Chapter 6
Inhibition of Bacterial and Fungal Phytopathogens Through Volatile Organic Compounds Produced by *Pseudomonas* sp.

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Abstract Plant growth-promoting rhizobacteria (PGPR) are being used as an alternative approach to combat plant diseases. About 80–90% of plant diseases are caused by bacterial and fungal pathogens, which remain an inevitable cause for the loss of several crops. Phytopathogenic bacteria and fungi are the major constraints to sustainable agriculture by adversely affecting crop growth and productivity. Owing to the increased pollution and harmful impacts of chemicals to control these pathogens, scientists are now centering on safer biological organisms and their byproducts. Secondary metabolites and volatile organic compounds (VOCs) emitted by various beneficial bacterial strains have a lot of potential for enhancing plant growth and preventing plant diseases. The VOCs produced by the most researched bacterial strains, such as *Pseudomonas* genera, are well recognized for protecting economically imperative plants and inducing resistance against bacterial and fungal phytopathogens. This chapter concentrates on throwing up a better grasp of biological activities of secondary metabolites such as hydrogen cyanide, siderophores, antibiotics, and VOCs produced by *Pseudomonas* spp. Hundreds of various bacterial VOCs, including alcohols, terpenoids, esters, and sulfur compounds, have been discovered. The VOCs emitted by *Pseudomonas* sp., for instance, acetophenone, 1,3-butadiene, 2-undecanone, benzaldehyde, 1,2-benzisothiazol-3(2H)-one, dimethyl trisulfide, dimethyl disulfide, benzothiazole, nonanal, N,N-dimethyldodecylamin, 3,5,5-trimethyl-1-hexanol, isovaleric acid, cyclohexanol, 2-ethyl 1-hexanol, n-decanal, decyl alcohol, etc., are reported for their antagonistic potential, inducing resistance in host plants against several bacterial and fungal

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pathogens. Crop growth enhancement and protection via VOCs is a promising and an ecofriendly method, substituting the harmful impacts of chemicals and ensuring the long-term sustainability in agriculture.

Keywords PGPR · VOCs · Induced systemic resistance · Antibiotics · HCN · Siderophore

1 Introduction

In the twenty-first century, according to United Nations the global population is increasing continuously which is projected to reach 9.7 billion in 2050,, which may lead to increase in global agricultural production, to fulfill the requirements of rapidly growing population (UNDESAP 2017; Rohr et al. 2019). Our agricultural sector largely depends upon the use of synthetic chemicals in order to revamp the crop production, i.e., synthetic fertilizers, which are used to increase the crop biomass, while synthetic pesticides are used to control pest and diseases in crops to reduce crop loss by 17–30%, particularly for the major staple crops (Naz and Bano 2014; Savary et al. 2019). However, these synthetic pesticides are unendurable due to their harmful residual effects and heavy manufacturing costs (Naz et al. 2014, 2018, 2021a). According to an estimation, around $250 million are required to take single active ingredients in market, having very low success rate about only 1 out of 140,000 synthetic compounds are successful, which is a very unsustainable way to develop synthetic pesticides (Lamberth et al. 2013).

Besides these, the continued use of pesticides makes them less effective because of the production of pesticide-resistant genes in plants (Butt et al. 2019; Ullah et al. 2020; Naz et al. 2021b). Furthermore, the continuous increase in global population has increased the demands for crops and agricultural growth, which has further caused increase in the applications of synthetic compounds. As projected increase in the demand for crops, agricultural growth might result in increased pesticide use of 10-fold and increased fertilizer application of 2.7-fold (Rohr et al. 2019; Jabborova et al. 2020).

Agronomic practices should be taken in consideration to lessen this dependency on synthetic compounds as well as to evolve the viable control measures, and different collaborative efforts should be made, i.e., improving agricultural practices by agronomic practices (Naz and Bano 2015; Ahluwalia et al. 2021). However, the introduction of soil beneficial microorganisms is another effective method to reduce the use of synthetic compounds in agricultural practices, as they have potential to antagonizing soil pathogenic microbes and are capable of increasing plant biomass (Yasmin et al. 2019; Luh Suriani et al. 2020). An extensive range of secondary metabolites is produced by these soil microorganisms which strengthen them to fight with other pathogenic soil microbes, as they compete with each other for same resources in soil (Naz et al. 2017; Garbeva and Weisskopf 2020; Hamid et al. 2021).

The production of antibiotics, volatile organic compounds (VOCs), and secondary metabolites during microbial lifecycles are some other microbial inhibition tools to cope with pathogenic microbes within soil (Naz et al. 2020; Ye et al. 2020; Khan et al. 2021). The scientific world requires more attention on the production of VOCs due to multiple benefits of their utilization. VOCs are a mixture of volatile metabolites that may be emitted by all living microorganisms and have been shown to be very potent to control the growth of phytopathogenic bacteria and fungus through cross-talk interactions and antibacterial activities. Their antimicrobial effects, along with the reduced hazard for both the environment and human beings and their possible application without the need of a supplemental spray or drench, make the use of VOCs a promising and sustainable approach to replace fungicides of synthetic origin in the control of plant pathogens (Parafati et al. 2017; Tilocca and Migheli 2020; Zhang et al. 2020).

Although numerous modes of action are involved in phytopathogen obliteration, this chapter will dig into novel visions and ideas in biological control of phytopathogens via PGPR by dint of antibiotics and VOCs. Some *Pseudomonas* spp. have been associated with plant growth, suppression of fungal pathogens affecting plants, and detrimental rhizobacteria presenting considerable upsurge in root colonization. These aspects suggest that *Pseudomonas* spp. can serve as excellent biocontrol agents (Gomez-Lama et al. 2018; Reshma et al. 2018).

In this chapter, we focus to explore the role of secondary metabolites, antibiotics, and VOCs produced by the *Pseudomonas* species to sustain plant health by directly suppressing pathogens, inducing plant resistance against phytopathogens, and promoting plant growth, emphasizing their potential as alternatives to synthetic fertilizers and pesticides.

2 Microorganisms Emitting Volatile Organic Compounds

The volatile metabolites emitted from both plant and microbial sources are receiving a steady increase in interest. The word “volatilome” has been relatively recently used to describe this diverse and heterogeneous collection of metabolites (Farbo et al. 2018; Tilocca and Migheli 2020). The volatile metabolites of plant and microbial origin are mainly differentiated into organic and inorganic volatile molecules. Among inorganic volatile molecules, most relevant are CO_2, H_2S, CO, HCN, SO_3, H_2, NH_3, NO_2^-, and SO_2. The inorganic volatile molecules play an important role in different biological functions, i.e., acting as defense compounds by donating/accepting electrons (Rad et al. 2016; Zhang et al. 2020). These metabolites also have a role in various ecological and biological features along with their antibiotic resistance potential (Avalos et al. 2019; Kenawy et al. 2019).

In agriculture, the application of VOCs with microbial source in the biological control of plants pathogens has been given an unintentional decrease over the last few years. However, the progress recently made and the general trend to an integrative approach have highlighted the potential advantages of microbiological VOCs in this area. The VOCs are known to be very effective at very low levels (Reshma et al. 2018; Tilocca and Migheli 2020).

In addition to pathogen inhibition and negative impact on fungal spore germination and function of morphogenesis enzymes, VOCs from microbial species have been found to play a role in a variety of biological processes (Deveau et al. 2018; Zhang et al. 2020). VOCs have the capability to kill nematodes which are known to be parasitic for plants (de Freitas Silva et al. 2020; Khoja et al. 2021) to increase plant growth (Hernández-León et al. 2015; Fincheira and Quiroz 2018) and to activate the mechanisms associated with resistance within plants, thus averting the plant from being infected by pathogens (Sharifi and Ryu 2016; Tahir et al. 2017; Zhang et al. 2020).

2.1 Production of VOCs by Consortium of Different Microbes

A single organism can produce a diverse mixture of VOCs when applied, which leads to different outcomes proved by many experiments (Tilocca et al. 2019), whereas in a single ecological niche, there reside many microbial entities through which unexpected achievements can be obtained by consortium application as compared to the application of single microbial strain (Khan et al. 2019). Microbial strains interact with each other irrespective of their genera, phyla, and kingdom (Shaikh et al. 2016; Schulz-Bohm et al. 2017). These interactions lead to the essential biological and ecological outcomes in ensembled role of all the microbiota as a single unique entity. The effectiveness of the interactions occurring between microbiota members *Pseudomonas helmanticensis* Sc-B94 and *Bacillus cereus* Rs-MS53 has been reported to control the pathogenic fungus *R. solani* (Mülner et al. 2019), which was proved to be a strong strain compatibility and cooperative interaction (Asari et al. 2016; Che and Men 2019; Kramer et al. 2020). The production of volatile and nonvolatile compounds by different strains of *Pseudomonas* and *Bacillus* spp. can directly inhibit the growth of pathogen or can help in the acclimatization of the microbial community already residing in the same ecological niche which can also inhibit growth and infection caused by pathogen (Schulz-Bohm et al. 2017; Tilocca et al. 2020; Dimkić et al. 2022).

3 Bacterial Volatiles: Tool to Biocontrol of Phytopathogens

Bacterial VOCs play a role in the complex network of interactions that are established between bacteria, bacterial species, and bacteria with other microorganisms as well as with plants. Similarly, these interactions play a variable ecological role including beneficial interaction as well as antagonistic interaction. However, beneficial cooperation encompasses symbiosis, mutualism, and host resistance interaction, while in antagonistic relationship, one of the interacting species exerts microbicidal activity on other species (Kanchiswamy et al. 2015; Tilocca et al. 2020). The useful bacterial-plant interaction has recently been recognized, which has extend new approaches for the use of bacterial volatilome in promoting plant growth. Furthermore, due to high flexibility of bacterial origin VOCs as well as their efficacy in controlling other pathogens, investigation is made on the utilization of VOCs produced by natural bacteria in defense against plant pathogenic microbes (Reshma et al. 2018; Mulero-Aparicio et al. 2019).

A wide variety of VOCs have been produced by rhizobacteria (*Serratia odorifera*, *S. plymuthica*, *Stenotrophomonas maltophilia*, *P. fluorescens*, *Stenotrophomonas rhizophila*, and *Pseudomonas trivialis*) which are active against an extensive variety of pathogenic microorganisms including bacteria and fungi (Kanchiswamy et al. 2015; Gotor-Vila et al. 2017; Mulero-Aparicio et al. 2019). Bacteria-fungi interaction usually produces some common volatile molecules including 1-octen3-ol, 2-nonanone, 2-undecanone, γ-patchoulene, 3-methylbutanoate, 3-methylbutanal, 2-methylbutan-1-ol, ethanethioic acid, dimethyl trisulfide 2,3,6-trimethylphenol, and 4-methyl-2-heptanone. Among these antifungal activities of some VOCs have already been tested (Tilocca et al. 2020).

4 Pseudomonas Volatilome

Various studies revealed that VOCs can inhibit a wide range of plant pathogens, also emphasizing VOCs as possible viable alternatives to pesticides and chemical fertilizers. One of the first examples of VOCs, produced by *Pseudomonas* species from canola and soyabean, exhibits plant growth stimulatory and inhibitory effect in case of plant pathogenic microbes (Agisha et al. 2019). About 23 VOCs are identified, which are produced by *Pseudomonas* species; among these six VOCs inhibited the mycelium growth of *S. sclerotiorum*, a pathogen of more than 400 plant species (Effmert et al. 2012; Thomas et al. 2020). A growth of widespread soil-borne *R. solani* pathogen was inhibited by VOCs from *Pseudomonas* spp. (Elkahoui et al. 2015) and by a variety of other rhizobacterial isolates (Velivelli et al. 2015). However, inhibitory activity against various bacterial pathogens exhibited by many VOCs is reported; for instance, nonanal, benzaldehyde, acetophenone, and benzothiazole are reported to inhibit the proliferation of *Clavibacter michiganensis*, a causative agent of bacterial ring rot disease of potato (Rajer et al. 2017). Similarly, *Xanthomonas oryzae* causing bacterial leaf blight of rice has been reported to be inhibited by 3,5,5-trimethyl-1-hexanol and decyl alcohol (Xie et al. 2018).

Moreover, the bacterial VOCs are also known to inhibit fungal mycelial growth; e.g., isovaleraldehyde, 3-methyl-1-butanol, isovaleric acid, 2-heptanone, and 2-ethylhexanol decrease the mycelium growth of *Phytophthora capsica* (Syed-Ab-Rahman et al. 2019; Freitas et al. 2022). Anti-oomycete activity is displayed by the VOCs of *Nodulisporium* against different *Pythium* species, while VOCs which are causing inhibition of pathogens were not assayed individually (Sánchez-Fernández et al. 2016). However, these studies spotlight inhibitory activity of VOCs against a wide range of bacterial and pathogens, which could be good alternatives to pesticides.

4.1 Role of **Pseudomonas** *Volatilome in Biocontrol of Phytopathogens*

Pseudomonas is widely recognized for having a diverse storage of plant growth-enhancing and antifungal metabolites, and many of these molecules are volatile compounds (Hernández-León et al. 2015; Yan et al. 2017; Dahiya et al. 2020). For instance, recently, it is reported by Hunziker et al. (2015) that *P. infestans* (a well-known oomycete phytopathogen of potato) can be inhibited by high potential volatiles emitted by *Pseudomonas*. The VOCs produced by *P. fluorescens* and *P. trivialis* are also reported to drastically inhibit the mycelial growth of *R. solani* (Kai et al. 2007). In recent studies, it was revealed that *P. donghuensis* P482 in the rhizosphere of tomato plants emits volatiles that play a significant role in inhibiting the growth of different plant pathogens for instance *Pythium ultimum*, *R. solani*, *Verticillium dahlia*, and *F. culmorum* (Ossowicki et al. 2017).

Evidences related to bacteriostatic were also found in the volatilomes of several strains of *Pseudomonas* spp. particularly in *P. chlororaphis*, which was tested against *Agrobacterium tumefaciens* and fungal, nematode, and insect pathogens for its antagonistic potential (Popova et al. 2014). The VOCs emitted from *P. putida* BP25 including 2-ethyl-5-methyl pyrazine, 2,5-dimethyl pyrazine, 2-ethyl-3,6-dimethyl pyrazine, 2-methyl pyrazine, and dimethyl trisulfide exhibited significant in vitro antimicrobial potential against several pathogens, for instance, *C. gloeosporioides*, *P. capsici*, *G. moniliformis*, *P. myriotylum*, *R. solani*, *R. pseudosolanacearum*, *A. rolfsii*, *R. similis*, and *M. oryzae* (Agisha et al. 2019).

From rhizosphere of soybean, common bean, and canola plants, the *Pseudomonas* strains were isolated and further reported for antagonistic potential against *S. sclerotiorum* owing to their VOCs including dimethyl trisulfide, n-decanal, benzothiazole, nonanal, cyclohexanol, and 2-ethyl 1-hexanol (Fernando et al. 2005; Giorgio et al. 2015). The antagonistic ability of VOCs produced by *P. fluorescens* B-4117 and *P. fluorescens* Q8r1-96 has been reported against plant pathogenic bacterial strains including *A. vitis* and *A. tumefaciens*. Here, it is suggested that *Pseudomonas* species are known to produce VOCs which can be used as a potential tool to control many diseases particularly the crown gall tumors which can be effectively prevented in tomato plants (Dandurishvili et al. 2011). The VOCs produced by *P. fluorescens* WR-1 are also reported to significantly affect and decrease the virulence characteristics of *R. solanacearum in tomato* (Raza et al. 2016). The active VOCs produced by *Pseudomonas* spp. and their biocontrol potential against target phytopathogens have been described in Table 6.1.

Table 6.1 Active VOCs produced by *Pseudomonas* spp. and their biocontrol potential against target phytopathogens

VOC-producing *Pseudomonas* sp.	Target pathogen	Active VOCs	References
P. fluorescens *P. chlororaphis O6*	*S. sclerotiorum* *E. carotovora/N. benthamiana*	Benzothiazole (2R, 3R)-Butanediol	Fernando et al. (2005) Han et al. (2006)
P. chlororaphis	*S. sclerotiorum*	Nonanal Cyclohexanol Benzothiazole Dimethyl trisulfide 2-Ethyl, 1-hexanol *n*-Decanal	Fernando et al. (2005)
P. donghuensis	*P. ultimum, R. solani, V. dahlia, and F. culmorum*	Dimethyl sulfide Methyl thiocyanate 1-Undecan S-Methyl thioacetate Dimethyl trisulfide	Ossowicki et al. (2017)
Pseudomonas sp. *P. fluorescens* L13-6-12	*P. infestans* *R. solani*	1-Undecene Undecene	Kai et al. (2007)
P. trivialis 3Re2-7	*R. solani*	UndecadieneUndeceneBenzyloxybenzonitrile	
P. fluorescens B-4117	*A. tumefaciens* *A. vitis*	Hydrocarbon 1-undecene Methanethiol Methyl thiol acetate	Dandurishvili et al. (2011)
P. fluorescens WR-1	*R. solanacearum*	Dodecane 1-Undecanol 1-Nonene Benzothiazole Naphthalene, 1-methyl Ethyl benzene Ethanone 1-(2-furanyl)-	Raza et al. (2016)

(continued)

Table 6.1 (continued)

VOC-producing *Pseudomonas* sp.	Target pathogen	Active VOCs	References
P. putida BP25	*C. gloeosporioides, P. capsici, G. moniliformis, P. myriotylum, R. solani, R. pseudosolanacearum, A. rolfsii, R. similis and M. oryzae*	2-Ethyl-5-methyl pyrazine 2,5-Dimethyl pyrazine 2-Ethyl 3,6-dimethyl pyrazine 2-Methyl pyrazine Dimethyl trisulphide	Agisha et al. (2019)
P. brassicacearum	*S. sclerotiorum*	1-Undecene dl-Limonene m-Cymene 2-Undecanone 2-Nonanone	Giorgio et al. (2015)
P. aurantiaca	*S. sclerotiorum*	Nonanal 2-Ethyl,1-hexanol *n*-Decanal	Fernando et al. (2005)
P. chlororaphis	*S. sclerotiorum*	Nonanal Cyclohexanol Benzothiazole Dimethyl trisulfide 2-Ethyl,1-hexanol *n*-Decanal	Fernando et al. (2005)
P. fluorescens	*B. cinerea* *S. sclerotiorum* *C. fimbriata*	Dimethyl disulfide 2-Ethyl,1-hexanol Phenylethyl alcohol 2-Methyl-1-butanol 3-Methyl-1-butanol	Hernández-León et al. (2015) Fernando et al. (2005) Zhang et al. (2019)
P. chlororaphis subsp. *aureofaciens* *P. stutzeri*	*B. cinerea*	Dimethyl disulfide	Rojas-Solís et al. (2018)

4.2 Role of Secondary Metabolites Produced by **Pseudomonas** *spp. in Plant Disease Control*

Fluorescent pseudomonads are predominant antagonistic bacteria that live in soil. Nowadays, the significance of these bacteria has been acknowledged all over the world, owing to the fact that they are capable of synthesizing a variety of antifungal compounds such as siderophores; fluorescent pigments along with volatile elements, namely, hydrocyanic acid (HCN); lytic enzymes; as well as antibiotics (Ciancio et al. 2016; Jadhav et al. 2017; Yasmin et al. 2020). Some of the noteworthy lytic enzymes produced by *Pseudomonas* spp. are chitinase, protease, and β-1,3-glucanase. These enzymes instigate lysis and hyperparasitism of antagonistic bacteria toward lethal fungal pathogens (Jadhav et al. 2017; Zia et al. 2021).

Various fluorescent pseudomonads are impervious to cyanide due to the existence of a thiosulfate (RhdA): cyanide sulfur transferase that modifies the cyanide to thiocyanate which is less toxic. In many *Pseudomonas* spp., approximately 300 μM cyanide is produced by the oxidative decarboxylation of glycine (Blumer and Haas 2000). Gupta et al. (2002) investigated the *Pseudomonas* to biologically control the charcoal rot instigated by *Macrophomina phaseolina* in peanut.

Sindhu et al. (1997) reported the role of secondary metabolites in the inhibition of phytopathogens and also the inhibiting role of siderophore-producing rhizobacteria and several fluorescent *Pseudomonas* spp. against many bacterial and fungal phytopathogens. Siderophore- producing pseudomonads have been reported in chickpea to markedly reduce the root rot disease (Akhtar and Siddiqui 2009).

Pseudomonas fluorescens are known to produce siderophore and control *Pythium ultimum*, and *Pseudomonas stutzeri* produces chitinase which lyse the cell wall of *Fusarium solani*. Antifungal metabolites produced by these *Rhizobacteria* were identified as antibiotics (iturin, surfactins, fengycin, DAPG, phenazine, etc.), cell wall degrading enzymes (proteses, chitinases, cellulases), plant growth-promoting enzymes and hormones (indole-3-acetic acid, ACC-deaminase, phosphatase, nitrogen fixation), N-acyl homoderine lactones, and siderophore (Dahiya et al. 2020).

Another siderophore as pseudobactin produced by *P. putida* was able to suppress the growth of *Fusarium oxysporum* in iron-deficient soil; this suppression/inhibition was abandoned when iron was provided in that soil (de Boer et al. 2003). Several studies have explained the inhibition of fungal pathogens by fluorescent pseudomonads from the excretion of siderophores (iron-chelating), making it inaccessible to other several microorganisms (Shaikh et al. 2014).

The biocontrol potential of siderophore as an antifungal metabolite produced by *Pseudomonas* spp. is shown in Table 6.2.

Table 6.2 Role of antifungal metabolites of *Pseudomonas* spp. in biocontrol of phytopathogens

Antifungal metabolites	Producing PGPR	Host	Target pathogen	References
Siderophore	*P. fluorescence*	Wheat	*G. graminis*	Sayyed et al. (2013)
		Wheat	*F. glycinia*	
		Soybean	*S. oryzae*	
	P. aeruginosa	Potato	*F. udum* *A. niger*	Sulochana et al. (2014)
	P. fluorescens	Soybean	*P. ultimum*	León et al. (2009)
	P. putida	Radish Cucumber	*Fusarium* spp. wilt	Sayyed et al. (2013)
		Beans	*F. solani*	
		Potato	*F. oxysporum*	
	P. cepacia	Onion	*F. oxysporum*	Sayyed et al. (2013)
	P. aureofaciens	Wheat	*G. graminis* var. *tritici*	
	P. fluorescence	beet root	*P. debaryanum*	Dodd and Stewart (1992)
		Cotton	*R. solani*	Hagedorn (1990)
		Tomato	*S. rolfsii*	Thiribhuvanamala et al. (1999)
	P. fluorescence	In vitro	*P. debaryanum, R. solani*, and *S. rolfsii*	Prasad et al. (2017)
HCN	*P. fluorescence*	Tobacco, wheat	*T. basicola* *G. graminis*	Voisard et al. (1989) Shaikh and Sayyed (2015)
	Pseudomonas spp. P76 and P124	Many crops	*S. rolfsii*	Priyanka et al. (2017)
	Pseudomonas spp. LBUM300	Tomato	*C. michiganensis* subspp. *michiganensis*	Lanteigne et al. (2012)
	Pseudomonas CF1 and CF5	In vitro	*M. phaseolina*	Reetha et al. (2014)
	P. corrugata and *P. mediterranea*	In vitro	*B. cinerea*	Strano et al. (2017)
	P. donghuensis P482	In vitro	*R. solani* AG2, *F. culmorum* PV and *P. ultimum* P17	Ossowicki et al. (2017)
	P. fluorescence	In vitro	*P. debaryanum, R. solani*, and *S. rolfsii*	Prasad et al. (2017)

4.3 *Antibiotics Produced by* Pseudomonas *spp.*

According to Haas and Défago (2005), six antibiotic classes are best to perform their biocontrol potential particularly to control root fungal diseases: pyoluteorin, phenazines, pyrrolnitrin, phloroglucinols, hydrogen cyanide (which is volatile), and cyclic lipopeptides. Most recently, lipopeptide biosurfactants produced by *Pseudomonas* spp. have been implied in biocontrol due to their potential positive impact on the competitive contacts with organisms involving fungi, bacteria, oomycetes, nematodes, protozoa, and plants (Raaijmakers et al. 2010; Shafi et al. 2017; Fira et al. 2018).

Many bacterial species are reported for the isolation of several antibiotics that are known to inhibit cell wall composition of the pathogen, interrupt the cell membrane structures, and impede the synthesis of ribosomal subunits (Maksimov et al. 2011). Fluorescent pseudomonads primarily achieve biocontrol of pathogens by synthesizing specific antibiotics like pyoluteorin, 2,4-diacetylphloroglucinol, pyrrolnitrin, 2-hydroxy phenazines, and phenazine-1-carboxamide and phenazine-1-carboxyclic acid (Mustafa et al. 2019). Antibiotics are not just solely involved in antipathogenic activity; they are also major contributors in instigating ISR in plants as they vigorously suppress disease by offering competitive leverage to biocontrol agents. Host resistance toward plant pathogens is enhanced significantly when ISR and antibiotics act synergistically (Hashem et al. 2019; Ullah et al. 2020).

More than 6000 compounds have been characterized and identified for strong antifungal potential, including phenazine (PHZ) as a key molecule and over 100 more derivatives of PHZ (Mavrodi et al. 2006). Moreover, the products containing PHZ (even more than 180) are known for their strong antifungal, antibiotic, anticancer, insecticidal, anti-protozoan, and antitumor potential (Briard et al. 2015; Guttenberger et al. 2017). Several studies attributed the antimicrobial potential of PHZ produced by *Pseudomonas* strain PCL1391 to the production of ROS (reactive oxygen species) (Laursen and Nielsen 2004) and found very effective against *Botrytis cinerea*, *Gaeumannomyces graminis*, and *F. oxysporum* (Schoonbeek et al. 2002; Chin-A-Woeng et al. 2003). Several PHZ and its derivatives are efficient in controlling numerous fungal diseases (Chincholkar et al. 2013). The *P. chlororaphis* PCL1391 strain has been reported to produce phenazine-1-carboxamide, which can nourish plants with soluble iron at neutral pH (Hernandez et al. 2004; Haas and Défago 2005).

The fluorescent pseudomonads producing DAPG are reported for their strong biocontrol potential (Weller et al. 2007; Troppens et al. 2013); several other research studies have confirmed DAPG as a key antimicrobial metabolite engaged in the biocontrol of fungal phytopathogens (Sonnleitner and Haas 2011; Khare et al. 2018). The DAPG is an efficient and extensively researched antibiotic which is released by pseudomonads to control oomycete and *Pythium* spp. (de Souza et al. 2003).

Pyoluteorin (PLT) is a phenolic polyketide, which has initially been isolated and identified from *P. aeruginosa* and then from fluorescent pseudomonads (Nowak-Thompson et al. 1997). PLT has herbicidal, bactericidal, and fungicidal properties (Takeda 1959). PLT has also been stated to function as an intercellular signal and auto-inducer among distinctive rhizospheric populations of bacterial strains (Brodhagen et al. 2004). It has recently been observed that phloroglucinol in *P.*

protegens has a significant impact on PLT gene expression and production (Clifford et al. 2016).

Different metabolites are produced at different concentration of phloroglucinol with distinct phytopathogenic target (Khare et al. 2018). Limited range of gram-negative bacteria are involved in the production of pyrrolnitrin from *Pseudomonas* species (Mujumdar et al. 2014; Weller et al. 2016). Fluorescent pseudomonads produce pyrrolnitrin which has antagonistic nature against fungi, yeast, and Gram-positive bacteria (Jani et al. 2015). *P. fluorescens* BL915 strain secretes pyrrolnitrin which has a property to protect *Rhizoctonia solani* during damping off of cotton (Hill et al. 1994).

Currently, cyclic lipopeptides (CLPs) have been identified as biosurfactant and antimicrobials which is found effective against broad spectrum of phytopathogen involving enveloped viruses, Gram-positive bacteria, and mycoplasmas (Raaijmakers et al. 2006; Tran et al. 2007; Raju et al. 2016). Research has reported that CLPs released by pseudomonads are involved in colonization of seeds and roots. In addition, it also contributes to the formation of biofilm and virulence (Li et al. 2013; Raaijmakers et al. 2010). Fluorescent pseudomonads release different types of CLPs; many of them have not characterized completely. The well-documented and studied groups of CLPs are amphisin, viscosin syringomycin, and tolaasin (Nybroe and Sørensen 2004).

CLPs secreted by *Pseudomonas* are categorized into eight different groups on the basis of variation in length and composition of the oligopeptide and fatty acid tails (Olorunleke et al. 2017). The ability to agitate biological membranes are associated with the antimicrobial properties (Raaijmakers et al. 2006; Dumée et al. 2015). *P. protegens* produce orfamide which is a type of potential CLPs having insecticidal property (Nandi et al. 2015). Fluorescent pseudomonads releasing several metabolites having broad-spectrum phytopathogenic activities are preferred in the field of agriculture. Currently, Izzah-Shahid et al. (2017) reported that application of PCA, CLP, and lahorenoic acid A substantially enhanced growth of wheat by producing *P. chlororaphis* and *P. aurantiaca* during development. Sharifazizi et al. (2017) also found that fluorescent pseudomonad strain Ps170 has the capability to control blight-causing pathogen in pear by releasing DAPG, PLT, PRN, and PCA. Metabolites of fluorescent pseudomonads are currently being used as biological controls to secure the plant from causative agents such as causing protozoa and nematodes (Meyer et al. 2009; Jousset et al. 2010; Clifford et al. 2016). Antibiotics produced by *Pseudomonas* spp. and their biocontrol potential against phytopathogens have been described in Table 6.3 and Fig. 6.1.

Table 6.3 Antibiotics produced by *Pseudomonas* spp. and their biocontrol potential against fungal pathogens

Antibiotics	*Pseudomonas* spp.	Host/disease	Targeted fungal phytopathogen	References
2,4-DAPG	*P. fluorescens*	Wheat	*G. graminis tritici*	Weller et al. (2007)
		Tobacco	*T. basicola*	Keel et al. (1992)
		Sugar beet	*P. ultimum*	Nielsen et al. (1998)
	Pseudomonas spp.	Sugar beet	*P. ultimum*	Shanahan et al. (1992)
	P. fluorescens (CHAO)	Tobacco	*T. basicola*	Keel et al. (1992)
	P. fluorescens CHAO	All diseases	*G. graminis* tritici	Fenton et al. (1992)
	P. fluorescens Q2-87 P. ßuorescens F	Sugar beet	*P. ultimum*	Rosales et al. (1995)
	P. fluorescens Pf	Sheath blight	*R. solani*	Rosales et al. (1995)
	P. aurantiaca	Wheat	*F. oxysporum*	Garagulia et al. (1974)
	P. fluorescens VUPf5	Wheat	*G. graminis* var. tritici	Lagzian et al. (2013)
	P. fluorescens	Rice	*X. oryzae* pv. oryzae (Xoo)	Velusamy and Gnanamanickam (2003)
	P. aeruginosa	Banana	*F. oxysporum* f. spp. cubense FOC	Ayyadurai et al. (2006)
	P. fluorescens	Groundnut	*A. niger, A. flavus*, *S. rolfsii*	Sherathia et al. (2016)
	P. brassicacearum	In vitro	*R. solanacearum*	Zhou et al. (2012)
	Pseudomonas spp.	Tomato	*C. michiganensis* subspp. *michiganensis*	Lanteigne et al. (2012)
Aerugine	*P. fluorescens*	Pepper Cucumber	*Phytophthora* *C. orbiculare*	Lee et al. *(*2003)
Pyrrolnitrin	*P. fluorescens*	Grass Cucumber Soybean	*S. homoeocarpa* *Pythium* spp. *P. ultimum*	León et al. (2009)
	P. cepacian	Maize Sugar beet In vitro only	*B. maydis* *A. cochliodes* *C. truncatum* and *F. sambucinum*	Homma (1994) Burkhead et al. (1994)
	P. chlororaphis O6	*Tomato*	*F. graminearum* and *R. solani*	Park et al. (2011)
	P. fluorescens	Cotton and cucumber	*R. solani*	Hammer et al. (1997)
	P. fluorescens	Cotton Cotton	*V. dahliae* *T. basicola*	Howell and Stipanovic (1979)

(continued)

Table 6.3 (continued)

Antibiotics	*Pseudomonas* spp.	Host/disease	Targeted fungal phytopathogen	References
	P. fluorescens Pf-5	Spring and fall disease of Kentucky bluegrass	*D. poae*	Rodriguez and Pfender (1997)
	P. cepacia	Potato	*F. sambucinum*	Burkhead et al. (1994)
	P. cepacia	Sunflower	*Sclerotinia sclerotiorum*	McLoughlin et al. (1992)
Viscosinam ide	*P. fluorescens*	Sugar beet	*R. solani* *P. ultimum*	Nielsen et al. (1998)
Pyoluteorin	*P. fluorescens*	Cotton Sugar beet	*Pythium* spp. *Pythium* spp.	Howell and Stipanovic (1980)
	P. fluorescens Pf-5	Damping off	Members of oomycetes spp. Pythium	Kraus and Loper (1995)
Phenazines	*P. fluorescens*	*Wheat*	*G. graminis* var. tritici.	Thomashow and Weller (1988) and Thomashow et al. (1990)
	P. aeruginosa	Pigeon pea and chickpea	*F. oxysporum* f. spp. ciceris and *F. udum*	Anjaiah et al. (2003)
	Pseudomonas spp. MCC 3145	In vitro	*C. circinans*, *C. dematium, F. oxysporum*	Patil et al. (2017)
	Pseudomonas spp.	*Wheat*	*R. solani*	Jaaffar et al. (2017)
	Pseudomonas spp.	*Tomato*	*F. oxysporum*	Chin-A-Woeng et al. (1998)
	P. fluorescens	Wheat	*G. g.* Var. *tritici*	Thomashow and Weller (1988)
Oomycin A	*Pseudomonas* spp.	Damping-off (cotton)	Pythium spp.	Gutterson et al. (1988)
3-de-epoxy-2,3-didehydro-rhizoxin	*Pseudomonas* spp.	Net blotch Wheat bunt	*Pyrenophora teres* Drechs *Tilletia caries* Tull	Wright et al. (1999)
Agrocin 84	*Pseudomonas* spp.	Crown gall (fruit trees)	*A. tumefaciens*	Kerr et al. (1984)
Pseudobactin B10	*Pseudomonas* spp.	Flax wilt	*F. oxysporum*	Kloepper et al. (1980)
Cyclic lipopeptides	*P. fluorescens*	Sugar beet	*R. solani* and *P. ultimum*	Nielsen et al. (2000, 2002)
	P. fluorescens	Tomato	*P. infestans*	Tran et al. (2007)
	Pseudomonas SH-C52	Groundnut	*S. rolfsii*	Le et al. (2012)

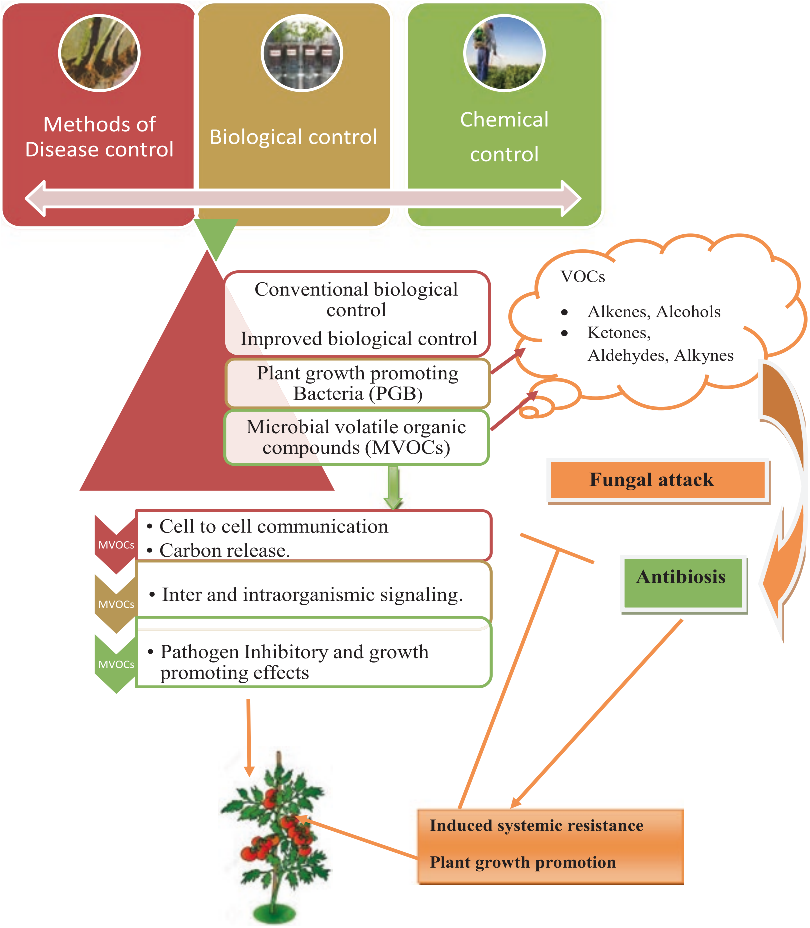

Fig. 6.1 Role of VOCs and antibiotics in plant growth promotion and induced systemic resistance

5 Conclusion

Pseudomonas spp. are **plant growth-stimulating** bacteria that are often observed with diverse phyto-beneficial characteristics. The biological activities of hydrogen cyanide, siderophore, antibiotics, and VOCs **produced by these species** highlight their potential to act as alternatives to unsustainable agricultural chemical inputs and to feed a continuously growing population. In this chapter, we have investigated the biocontrol potential of secondary metabolites and VOCs produced by *Pseudomonas* species (Tables 6.1, 6.2, and 6.3), which have more and diverse abilities to fight phytopathogens. Therefore, future research should focus on the growth-stimulating effects of antibiotics and VOCs on various crop and vegetable species. This chapter represented here focuses on the antibiotics and particularly VOCs emitted by *Pseudomonas* spp. in axenic culture conditions, whereas growing evidence suggests that interaction between different microorganisms could boost the production of VOCs which have been shown to have inhibition against pathogens. This will allow to identify the biologically relevant VOCs that are effectively involved in the inhibition of microbial pathogens. While a number of studies have also investigated the impact of VOCs in one biological function, there are likely to be similarities in the functions of these VOCs. For instance, nonadecane and heptadecane exhibited their role in pathogen suppression, plant growth promotion, and induced resistance, which suggests that the biological activities are not the isolated entity. Studies have shown the pathogenic suppression in the presence of the VOCs, but it is also important to know the involvement of these inhibitory VOCs on plant growth. Further investigation on the efficacy of VOC under field conditions can be a promising approach. There is a dire need for further exploration for the testing of a wider range of VOCs for field applications.

In conclusion, studies reviewed here demonstrate antibiotics, siderophore, hydrogen cyanide, and VOCs can be manipulated to serve as sustainable alternatives to agricultural chemical inputs, which can potentially reduce our overreliance on the current unsustainable methods at a time when population growth, and food demand, is likely to substantially increase.

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