated from *Convolvulus arvensis* L. are effective against phytopathogens like *Alternaria alternata*, *F. oxysporum*, *Curvularia lunata* (Hassan et al. 2018, 2019). Similarly, endophytic *S. coelicolor* isolated from *Ocimum sanctum* is capable of synthesizing magnesium nanoparticle effective against *R. solanacearum* in tomato (El-Moslamy et al. 2019). Despite the growing interest in endophytic nanoparticles, these are largely unexplored, and more attention should be drawn to these. These innovative technologies suggest the unlimited potential of endophytic bacteria for producing more effective and cost-effective nano-formulations in the future for controlling plant diseases (Tewari et al. 2019).

Rhizobia are perhaps the most extensively investigated rhizobacteria due to their ability to form successful symbiotic interactions with leguminous plants (Das et al. 2017). It is now known that apart from their classical biological N-fixation, rhizobia can also suppress plant pathogens/diseases (Akhtar and Siddiqui 2008; Aeron et al. 2017; Volpiano et al. 2018; Jack et al. 2019). However, their exploitation for plant defense against phytopathogens is still underexplored and is a promising research niche (Tewari et al. 2019). Indisputably, more research is essential to further establish the characteristics of these special endophytes to exploit their benefits to the maximum for plant protection. Undoubtedly, the rhizobial inoculants with dual functions of N-fixation and phytopathogen suppression can contribute to enhanced

plant productivity (Das et al. 2017), and the sustainability of various agricultural systems.

While both endophytic and external rhizobacteria have important PGP abilities and the suppression of plant pathogens, endophytic bacteria have certain advantages over their external counterparts, especially because of protection from the biotic and abiotic environmental stresses in the rhizosphere (Rajkumar et al. 2009; Suman et al. 2016; Waghunde et al. 2017; Lata et al. 2019; Dubey et al. 2020). Besides, endophytes can vertically be transmitted to subsequent plant generations, providing the progeny with endosymbionts effective in defense against phytopathogens. Cognizant of this, innovative strategies can be developed to generate planting materials with beneficial rhizobacterial endophytes as plant bioprotectors (Mitter et al. 2016). This kind of engineering is promising to eliminate the need for agrochemicals (Orozco-Mosqueda et al. 2018).

Even though there is voluminous information on the characterization of endophytic bacterial diversity and their mechanisms of plant disease suppression, their successful application under field conditions is still wanting (Liu et al. 2017). Generally, a deeper understanding of plant colonization by endophytic bacteria has to be achieved to predict their successful establishment in the plant as biocontrol agents after field application (Compant et al. 2010). Finally, the biocontrol mechanisms discussed in this chapter apply to both endophytic bacteria and other rhizobacteria, and there is an opportunity to explore those mechanisms that are unique and exclusive to endophytes (Morales-Cedeño et al. 2021).

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## 4.6 Concluding Remarks

Plant-bacteria interactions have been studied for several decades now. However, the complete understanding of rhizobacterial endophytes remains somewhat elusive, hindering their utilization in phytopathogen control. Although the role of endophytic bacteria in plant disease management is undisputed, their diversity is only starting to be explored. The community dynamics of endophytes remain an important area for further research. Other promising areas for research are rhizo-engineering of the endophytic microbiomes and a better understanding of key endophytic bacterial genera and species with important biocontrol activities. Hence, futuristic research should focus on bioprospecting of endophytic bacteria and isolating them from wild and unexplored plants. Comprehensive knowledge on this subject will facilitate and advance the application of endophytes in contemporary agricultural practices for the development of sustainable food production systems. Endophytic bacteria have opened a new avenue in the area of plant defense against phytopathogens and are now designated as the future “plant probiotics” since they live within plants and leverage numerous beneficial effects to plants without causing any apparent harm to their hosts. While substantial work remains to be done, it is envisioned that soon, formulations of endophytic bacteria can be partial substitutes to chemical pesticides and bring forward a paradigm shift for the overall sustainability of agricultural systems.

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