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Research review paper

Bacterial volatile organic compounds as biopesticides, growth promoters and plant-defense elicitors: Current understanding and future scope

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ABSTRACT

Bacteria produce a large number of volatile organic compounds (VOCs) into the environment. VOCs are species-specific and their emission depends on environmental conditions, such as growth medium, pH, temperature, incubation time and interaction with other microorganisms. These VOCs can enhance plant growth, suppress pathogens and act as signaling molecules during plant–microorganism interactions. Bacterial VOCs have been reported to show strong antimicrobial, nematicidal, pesticidal, plant defense, induced tolerance and plant-growth-promoting activities under controlled conditions. Commonly produced antifungal VOCs include dimethyl trisulfide, dimethyl disulfide, benzothiazole, nonane, decanone and 1-butanol. Species of *Bacillus*, *Pseudomonas, Arthrobacter, Enterobacter* and *Burkholderia* produce plant growth promoting VOCs, such as acetoin and 2,3-butenediol. These VOCs affect genes involved in defense and development in plant species (i.e., *Arabidopsis*, tobacco, tomato, potato, millet and maize). VOCs are also implicated in altering pathogenesis-related genes, inducing systemic resistance, modulating plant metabolic pathways and acquiring nutrients. However, detailed mechanisms of action of VOCs need to be explored. This review summarizes the bioactive VOCs produced by diverse bacterial species as an alternative to agrochemicals, their mechanism of action and challenges for employment of bacterial VOCs for sustainable agricultural practices. Future studies on technological improvements for bacterial VOC application under greenhouse and open field conditions are warranted.

1. Introduction

Bacterial species emit volatile organic compounds (VOCs), which play an important role in communication between microorganisms and plants by modulating metabolic and other regulatory pathways involved in plant defense (Wu et al., 2018), growth and development (Tahir et al., 2017b). VOCs are low-molecular-weight compounds (<300 Da) that can travel through soil and air for long distances, due to their high vapor pressure and their ability to diffuse through air and water-filled pores at ambient temperature. VOCs are produced by catabolic pathways, such as glycolysis, lipolysis, proteolysis, fermentation, fatty acid biosynthesis and sulfur metabolism (Weisskopf et al., 2021). Bacterial VOCs commonly belong to classes such as hydrocarbons, aldehydes, ketones, esters, organic acids, and sulfur- or nitrogen-containing compounds, alcohols and terpenes (Table 1). The most commonly studied VOCs emitted by soil bacteria are fatty acid derivatives (including alcohols, alkanes, and alkenes), aromatic compounds, terpenes, nitrogen-based compounds (such as indole) and sulfur-containing com-

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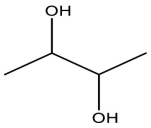
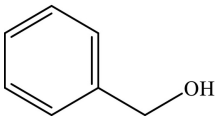
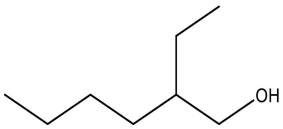
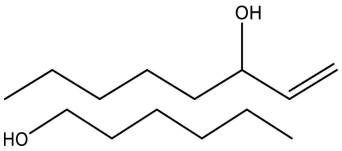
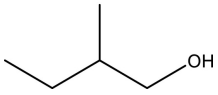
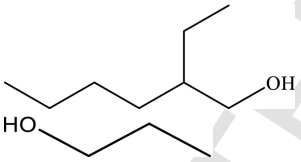
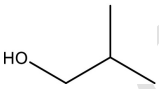
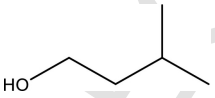
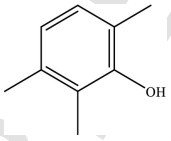
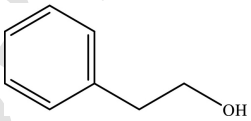
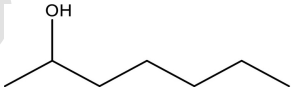
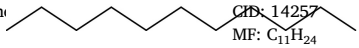
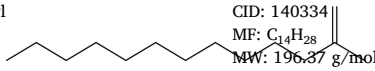
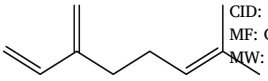
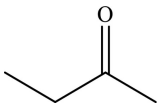
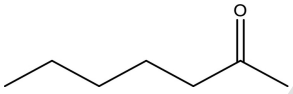
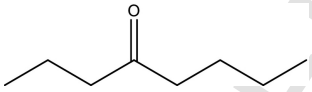
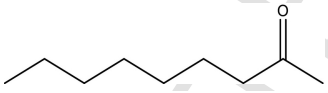
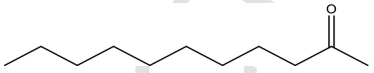
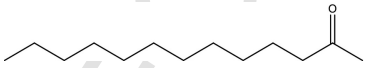
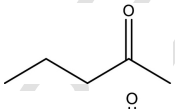
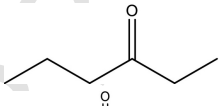
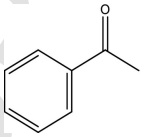
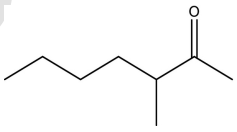
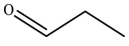
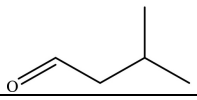
Table 1
Classification of bacterial volatile organic compounds and their biological activity.

Sr. No	Compound	Structure	Molecular weight and compound CID no	Biological activity
Alcohols				
	2,3-Butanediol		CID: 262 MF: $C_4H_{10}O_2$ MW: 90.12 g/mol	Plant growth promotion Antifungal
	Benzyl alcohol		CID: 244 MF: C_7H_8O MW: 108.14 g/mol	Plant growth promotion
	2-Ethylhexanol		CID: 7720 MF: $C_8H_{18}O$ MW:130.229 g/mo	Plant growth promotion
	1-octen-3-ol		CID: 18827 MF: $C_8H_{16}O$ MW: 128.21 g/mol	Antifungal
	1-Hexanol		CID: 8103 MF:$C_6H_{14}O$ MW: 102.17 g/mol	Plant growth promotion
	2-Methylbutanol		CID: 8723 MF: $C_5H_{12}O$ MW: 88.15 g/mol	Plant growth promotion
	2-Ethyl-1-hexanol		CID: 7720 MF: C8H18O MW: 130.229 g/mol	Plant growth promotion Antifungal
	1-Propanol		CID: 1031 MF: C_3H_8O MW: 60.1 g/mol	Antifungal
	Isobutyl alcohol		CID: 6560 MF: $C_4H_{10}O$ MW: 74.12 g/mol	Antifungal
	Isopentyl alcohol		CID: 31260 MF: $C_5H_{12}O$ MW: 88.15 g/mol	Plant growth promotion
	2,3,6- Trimethylphenol		CID: 17016 MF: $C_9H_{12}O$ MW: 136.19 g/mol	Antifungal
	2-Phenyl ethanol		CID: 6054 MF: $C_8H_{10}O$ MW: 122.16 g/mol	Plant growth promotion
	2-Heptanol		CID: 10976 MF: $C_7H_{16}O$ MW: 116.2 g/mol	Salt tolerance in plants
Hydrocarbons				
	Pentadecane		CID: 12391 MF: $C_{15}H_{32}$ MW: 212.41 g/mol	Antifungal
	Hexadecane		CID: 11006 MF: $C_{16}H_{34}$ MW: 226.44 g/mol	Antifungal
	Heptadecane		CID: 12398 MF: $C_{17}H_{36}$ MW: 240.5 g/mol	Nematicidal

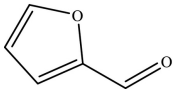
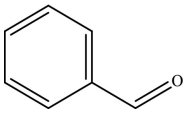
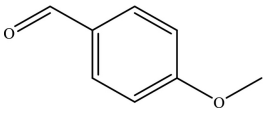
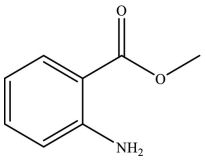
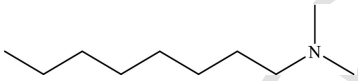
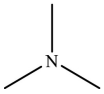
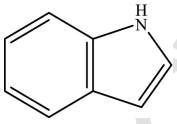
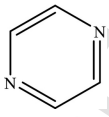
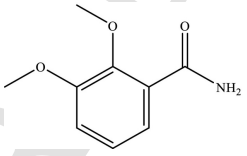
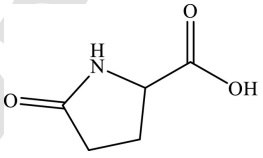
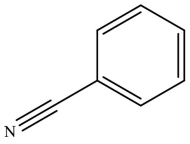
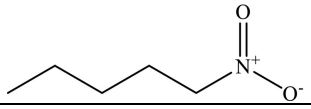
(*continued on next page*)

Table 1 (*continued*)

Sr. No	Compound	Structure	Molecular weight and compound CID no	Biological activity
	Undecan		CID: 14257 MF: $C_{11}H_{24}$ MW: 156.31 g/mol	Plant growth promotion Antifungal
	Tetradec		CID: 12389 MF: $C_{14}H_{30}$ MW: 198.39 g/mol	Antifungal
	Tridecan		CID: 12388 MF: $C_{13}H_{28}$ MW: 184.36 g/mol	Antibacterial Plant growth promotion
	2-Methyl		CID: 140334 MF: $C_{14}H_{28}$ MW: 196.37 g/mol	Plant growth promotion
	Myrcene		CID: 31253 MF: $C_{10}H_{16}$ MW: 136.23 g/mol	Bacteria-bacteria interaction
Ketones and Aldehydes				
	2-Propanone (Acetone)		CID: 180 MF: C_3H_6O MW: 58.08 g/mol	Plant growth promotion Salt tolerance
	2-Butanone		CID: 6569 MF: C_4H_8O MW: 72.11 g/mol	Antifungal
	2-Heptanone		CID: 8051 MF: $C_7H_{14}O$ MW: 114.19 g/mol	Plant growth promotion Antifungal
	4-Octanone		CID: 11516 MF: $C_8H_{16}O$ MW: 128.21 g/mol	Antifungal
	2-Nonanone		CID: 13187 MF: $C_9H_{18}O$ MW: 142.24 g/mol	Antifungal
	2-Undecanone		CID: 8163 MF: $C_{11}H_{22}O$ MW: 170.29 g/mo	Plant growth promotion Antifungal
	2-Tridecanone		CID: 11622 MF: $C_{13}H_{26}O$ MW: 198.34 g/mol	Antifungal
	2-Pentanone		CID: 7895 MF: $C_5H_{10}O$ MW: 86.13 g/mol	Plant growth promotion
	3-Hexanone		CID: 11509 MF: $C_6H_{12}O$ MW: 100.16 g/mol	Antifungal
	Acetophenone		CID: 7410 MF: C_8H_8O MW: 120.15 g/mol	Antibacterial activity
	3-Methyl-2-heptanone		CID: 92927 MF: $C_8H_{16}O$ MW: 128.21 g/mol	Insecticidal
	Propanal		CID: 527 MF: C_3H_6O MW: 58.08 g/mol	Antifungal
	3-Methyl butanal		CID: 11552 MF: $C_5H_{10}O$ MW: 86.13 g/mol	Antifungal

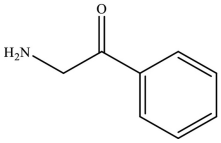
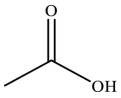
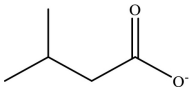
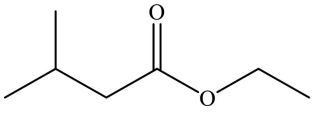
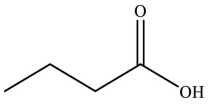
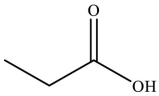
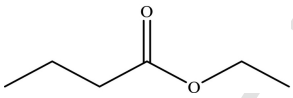
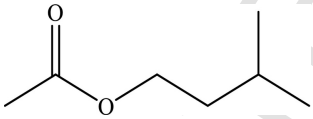
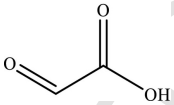
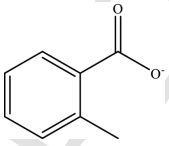
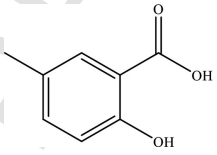
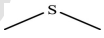
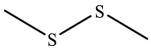
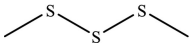
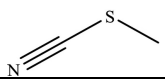
(*continued on next page*)

Table 1 (*continued*)

Sr. No	Compound	Structure	Molecular weight and compound CID no	Biological activity
	Furfural		CID: 7362 MF: $C_5H_4O_2$ MW: 96.08 g/mol	Antibacterial
	Benzaldehyde		CID: 240 MF: C_7H_6O MW: 106.12 g/mol	Antifungal Antibacterial Plant growth promotion
	Anisaldehyde		CID: 31244 MF: $C_8H_8O_2$ MW: 136.15 g/mol	Antifungal
	Tridecanal		CID: 25311 MF: $C_{13}H_{26}O$ MW: 198.34 g/mol	Plant growth promotion
	Tetradecanal		CID: 31291 MF: $C_{14}H_{28}O$ MW: 212.37 g/mol	Plant growth promotion
Nitrogen-containing compounds				
	Methyl anthranilate		CID: 8635 MF: $C_8H_9NO_2$ MW: 151.16 g/mol	Antifungal
	N,*N*-Dimethyloctylamine		CID: 16224 MF: $C_{10}H_{23}N$ MW: 157.3 g/mol	Antifungal
	Trimethyl amine		CID: 1146 MF: C_3H_9N MW: 59.11 g/mol	Antibiotic resistance
	Indole		CID: 798 MF: C_8H_7N MW: 117.15 g/mol	Auxin signaling Growth promotion
	Pyrazine		CID: 9261 MF: $C_4H_4N_2$ MW: 80.09 g/mol	Antibacterial
	2,3-Dimethoxybenzamide		CID: 220089 MF: $C_9H_{11}NO_3$ MW: 181.19 g/mol	Antifungal
	DL-Proline, 5-oxo		CID: 120115 MF: $C_{11}H_6Cl_5NO_3$ MW: 377.4 g/mol	Antifungal
	Benzonitrile		CID: 7505 MF: C_7H_5N MW: 103.12 g/mol	Herbicide Antifungal
	Nitropentane		CID: 220639 MF: $C_5H_{11}NO_2$ MW: 117.15 g/mol	Antifungal

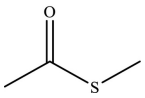
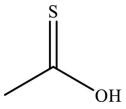
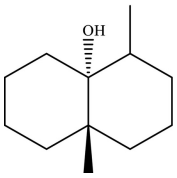
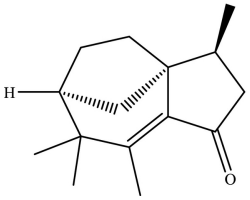
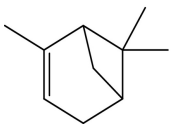
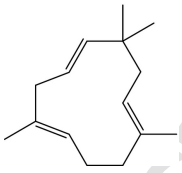
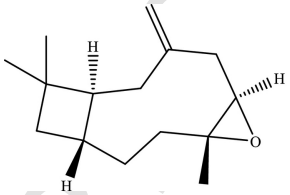
(*continued on next page*)

Table 1 (*continued*)

Sr. No	Compound	Structure	Molecular weight and compound CID no	Biological activity
	2-amino-acetophenone		CID: 11952 MF: C_8H_9NO MW: 135.16 g/mol	Quorum sensing molecule Promote antibiotic tolerance
Organic Acids and Esters				
	Acetic acid		CID: 176 MF: $C_2H_4O_2$ MW: 60.05 g/mol	Antifungal
	3-methyl butanoate		CID: 10430 MF: $C_5H_{10}O_2$ MW: 102.13 g/mol	Antibacterial
	Ethyl isovalerate		CID: 7945 MF: $C_7H_{14}O_2$ MW: 130.18 g/mol	Plant growth promotion
	Butyric acid		CID: 264 MF: $C_4H_8O_2$ MW: 88.11 g/mol	Antibacterial
	Propionic acid		CID: 1032 MF: $C_3H_6O_2$ MW: 74.08 g/mol	Inhibits growth of molds Antibacterial
	Ethyl butanoate		CID: 7762 MF: $C_6H_{12}O_2$ MW: 116.16 g/mol	Antibacterial
	Isoamyl acetate		CID: 31276 MF: $C_7H_{14}O_2$ MW: 130.18 g/mol	Plant growth promotion
	Glyoxylic acid		CID: 760 MF: $C_2H_2O_3$ MW: 74.04 g/mol	Salt tolerance
	Methylbenzoate		CID: 7150 MF: $C_8H_8O_2$ MW: 136.15 g/mo	Induction of systemic resistance
	5-Methylsalicylic acid		CID: 6973 MF: $C_8H_8O_3$ MW: 152.15 g/mol	Antibacterial
Sulfur containing compounds				
	Dimethyl sulfide		CID: 1068 MF: C_2H_6S MW: 62.14 g/mol	Antifungal
	Dimethyl disulfide		CID: 12232 MF: $C_2H_6S_2$ MW: 94.2 g/mol	Antifungal Plant growth promotion
	Dimethyl trisulfide		CID: 19310 MF: $C_2H_6S_3$ MW: 126.3 g/mol	Antifungal
	Methyl thiocyanate		CID: 11168 MF: C_2H_3NS MW: 73.12 g/mol	Antifungal

(*continued on next page*)

Table 1 (*continued*)

Sr. No	Compound	Structure	Molecular weight and compound CID no	Biological activity
	S-methyl thioacetate		CID: 73750 MF: C_3H_6OS MW: 90.15 g/mol	Antifungal
	Ethanethioic acid		CID: 10484 MF: C_2H_4OS MW: 76.12 g/mol	Antifungal Nematicidal
Terpenes				
	Geosmin		CID: 29746 MF: $C_{12}H_{22}O$ MW: 182.3 g/mol	Antibacterial Indicator of microbial Activity Attract soil arthropod
	albaflavenone		CID: 25137938 MF: $C_{15}H_{22}O$ MW: 218.33 g/mol	Antibiotics Flavor agent Pigments
	Alpha-pinene		CID: 6654 MF: $C_{10}H_{16}$ MW: 136.23 g/mol	Antifungal
	Alpha-humulene		CID: 5281520 MF: $C_{15}H_{24}$ MW: 204.35 g/mol	Antimicrobial
	Beta-caryophyllene		CID: 5281515 MF: $C_{15}H_{24}$ MW: 204.35 g/mol	Antimicrobial

CID: Compound Identification Number, MF: Molecular Formula, MW: Molecular Weight.

pounds (such as dimethyl disulfide) (Tyc et al., 2017b). The role of bacterial VOC (such as dimethyl disulfide) in quorum sensing has been explored across the bacterial kingdom in intra and interspecies communication. VOCs produced by *Pseudomonas fluorescens* and *Serratia plymuthica* inhibit cell-cell communication by interfering with the quorum-sensing pathway through suppression of transcription of *N*-acetylhomoserine lactone (AHL)-responsive genes *phzI* and *csaI* (Chernin et al., 2011).

Many pathogenic microorganisms hinder plant growth, disturb their functioning and cause diseases, resulting in crop yield reduction. Among these, many fungal phytopathogens cause severe diseases in a broad spectrum of plant species. They can survive in adverse environmental conditions and produce spores that remain dormant for many years. Such pathogens can be controlled in an environmentally friendly manner using biocontrol agents (Heenan-Daly et al., 2021; Song and Ryu, 2013). Some bacteria, acting as biocontrol agents, can kill or suppress the growth of plant pathogens without direct contact, via exposure to VOCs (Weisskopf et al., 2021). For example, bacteria and their VOCs have antagonistic effects on several fungal phytopathogens such as *Aspergillus flavus, Botrytis cinerea, Aspergillus fumigatus, Penicillium citrinum, Fusarium oxysporum* and *Rhizopus stolonifera* by inhibition of growth and development of fungi (Erjaee et al., 2019; Rojas-Solís et al., 2018; Vaca et al., 2020).

Bacterial VOCs can also improve plant growth and development by providing certain mineral nutrients, or triggering seed germination or plant immunity (Weisskopf et al., 2021). VOCs such as dimethyl trisulfide and ketones produced by a root-associated *Microbacterium* sp. were reported to induce significant increase in shoot and root biomass, and changes in the root architecture of *Arabidopsis thaliana* (Cordovez et al., 2017). Similarly, 2,3-butanediol exposed pepper roots had shown enhanced plant growth and inhibition of saprophytic fungi (*Trichoderma* sp.) and plant pathogen *Ralstonia solanacearum*. Exposure with 2,3-butanediol also modulated root exudates and rhizospheric microorganisms (Yi et al., 2016). The effect of VOCs is concentration-dependent and may have positive or negative effect on plant growth (Park et al., 2015). VOCs (13-tetradecadien-1-ol, 2-butanone and 2-methyl-n-1-tridecene) derived from the plant-growth-promoting rhizobacterium *Pseudomonas fluorescens*, enhanced growth of *Nicotiana tabacum* and also induced systemic resistance (ISR) against pathogens (Park et al., 2015). Bacterial species from diverse genera, including *Pseudomonas,*

Table 2
Antifungal activity of bacterial VOCs.

Bacteria (source)	Antifungal VOCs	Phytopathogens	Plant	References
Pseudomonas	Nonanal; Cyclohexanol; Benzothiazole; 2-ethyl, 1-hexanol; n-Decanal; Dimethyl trisulfide	*Sclerotinia Sclerotiorum*	Canola; Soybean	(Fernando et al., 2005)
Bacillus amyloliquefaciens	2,3,6-trimethyl-phenol; pentadecane; tetradecane	*Fusarium oxysporum*	Banana	(Yuan et al., 2012)
Burkholderia ambifaria	Dimethyl disulfide; 2-Undecanone; Dimethyltrisulfide; 4-Octanone; Methylmethane thiosulfate; Phenyl propane	*Rhizoctonia solani; Aleternaria alternate*	Pea; Maize; *Arabidopsis*	(Groenhagen et al., 2013)
Burkholderia tropica	Limonene; α-Pinene; Ocimene	*Collectotrichum gloeosporioides; F. oxysporum; F. culmorum*	Maize	(Tenorio-Salgado et al., 2013)
B. atrophaaeus	Hexadecane; 2,3-Dimethyloxybenzamide; Oanisaldehyde	*Botrytis cinera*	Tomato; Cucumber	(Zhang et al., 2013)
Aurebasidium pullalans	2-phenyl,1-butanol-3-methyl; 1-butanol-2-methyl; 1-Propanol-2-Methyl; 2-Phenethyl Alcohol	*Botrytis cinerea; Colletotrichum acutatum; P. expansum; P. italicum; P. digitatum*	Citrus fruit	(D'Alessandro et al., 2014)
Enterobacter aerogenes	2,3-Butanediol	*Exserohilum turcicum*	Maize	(D'Alessandro et al., 2014)
Paenibacillus polymyxa	Benzothiazole; Benzaldehyde; Undecanal; Dodecanal; Hexadecanal, 2-Tridecanone; Phenol	*F. oxysporum*	Watermelon (*Citrullus lanatus*)	(Raza et al., 2015)
P. fluorescence	Phenazines; Cyanogens; Dimethylhexadecylamin, ACC deaminase	*B. Cinerea*	*Medicago truncatula*	(Hernández-León et al., 2015)
B. amyloliquefaciens CPA-8	1,3 pentadiene; Acetoin; Thiophene	*Monilinia laxa; M. fructicola; B. cinera*	Cherry	(Gotor-Vila et al., 2017)
B. acidiceler	2,3,5-trimethylpyrazine; 6,10-dimethyl-5; 9-undecadien-2-one; 3-amino-1,3-oxazolidin-2-one	*Phytophthora Cinnamomi*	Avocado; *Arabidopsis*	(Mendez-Bravo et al., 2018)
Bacillus; Pseudomonas	(2,3,5-Trimethylpyrazine; 2-Nonanone; 2-Decanone; 2-Dodecanone; Dimethyl disulfide; Dimethyl trisulfide	*Colletotrichum gloeosporioides; Phytophthora Cinnamomi; Fusarium solani*	Avocado; Orchard	(Guevara-Avendano et al., 2018)
B. mojavensis	DL-proline-5oxo	*F. oxysporum f.* sp. *Cubense*	Banana	(Seethapathy et al., 2019)
B. pumilus	Methyl isobutyl ketone; Ethanol; 5-methyl-2-heptanone; S-2-methylbutyl amine	*Alternaria alternate; Curvularia lunata; F. oxysporum; Cladosporium cladosporioides; P. italicum*	Soil; Manure; Grease traps	(Morita et al., 2019)
B. subtilis; Bacillus safensis	Butanal; 3- Methylpropene; 2-Butene; 2-Heptanone; 6-Methyl-5-methylene; 6-Oxabicyclohexane	*F. oxysporum; Aspergillus flavus; A. fumigatus; Penicillium citrinum; Rhizopus stolonifers*	*Thymus vulgaris; Matricaria chamomilla*	(Erjaee et al., 2019)
Exiguobacterium acetylicum	1-(2-Aminophenyl) ethanone; Benzothiazole; α-Farnesene	*P. litchi*	Litchi	(Zheng et al., 2019)
B. subtilis	2-Methylbutyric acid; 2-Heptanone; Isopentyle acetate	*Curvularia lunata*	Maize	(Xie et al., 2020)

(*continued on next page*)

Table 2 (*continued*)

Bacteria (source)	Antifungal VOCs	Phytopathogens	Plant	References
Pseudomonas moorei; P. soli; P. umsongensis	2-Nonanone; 2-Tridecanone; DMTS; Benzeneacetaldehyde; Benzaldehyde; 2-undecanol; DMDS; 1-Undecene	*Thielaviopsis ethacetica*	*Saccharum officinarum*	(Freitas et al., 2022)
Paenibacillus polymyxa	1-Undecene; (Methyldisulfanyl) methane; 1-Decene 1-Tridecyne; 2-Undecanone	*R. solani; Sclerotinia sclerotium; F. oxysporum*; *Verticillium longisporum*	*Olea europaea*	(Montes-Osuna et al., 2022)
Streptomyces angustmyceticus	[2,2-Dimethyl-4-(3-methylbut-2-enyl)-6-methylidenecyclohexyl]methanol	*Lasiodiplodia theobromae*	*Anthurium andraeanum*	(Ruangwong et al., 2022)

Bacillus, Arthrobacter and *Serratia,* were shown to produce VOCs (acetoin, 2,3-butanediol, dimethylhexadecylamine and 2-pentylfuran) that enhance plant growth and ISR. However, *Stenotrophomonas, Chromobacterium* and *Burkholderia* were shown to emit VOCs (dimethyl disulfide) that inhibit plant growth and development in several plant species (*Medicago sativa*, *A. thaliana* and *N. tabacum*) (Bailly and Weisskopf, 2012). VOC, 2,3-butanediol derived from endophytic bacteria *Enterobacter aerogenes* promoted maize growth, controlled herbivores at a higher trophic level, and ISR to the corn leaf blight fungus *Setosphaeria turcica* (D'Alessandro et al., 2014).

As VOCs are often reactive molecules and thus, we do not know their fate once emitted. In several cases, they can be oxidized or photochemically react thus forming reactive oxygen species which also have a biological activity (Tyagi et al., 2020; Das et al., 2022). Soil characteristics (clay content, nutrients, minerals and humic acids), environmental factors (pH, moisture, temperature) and physiochemical properties of VOCs (vapor pressure and water solubility) influence the production and release of bacterial VOCs (Insam and Seewald, 2010). Changes in VOC profiles in a specific bacterial species have also been observed due to changes in culture conditions, such as the type of growth medium, pH, salts, sugars, temperature or incubation time (Morita et al., 2019; Tyc et al., 2017b; van Agtmaal et al., 2015). Garbeva and Weisskopf (2020) described the direct and indirect effects of microbial volatiles on plant health, including their impact under stress conditions. Cellini et al. (2021) described the use of VOCs for phytosanitary inspection, biological control, plant growth and assessing crop quality. They further validated the effects of VOCs on plant-pathogen interactions (Cellini et al., 2021). Weisskopf and others (Weisskopf et al., 2021) discussed VOCs in intrakingdom and interkingdom interactions with microbes, plants and insects, highlighting the potential biotechnological application of microbial VOCs. Role of VOCs were described in plant-microbe communication that affects plant growth, ISR and associated regulatory metabolic pathways for cellular function in plants (Fincheira et al., 2021; Gamez-Arcas et al., 2022). In the present review, we critically compiled the recent scientific studies specific to bacterial VOCs and their potential role in different metabolic pathways, hormone signaling and plant-microbe and microbe-microbe interactions. We further emphasize the detailed mechanisms involved in VOCs-microbe-plant interactions and highlight the application of not only mixed VOCs, but also individual VOC, and the responses of plants and their pathogens. The information regarding potential VOCs will help to select specific VOCs for growth promotion, ISR and pathogen suppression. This review may thus contribute to future scientific studies and pave the way for new research possibilities that will help fill the gaps in our understanding in this exciting field.

2. Role of bacterial VOCs in agriculture

Bacteria often produce a spectrum of VOCs, some of which influence neighboring organisms. Here we describe the application of VOCs produced by different genera of bacteria in agriculture for pathogen control, growth promotion, abiotic stress tolerance and ISR in plants, as well as cell to cell communication.

2.1. Bacterial VOCs-mediated antifungal activity

A great deal of information is available on the antifungal activity of bacterial VOCs. VOCs produced by different bacterial species has ability to control plant infection caused by pathogenic fungi. DMDS, 1-undecene, 4-hydroxy-2-pentanone and benzaldehyde were emitted by 16 different *Pseudomonas* strains controlled *Phytophthora infestans* infection in potato (De Vrieze et al., 2015). Another potato pathogen *Rhizoctonia solani* was significantly inhibited by VOCs emitted by *Pseudomonas palleroniana*, *Bacillus* strains and a *Paenibacillus* sp. B3a (Velivelli et al., 2015). VOCs produced by *Pseudomonas* strains inhibited mycelial growth of the pathogenic fungus *Thielaviopsis ethacetica,* which causes the disease-pineapple sett rot in sugarcane. It was observed that 5 mM of each individual VOC (2-nonanone, 2-ethyl, 1-hexanol, 2-nonanol, 2-tridecanone, dimethyl trisulfide, benzeneacetaldehyde, benzaldehyde, 2-undecanol, dimethyl disulfide and 1-undecene) inhibited mycelial growth up to 80% by altering the structural morphology of the fungus (Freitas et al., 2022).

Pseudomonas strains (P482 and AD21) produced VOCs (1-undecene, methyldisulfanyl-methane and 1-decene) that reduced mycelial growth of *Verticillium dahliae* (41%) and *Verticillium longisporum* (33%). *P. donghuensis* P482 emits a blend of VOCs that strongly inhibits the growth of many plant-pathogenic bacteria, fungi and oomycetes, such as *Xanthomonas oryzae, R. solani, Fusarium culmorum, V. dahliae,* and *Pythium ultimum* (Ossowicki et al., 2017). Interestingly, a distinct VOCs profile of antifungal compounds was analyzed through volatilome analysis of wild-type and mutant strains of *P. donghuensis* (Ossowicki et al., 2017). Furthermore, VOC emission was correlated with HCN production, regulated by the *Gac*A/*Gac*S two-component regulatory system, while the *Gac*A mutant entirely lost production of antifungal compounds. Thus, the production of antifungal VOCs is dependent on the *Gac*A/*Gac*S regulatory system in bacteria. (Ossowicki et al., 2017). The compounds, namely dimethyl disulfide, *S*-methyl thioacetate, methyl thiocyanate, dimethyl trisulfide, and 1-undecane were present only in the wild-type strain (Ossowicki et al., 2017). The role of *Gac*A/*Gac*S system was also investigated in *Pseudomonas chlororaphis* 449 that regulate VOC emission and affected the growth of *Arabidopsis thaliana* (Plyuta et al., 2021). However, the precise effect of the *Gac*S mutation on the biosynthesis of individual volatiles in bacteria requires further study (Plyuta et al., 2021). However, Popova et al. (2014) did not observe any inhibitory effect of HCN on the fungal pathogen *R. solani* using HCN-producing and non-HCN-producing bacteria (*Pseudomonas chlororaphis* strains, *Pseudomonas fluorescens* B4117 and *Serratia plymuthica* IC1270 strains). Moreover, *P. chlororaphis* produced VOCs (2-nonanone, 2-heptanone, 2-undecanone and dimethyl disulfide) inhibited the growth of fungi (*R. solani*), flies (*Drosophila melanogaster*), ne-

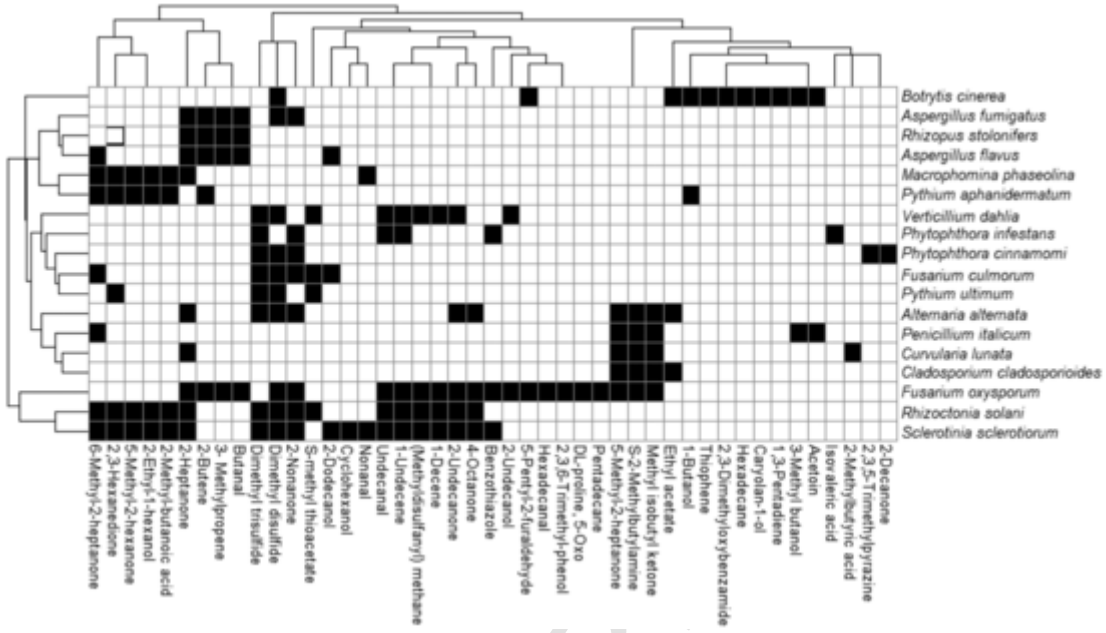


Fig. 1. Antifungal potential of selected bacterial VOCs against fungal plant pathogens. Black square indicates a compound checked against a specific pathogen and found to be effective in at least one study.

matodes (*Caenorhabditis elegans*) and bacteria (*Agrobacterium tumefaciens*) (Popova et al., 2014).

Notably, a different volatilome profile was identified when the bacteria (*Pseudomonas* spp.) were co-cultivated with the fungi (*V. dahliae*), with some specific antimicrobial VOCs (4-methyl-2,6-bis(2-methyl-2-propanyl)phenol, 10-methyl-1-undecene) produced only during co-cultivation (Montes-Osuna et al., 2022). Interestingly, some compounds that were emitted in smaller quantity such as isovaleric acid, nitropentane, propiophenone, undecanal, phenylpropanedione, dimethyl trisulfide and *S*-methyl methanethiosulfonate were tested more efficient in inhibiting *P. infestans* (De Vrieze et al., 2015). A fungistatic effect of *Serratia plymuthica*-produced VOCs was described both on plant-beneficial (*Neurospora crassa*) and plant-pathogenic (*R. solani, S. sclerotiorum* and *Juxtiphoma eupyrena*) fungi. However, there was no significant difference in the growth inhibition of pathogenic and nonpathogenic fungi. The fungi exposed to the VOCs showed loss of membrane integrity due to increased concentration of oxidative stress-responsive enzymes (superoxide dismutase, catalase and laccase) and lipid peroxidation (Das et al., 2022).

Bacillus represents a prominent genus for production of antifungal VOCs as reported in different studies to control diversity of pathogens. *Bacillus pumilus*- and *Bacillus safensis*-derived VOCs effectively inhibited the growth of *Aspergillus flavus, Aspergillus fumigatus, Penicillium citrinum, Fusarium oxysporum* and *Rhizopus stolonifera* (Erjaee et al., 2019). The application of these bacterial VOCs mixture showed antifungal activity, while individual compound did not reflect any inhibition. Therefore, the combined effect of mixture of VOCs were found more effective for their biological activity as compared to individual one (Erjaee et al., 2019). *Paenibacillus polymyxa* emitted VOCs inhibited growth (by 51–72%) of four plant-pathogenic fungi (*Rhizoctonia solani, Sclerotinia sclerotiorum, Fusarium oxysporum*, and *Verticillium longisporum*) (Montes-Osuna et al., 2022).

Some studies on efficacy testing of VOCs producing bacteria in pot and field experiments has been undertaken. The organic matter status of soil, crop rotation, tillage, application of soil amendments along with soil physico-chemical properties affects the production and release of VOCs by soil microbial communities (Insam and Seewald, 2010). VOC profiles were found to differ according to oxygen availability in the soil (Insam and Seewald, 2010). Under aerobic conditions, bacteria produced and utilized CO_2 as a source of carbon for cell growth, and only a small fraction was used for VOC production. Under microaerophilic and anaerobic conditions, bacteria produced fermentation products as end products from the carbon sources, and these were further involved in the biosynthesis and emission of diverse VOCs (Insam and Seewald, 2010).

VOCs produced by *Bacillus pumilus* were shown to suppress the growth of post-harvest spoilage caused by *Alternaria alternata, Fusarium oxysporum, Curvularia lunata, Cladosporium cladosporioides* and *Penicillium italicum* (Morita et al., 2019). Most predominant antifungal VOCs produced by this bacterium were 5-methyl-2-heptanone, methyl isobutyl ketone, ethanol and S-(−)-2-methylbutylamine (Morita et al., 2019).

The predominant antifungal VOCs identified in *B. pumilus* (S-2-methylbutylamine, 5-methyl-2-heptanone, ethanol and methyl isobutyl ketone) were screened by testing the growth inhibition of *P. italicum*. A different *Bacillus* sp. produced the antifungal VOC 5-oxo-DL-proline, which inhibited the banana wilt-causing fungus *F. oxysporum* f. sp. *cubense* (Seethapathy et al., 2019). VOCs derived from the endophyte *Bacillus subtilis* DZSY21 also demonstrated antifungal activity against the maize pathogen *C. lunata*. This *Bacillus* produced a VOC mixture of isopentyl acetate and 2-heptanone, which strongly inhibited sporulation and germination, while 2-methyl butyric acid inhibited sporulation of *C. lunata* and reduced the disease index by up to 44% in maize crops (Xie et al., 2020). The mechanism of antifungal activity was also analyzed and it was revealed that isopentyl acetate caused accumulation of ROS in the conidia of *C. lunata,* which damage DNA replication and cell membrane and lead to cell death. Additionally, VOCs downregulated the expression of fungal virulence associated genes such as *clk1, scd, clm1* and *brn1* (Xie et al., 2020).

A newly described compound, caryolan-1-ol, produced by *Streptomyces* spp., was effective against the fungus *Botrytis cinerea*, a major pathogen of grapes. Pure caryolan-1-ol (0.005–0.075 mM ml^{-1}) inhibited mycelia growth in a dose-dependent manner. The maximum inhibitory concentration of the compound was 0.026 mM ml^{-1} after 4 days of exposure. The compound affected fungal endomembrane system by disrupting sphingolipid synthesis, vesicle trafficking, membrane localization and mycelial growth due to damage to the fungal spitzenkorper (point of origin of fungal hyphae) (Cho et al., 2017).

Table 3
Nematicidal activity of bacterial VOCs against *Ceanorhabditis elegans* and *Meloidogyne incognita*.

Compound	Effective concentration	Experimental condition	Activity	Target organisms	Reference
2-Nonanone 2-Undecanone Dimethyl disulfide	0.50 mM	Plate assay, Pot experiment	Nematicidal, Egg hatching	*Meloidogyne incognita*	(Huang et al., 2009)
S-methyl thiobutyrate	0.27 mM	Plate assay		*M. incognita*, *Caenorhabditis elegans*	(Xu et al., 2015)
2-Decanone	100.00 mg/L	Compartment petri dishes	Nematicidal	*M. incognita*	(Cheng et al., 2017)
Furfural acetone	75.10 mg/L		Nematicidal, Fumigant, Chemoattractant		
2-Nonanone	250.00 mg/L		Nematicidal		
Furfural acetone	4.44 mg/L		Contact nematicidal		
2-Undecanol	5.05 mg/L				
4-Acetylbenzoic	16.24 mg/L				
2-Decanol acid	23.12 mg/L				
Dimethyl disulfide	139.08 mg/L	Plate assay	Inhibit juvenile, Nematicidal	*M. incognita*	(Zhai et al., 2018)
Z)-hexen-1-ol acetate	32.35 mg/L				
2-Octanone	22.71 mg/L				
2-Nonanone	63.32 mg/L				
2-Undecanone	22.87 mg/L				
	185.00 mg/L		Fumigant		
	40.00 mg/L		Egg hatching		
Acetaldehyde	141.4 μg/mL	Plate assay	Nematicidal	*M. incognita*	(Huang et al., 2020)
	10.00 mg/L		Fumigant Egg hatching		
Dimethyl disulfide	139.10 μg/mL		Nematicidal		
Acetaldehyde; Dimethyl disulfide; Ethylbenzene	3.00 mg/L		Chemo attractant		
2-Butanone			Repellent		
Methyl thioacetate	0.01 mg/mL	Plate assay	Contact nematicidal	*M. incognita*	(Chen et al., 2021)
	10.00 mg/mL		Repellent		
	0.50–5.00 mg/mL		Inhibit egg hatching		
Octanoic acid	0.03 μL/mL	Broth medium	Nematicidal	*M. incognita*	(Ye et al., 2022)
Acetic acid	0.05 μL/mL				
2,3-Butanedione	0.05 μL/mL				

Moreover, caryolan-1-ol affected the genes responsive to lipid synthesis (*scs7, sur4, iro1*), osmotic stress (*ste11* and *smp1*), vesicular trafficking (*eug1, vps4, sip3,* cot*1, did4, vid22, vma9, vps52, vms1, rer1* and *csg2*), chromatin remodeling (*eaf1* and *hpr1*) and DNA replication (*ste11, mgs1, cot1, csg2*) (Cho et al., 2017).

Streptomyces setonii, producing 2-ethyl-5-methylpyrazine and dimethyl disulfide, significantly inhibited mycelial growth and spore germination of the sweet potato-pathogenic fungus *Ceratocystis fimbriata* in a dose dependent manner (Gong et al., 2022). Fumigation with 2-ethyl-5-methylpyrazine completely inhibited the growth (50 μL) and sporulation (10 μL) of *C. fimbriata* in plate assay while dimethyl disulfide (100 μL) was less inhibitory than 2-ethyl-5- methylpyrazine. Interestingly, fumigation with a mixture of these VOCs (100 μL/L) completely controlled black spot of sweet potato for up to 10 days of storage at ambient temperature in closed-box experiments (Gong et al., 2022). Additionally, VOCs exposure to sweet potato induced defense related enzymes, phenylalaline ammonia lyase (PAL) (91%), polyphenol oxidase (PPO) (84%) and catalase (44%) in the roots after 20 days of exposure. Moreover, flavonoids content was enhanced which further improved plant resistance against fungi. These complex effects indicated the diverse mode of volatiles action against *C. fimbriata*. Actinomycetes are also very effective biocontrol agents. *Streptomyces*-produced [2,2-dimethyl-4-(3-methylbut-2-enyl)-6-methylidenecyclohexyl]methanol inhibited (by 79%) mycelial growth of *Lasiodiplodia theobromae*, the causative agent of spadix rot of flamingo flowers (Ruangwong et al., 2022).

The reports on antifungal activity of VOCs derived from pure bacterial cultures and mixed population are available in the literature. These VOCs have suppressed the growth of plant pathogenic fungi. Chuankun et al. (2004) reported the fungistatic effect of mixture of VOCs emitted from different soil samples. Synthetic analogues of VOCs detected in soil, such as trimethylamine, dimethyl disulfide, benzaldehyde and *N,N*-dimethyloctylamine showed fungal growth inhibition in vitro (Chuankun et al., 2004). Agtmaal et al. (2018) showed that VOCs suppress the soil-borne plant-pathogenic fungi *R. solani* and *F. oxysporum*, and the oomycete *Pythium intermedium*, and the effect was positively correlated with soil organic matter and microbial biomass, and negatively correlated with pH, microbial diversity, tillage, crop rotation, solid manure and proportion of *Acidobacteria* in the microbial community (Agtmaal et al., 2018). The role of Burkholderiaceae family members was investigated in the suppression of *R. solani* in two different soil due to emission of sulfur-containing VOCs produced by *Paraburkholderia graminis*; the fungi suppression was more in suppressive soil than conducive soil which might be due to more production of VOCs (Carrion et al., 2018). Nevertheless, the soil properties and management practices that influence VOC-mediated pathogen suppression in soil have not yet been fully deciphered. Moreover, the nature and composition of VOCs were found to differ when a bacterium was grown individually or simultaneously with other microorganism (including fungal pathogen) (Rybakova et al., 2017). Therefore, there is need of depth investigations for profiling of VOCs emitted by the bacterium in natural conditions with the host. While bacteria emitting mixed VOCs have been explored for their antifungal activity against many fungal phytopathogens, as already noted, and summarized in Table 2 and Fig. 1, the biological activity of individual VOCs has been relatively less explored (Table 4). The identified chemical structures of the most commonly studied antifungal bacterial VOCs are presented in Table 1.

2.2. Effect of bacterial VOCs on neighboring bacterial communities

Bacterial VOCs readily diffuse in the environment and influence interspecific and intraspecific bacterial communication and behavior, al-

Table 4
Pathogen suppressive and plant growth promoting activities of pure VOCs.

Compound	Effective concentration	Experimental conditions	Activity	Targeted organisms	Reference
2,3-Butanediol	0.2 μg	Seedling treatment	ISR	*Arabidopsis*	(Ryu et al., 2004)
Dimethyl disulfide (DMDS)	50–100 μmol	Dual plate assay	Inhibit quorum sensing signaling	*Agrobacterium; Chromobacterium; Pectobacterium; Pseudomonas*	(Chernin et al., 2011)
Dimethyl disulfide	1.0 mM	Soil amendment	ISR in corn and tobacco	*Botrytis cinerea; Cochliobolus heterostrophus*	(Huang et al., 2012)
Tridecane	100 μM - 10 mM	Plate assay	PGP and ISR (*Arabidopsis*)	*Pseudomonas syringae*	(Lee et al., 2012)
3-Pentanol	2.0 mM	Field	Bactericide; nematicide	*Pseudomonas syringae; Myzus persicae*	(Song and Ryu, 2013)
2-Butanone	0.1 μM				
3-Pentanol	1.0 mM	Seedling root drench	PGP and ISR (pepper)	*Xanthomonas axonopodis*; Cucumber mosaic virus	(Choi et al., 2014)
Indole	0.1 μg	Plate assay	PGP	*A. thaliana*	(Bhattacharyya et al., 2014)
DMDS	100 μmol	Plate assay	Anti-cyanobacterium	*Synechococcus* sp.	(Popova et al., 2014)
2- Undecanone	100 μmol		Antifungal	*R. solani*	
Nitropentane; isovaleric acid; Undecanal; Phenylpropanedione; Propiophenone; Dimethyl trisulfide (DMTS) and *S*-methyl methanethiosulfonate (MMTS)	1.0 mg	Plate assay	Antifungal	*Phytophthora infestans*	(De Vrieze et al., 2015)
3-Pentanol	100 nM	Plate assay	Bactericidal; ISR	*Pseudomonas syringae*	(Song et al., 2015)
Diacetyl	75 μg/mL	Plate assay	Antifungal	*Penicillium solitum*	(Aunsbjerg et al., 2015a)
Propionic Acid	0.5 mg/mL	Microtitre plate assay	Antifungal	*Penicillium* spp.	(Aunsbjerg et al., 2015b)
Diacetyl	0.075 mg/mL				
13- Tetradecadien-1-ol	50 ng	Partition plate assay	PGP	Tobacco seedlings	(Park et al., 2015)
2-Methyl-n-1- tridecene	5.0 ng				
2-Undecanone 1-Heptanol 3-Methyl-butanol DMDS	100 ng - 1.0 mg	Plate assay	PGP; Salt tolerance	*A. thaliana*	(Ledger et al., 2016)
Caryolan-1-ol	0.25 μmol/ml	Plate assay	Antifungal	*Botrytis cinerea*	(Cho et al., 2017)
S-methyl thioacetate (MTA)	11.4 μM	Plate assay	Antibacterial; Antifungal	*Rhizoctonia solani; Fusarium culmorum; Verticillium dahlia; Pythium ultimum*	(Ossowicki et al., 2017)
Dimethyl disulfide (DMDS)	11.1 μM				
Dimethyl trisulfide (DMTS)	9.5 μM				
Benzaldehyde	0.20 mg	Plate assay	Antibacterial	*Ralstonia solanacearum*	(Tahir et al., 2017a)
1,2-Benzisothiazol-3(2H)-one	0.50 mg				
1,3–butadiene	0.57 mg				
2-Nonanone	50 ppm	Plate assay	PGP	*Lactuca sativa*	(Fincheira et al., 2017)
2-undecanone	0.05 ppm				
Dimethyl trisulfide	1.0 μM >1.0 mM	Climate cabinet	PGP Anti-PGP	*Arabidopsis thaliana*	(Cordovez et al., 2017)
DMDS	10 μM	Partition plate assay	Antifungal	*B. cinerea*	(Rojas-Solís et al., 2018)
Acetoin	112.9 μM	Pot experiment	ISR; Stomata closure	*Arabidopsis*; *Nicotiana*	(Wu et al., 2018)
2,3-Butanediol	297.5 μM				
Tetrahydrofuran-3-ol	1.0 μg/μl	Seedling treatment	PGP	*A. thaliana; Solanum lycopersicum*	(Jiang et al., 2019)
2-Heptanone	10 ng/μl				
2-Ethyl-1-hexanol	1.0 μg/μl				
3-Methyl-1-butanol	50 μM	Plate assay	Increase fresh shoot and total biomass	*A. thaliana; N. benthamiana;*	(Camarena-Pozos et al., 2019)
3-Methyl-1-butanol; Isoamyl acetate	1000 μM		Increase chlorophyll content	*Agave salmiana*	
Isoamyl acetate	5.0 μM		Increase length of primary root		
DMDS; Dimethylthiomethane; Propiophenone; Benzothiazole	7.5 μL	Plate assay and seedling exposure	Antifungal	*Cytospora chrysosperma; Phomopsis macrospora; Fusicoccum aesculi*	(Liu et al., 2020)
DMDS	50 μM	I-plate and pot assay	Antifungal, plant growth promotion (PGP)	*Sclerotinia minor*	(Tyagi et al., 2020)
2-Methyl butyric acid	10 μL	Plate assay	Antifungal	*Curvularia lunata*	(Xie et al., 2020)
2-Heptanone	20 μL				
Isopentyl acetate	35 μL				

(*continued on next page*)

Table 4 (*continued*)

Compound	Effective concentration	Experimental conditions	Activity	Targeted organisms	Reference
2-Nonanone; 2-Tridecanone; DMTS; Benzeneacetaldehyde; Benzaldehyde; 2-undecanol; DMDS; 1-Undecene	5.0 mM		Antifungal	*Thielaviopsis ethacetica*	(Freitas et al., 2022)
2-Ethyl-5-methyl pyrazine	10 μL	Plate assay	Antifungal	*Ceratocystis fimbriata*	(Gong et al., 2022)
Dimethyl disulfide	25 μL				

PGP- Plant Growth Promotion, ISR- Induced Systemic Resistance.

ter gene expression in neighboring bacterial communities, and modulate growth and nutrient availability in the surrounding environment (Netzker et al., 2020; Schulz-Bohm et al., 2017b). Among other things, bacterial VOCs play an important role in long-distance interactions among bacterial communities, and affect biofilm formation, antibiotic resistance and virulence (Hou et al., 2021; Kim et al., 2013; Letoffe et al., 2014; Xie et al., 2018). Long-distance effects of *Escherichia coli* VOCs have been observed on growth, motility and adhesion properties of exposed *Bacillus subtilis*, *Staphylococcus aureus* and *Pseudomonas aeruginosa*. In addition, exposure to the pure VOC trimethylamine (produced by *E. coli*) reduced antibiotic resistance in these bacteria, and increased the pH of the surrounding environment (Letoffe et al., 2014). Kim et al. (2013) reported that *Bacillus subtilis*-emitted 2,3-butanediol and glyoxylic acid which downregulated the expression of the regulatory gene *ypdB* (responsible for swarming and swimming motility and antibiotic resistance) in a neighboring *E. coli* population. In vitro study, the application of 10 nM of each 2,3-butanediol and glyoxylic acid reduced the swarming motility by 32% and swimming motility by 60% (Kim et al., 2013). In a study, monoculture of *Burkholderia* and *Paenibacillus* produced different VOCs profile, while a new compound 2,5-bis(1-methylethyl)-pyrazine was emitted only during cocultivation. The interaction between these two bacteria altered *Paenibacillus* gene expression and metabolic profile, which led to the production of this novel volatile antimicrobial compound (Tyc et al., 2017a). *Pseudomonas fluorescens*-derived 1-undecene and *Serratia plymuthica*-produced dimethyl disulfide inhibited the growth of *Agrobacterium tumefaciens* and *Agrobacterium vitis* in vitro and *in planta* (Dandurishvili et al., 2011). VOCs produced by *P. fluorescens* and *S. plymuthica* suppressed cell–cell communication (quorum sensing) among plant-pathogenic and plant-beneficial bacterial genera such as *Agrobacterium, Pectobacterium, Chromobacterium* and *Pseudomonas*. *P. fluorescens*-derived dimethyl disulfide was the most effective compound at reducing AHL production by suppressing the expression of genes *phzI* and *csaI* (Chernin et al., 2011). VOCs produced by a plant-growth-promoting *Bacillus* reduced cell motility and colony diameter of plant-pathogenic bacterium *X. oryzae*. A blend of 3,5,5-trimethylhexanol (2.4 mg) and decyl alcohol (0.48 mg), both identified in this *Bacillus* VOCs, inhibited the growth of *X. oryzae* via condensation of the cytoplasm and an increase in membrane permeability, as well as repressed virulence related genes (Xie et al., 2018). Genes, *motA* (encoding flagellar motor component) and *motC* (encoding flagellar motor protein) required for cell motility, and *rpfC* responsible for virulence and biofilm formation were significantly repressed as a result of exposure to these two VOCs individually (Xie et al., 2018).

VOCs produced by *Bacillus amyloliquefaciens* significantly inhibited the motility traits, and suppressed the production of antioxidant enzymes and exopolysaccharides, as well as biofilm formation and root colonization by *Ralstonia solanacearum* (Raza et al., 2016). The pure form of each of the nine VOCs produced by this *B. amyloliquefaciens* showed some antagonistic activity (1–11% growth inhibition) whereas their mixture showed 70% growth inhibition of *R. solanacearum* under in-vitro conditions (Raza et al., 2016). Exposure to VOCs mixture produced by this strain downregulated the proteins involved in carbohydrate and amino acids metabolism, translation and protein folding while upregulated the proteins involved in ABC transporter, amino acid synthesis and methylation in *R. solanacearum* (Raza et al., 2016).

2.3. Nematicidal activity of bacterial VOCs

Nematodes comprise a group of microorganisms, of which some cause devastating plant diseases such as root-knot, cyst, etc. Bacterial VOCs have been reported as fumigant and strong nematicidal agent that diffuse in soil air pockets causing long distances effects within the soil. For example, *Bacillus aryabhattai* was shown to emit VOCs with nematicidal and fumigant activities against *Meloidogyne incognita* (Chen et al., 2021). Of these, pentane, 1-butanol, methyl thioacetate, and dimethyl disulfide, when added to growth medium have exhibited strongest activity against *M. incognita*. Moreover, methyl thioacetate has been reported as contact nematicidal (87.9% mortality, 0.01 mg/mL, 72 h), repellent (0.01–10 mg/mL) and fumigant (mortality 91.1%, 1 mg/mL, 48 h) against *M. incognita* and inhibited egg hatching up to 100% (0.5–5.0 mg/mL) (Chen et al., 2021). Volatiles produced by *Bacillus* strain GBSC56 were potent nematicidal causing 90% mortality against *M. incognita* in a partition plate assay (Ayaz et al., 2021). Pure VOCs dimethyl disulfide, methyl isovalerate, and 2-undecanone, identified in *Bacillus*, exhibited strong nematicidal activity against *M. incognita* with mortality rate of 87%, 83%, and 80%, respectively. These VOCs were shown to kill the nematodes by inducing oxidative stress responsive proteins. Additionally, VOCs exposure induced the expression of defense related genes in plants (Ayaz et al., 2021). VOCs emitted during fermentation by *Bacillus cereus* showed nematicidal activity against *M. incognita* with mortality as 91% (24 h) and 97% (48 h) (Yin et al., 2021). Pure dimethyl disulfide (30.6%) and *S*-methyl ester butanethioic acid (30.29%) showed highest nematicidal activity. VOCs collected from *B. cereus* decreased root galls on cucumber roots up to 46% in pot experiment (Yin et al., 2021). *Paenibacillus polymyxa* VOCs showed a comprehensive array of nematicidal activities. VOCs such as furfural acetone, 2-undecanol, 4-acetylbenzoic, and 2-decanol acid showed 50% contact dependent nematicidal activity at concentration of 4.44, 5.05, 16.24, and 23.12 mg/L, respectively, in plate assay against *M. incognita* (Cheng et al., 2017). Application of furfural acetone (75.1 mg/L) as fumigant showed strong nematicidal activity in soil. Further, furfural acetone, 2-decanol and acetone act as chemoattractant while 2-undecanone (also produced by *P. polymyxa)* acted as chemo-repellent towards *M. incognita* (Cheng et al., 2017). Microscopic studies showed disrupted morphological changes such as indistinct intestine and shrunken pharyngeal tissues exposure to 2-nonanone (250 mg/L) and 2-decanone (100 mg/L) in J2 nematode juvenile (Cheng et al., 2017). VOCs such as acetic acid, 3-methylbutyric acid, octanoic acid, 2,3-butanedione, 2-isopropoxy ethylamine and 2-methylbutyric acid produced by *Bacillus altutudinis* showed nematicidal activity against *M. incognita* (Ye et al., 2022). Octanoic acid and acetic acid showed highest activity at a concentration of 0.03 μL/mL and 0.05 μL/mL, respectively. Other organic acids, produced by this bacterium- 2-methylbutyric acid (0.03 μL/mL) and 3-methylbutyric acid (0.03 μL/mL), and ketones (2,3-butanedione, 0.5 μL/mL and 2-isopropoxy ethylamine, 1 μL/mL) showed significant nematcidal activity against *M. incognita* (Ye et al., 2022). *Virgibacillus dokdenesis* produced VOCs with multiple nematici-

Table 5
Effect of bacterial VOCs on plant growth and induced systemic resistance.

Bacteria	VOCs	Plants	Effect	Reference
Bacillus amyloliquefaciens	2,3-Butanediol	*Arabidopsis thaliana*	Growth promotion	(Ryu et al., 2003)
B. amyloliquefaciens; B. subtilis	2,3-Butanediol; Acetoin	*Arabidopsis*	ISR; PGP	(Ryu et al., 2004)
B. subtilis	VOCs mixture	*A. thaliana*	Over expression of ion transporter, reduced expression of High-affinity K+ transporter; Salt tolerance	(Zhang et al., 2009a)
Arthrobacter agilis	Dimethylhexadecylamine	*Medicago sativa*	Growth promotion	(Velázquez-Becerra et al., 2010)
Sinorhizobium meliloti	2-Heptanone; 2-Nonanone; 3-Methyl-1- butanol; Phenylpropiolic acid; 1-Nonanol; Methyl-7 (*Z*)- hexadecenoate	*Medicago truncatula*	Increase plant biomass, rhizosphere acidification, ferric reductase activity, Chlorophyll content	(Orozco-Mosqueda Mdel et al., 2013)
Enterobacter aerogenes	2,3-Butanediol	maize	ISR; Parasitoid attraction against pathogen	(D'Alessandro et al., 2014)
Proteus vulgaris	Indole	*A. thaliana*	Increase fresh weight; Induction of auxin, cytokinin and brassinosteroid pathway	(Bhattacharyya et al., 2014)
Enterobacter cloacae; Bacillus spp.	VOCs mixture	*Brachypodium distachyon*	Increase total root length, fresh biomass	(Delaplace et al., 2015)
Pseudomonas fluorescens	13-Tetradecadien-1-ol; 2-Butanone; 2- Methyl-n-1-tridecene	Tobacco	Increase total biomass	(Park et al., 2015)
P. fluorescens	Dimethyl disulfide; Dimethyl-hexadecylamine	*M. truncatula*	Increase total biomass and chlorophyll content	(Hernández-León et al., 2015)
Pseudomonas simiae	VOCs mixture	*Glycine max*	Induce systemic tolerance to high sodic conditions; Accumulation of proline and chlorophyll content	(Vaishnav et al., 2015)
B. amyloliquefaciens	2,3- Butanedione; Acetoin; 5-Methyl-heptanone; 2-Pentanopne; 2-Methylpyridine	*Arabidopsis*	Increase root length; Total fresh weight	(Asari et al., 2016)
P. fluorescens	3-Nonene; 4-Undecyne; 1-Undecene; S-2-S-butylfuran; Dimethyl sulfide	*Arabidopsis*, Tobacco	Increase root and shoot biomass; ISR	(Cheng et al., 2016)
Azospirillum brasilense; Bacilus pumilus	2,3-Butanediol; Acetoin	Green microalga *Chlorella sorokiniana*	Increase total lipid, carbohydrates, chlorophyll *a*	(Amavizca et al., 2017)
B. subtilis	Albuterol; 1,3-Propanediol	*Nicotiana benthamiana*	ISR against *Ralstonia solanacearum* by upregulating the genes related to wilt resistance and defense	(Tahir et al., 2017b)
Pseudomonas aeruginosa	3-Hydroxy-5-methoxy benzene methanol (HMB)	Tomato	Induce defense mechanism	(Fatima and Anjum, 2017)
Arthrobacter agilis; Bacillus methylotrophicus; Sinorhizobium meliloti	VOCs mixture	*Sorghum bicolor*	Growth promotion; Induction of iron-transporters; plant defense pathways	(Hernandez-Calderon et al., 2018)
B. amyloliquefaciens	2,3-Butanediol	*Nicotiana benthamiana; A. thaliana*	ISR; Stomata closure	(Wu et al., 2018)
Pseudomonas stutzeri; Stenotrophomonas maltophilia	Dimethyl disulfide (DMDS)	Tomato	Increase root, Shoot biomass, Chlorophyll content, Total biomass	(Rojas-Solís et al., 2018)
Bacillus sp.	Tetrahydrofuran-3-ol; 2-Heptanone; 2-Ethyl-1-hexanol	*A. thaliana*; Tomato	Growth promotion through the action of auxin and strigolactone	(Jiang et al., 2019)
Staphyloccocus hominis; Belnapia rosea; Psychrobacillus psychrodurans; E. cloacae	Ethyl isovalerate; Isoamyl acetate; 3-Methyl-1-butanol; Benzyl alcohol; 2-Phenylethyl alcohol; 3-(Methylthio)-1-propanol	*A. thaliana; N. benthamiana; Agave salmiana; Cacti*	Increase lateral root formation, fresh shoot and total biomass, chlorophyll content	(Camarena-Pozos et al., 2019)

VOCs- Volatile Organic Compounds, PGP- Plant Growth Promotion, ISR- Induced Systemic Resistance.

dal activity against *M. incognita*. Acetaldehyde was strong nematicide by contact killing against juvenile after 6 h at 141.4 μg/mL, <10 μg/mL at 24 h; while dimethyl disulfide showed strongest activity at a concentration of 139.1 μg/mL after 24 h (Huang et al., 2020). Acetaldehyde at a concentration of 10 mg/L acted as strong fumigant by inhibiting juvenile and egg hatching with 100% mortality rate at 6 h and even at a low concentration of 1 mg/L showed 71% mortality rate at 6 h and 98% at 24 h (Huang et al., 2020). Moreover, acetaldehyde, dimethyl disulfide and ethylbenzene acted as a chemoattractant while 2-butanone acted as repellent of juvenile at a concentration of 3 mg/L (Huang et al., 2020).

Several studies showed nematicidal activities of VOCs produced by numerous *Pseudomonas* strains. For example, VOCs emitted by *P. putida* inhibited *M. incognita* juvenile and egg hatching (Zhai et al., 2018). Dimethyl disulfide (139.08 mg/L), (*Z*)-hexen-1-ol acetate (32.35 mg/L), 2-undecanone (22.87 mg/L), 2-octanone (22.71 mg/L) and 2-nonanone (63.32 mg/L) showed strong nematicidal effect against *M. incognita* juvenile by direct contact; while 2-undecanone (185 mg/L)

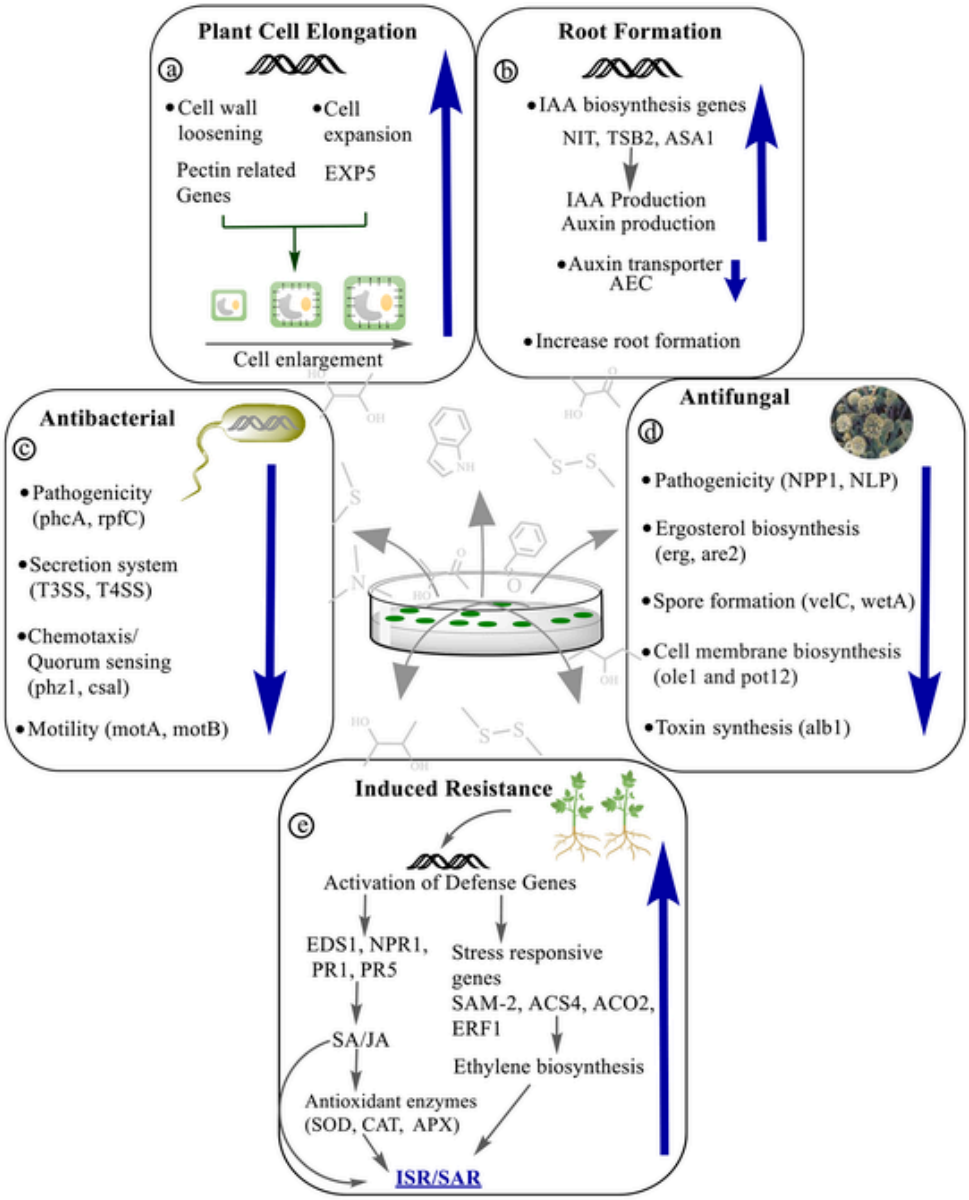


Fig. 2. Antimicrobial and plant growth mechanism of bacterial VOCs: (a) Bacterial VOCs induced expression of expansin gene (*EXP5*) and pectin related genes. (b) VOCs exposure enhanced expression of indole acetic acid (IAA) biosynthesis pathway regulatory genes such as nitrilases (*NIT*), tryptophan synthase (*TSB2*) and anthranilate synthase (*ASA1*). It also reduced expression of auxin efflux carrier (*AEC*) which enhance accumulation of auxin in roots. (c) VOCs exposure reduced the growth and virulence of bacterial pathogens via downregulation of pathogenicity responsible genes such as *phcA* and *rpfC*, genes responsible to secretory systems type III (*T3SS*) and IV (*T4SS*), quorum sensing *N*-acetyl homoserine lactone (AHL) biosynthesis genes (*phz1, csal*) and motility genes (*motA, motB*). (d) Bacterial VOCs exposure to pathogenic fungi downregulate the genes responsible for pathogenicity (*NPP1, NLP*), ergosterol biosynthesis (*ERG, ARE2*), spore formation (*velC, wetA*), cell membrane biosynthesis (*OLE1, POT12*) and toxin biosynthesis (*ALB1*). (e) VOCs exposed plants developed systemic acquired resistance (SAR), induced systemic resistance (ISR), ethylene biosynthesis and production of antioxidant enzymes in plants. Up and down blue arrows, represent upregulation and downregulation of responsive genes respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

acted as strong fumigant. The 2-nonanone, (Z)-hexen-1-ol acetate, dimethyl disulfide and 2-octanone significantly inhibited nematode egg hatching at concentrations 50–200 mg/L whereas 2-undecanone strongly inhibited the egg hatching at concentration of 40 mg/L (Zhai et al., 2018). *Pseudomonas koreensis* produced pyrazine (3-methoxy-2,5-dimethylpyrazine) which showed highest nematicidal activity against *Caenorhabditis elegans* and *M. incognita* (Wolfgang et al., 2019). In other study, 1-undecene (produced by *Comamonas sediminis*, *Pseudomonas monteilii*, and *Pseudomonas soli)* and dimethyl disulfide (by *P. monteilii)* showed nematicidal activity against both *C. elegans* and *M. incognita* (Wolfgang et al., 2019). *Pseudomonas chlororaphis* and *Serratia proteamaculans* produced 2-nonanone, 2-undecanone and dimethyl disulfide that killed *C. elegans* at 25 μM each after 3 days exposure. 1-undecene also produced by these bacteria showed inhibitory effect at 25 μM while it killed nematodes at 100 μM concentration within 3 days (Popova et al., 2014). VOCs (acetophenone, *S*-methyl thiobutyrate, dimethyl disulfide, ethyl 3,3-dimethylacrylate, nonan-2-one, 1-methoxy-4-methylbenzene, and butyl isovalerate), produced by *Pseudochrobactrum saccharolyticum, Wautersiella falsenii, Proteus hauseri, Arthrobacter nicotianae,* and *Achromobacter xylosoxidans* exhibited nematicidal activity against *C. elegans* and *M. incognita* (Xu et al., 2015). Among these VOCs, *S*-methyl thiobutyrate showed a stronger nematicidal activity

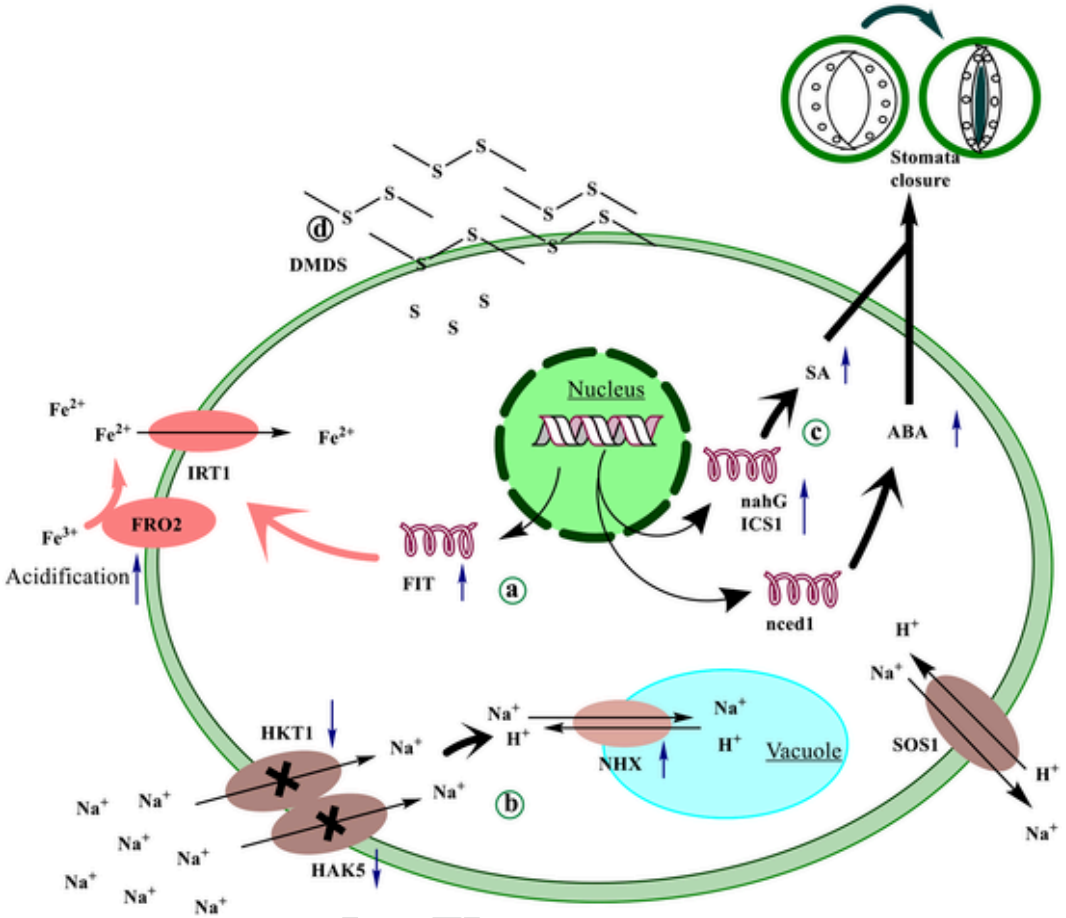


Fig. 3. Mechanism of action of bacterial VOCs in alleviating abiotic stress in plants. (a) Bacterial VOCs induce rhizospheric acidification and upregulation of transcription factor *FIT* to modulate expression of ferric reductase (*FRO2*) and iron transporter (*IRT1*) for iron sequestration. *FRO2* converts Fe^{3+} to Fe^{2+}, which is further transported into the cell by iron transporter *IRT1*. (b) Downregulation of high-affinity K^+ transporter (*HKT1* and *HAK5*) in roots, to maintain Na^+/K^+ homeostasis for salt tolerance. Excess Na^+ is stored inside the vacuole via sodium proton exchanger *NHX*, or removed from the cell via antiporter *SOS1*. (c) Induced expression of genes responsible for biosynthesis of ABA (*nced1*), SA (*ICS1*) and salicylate hydroxylase (*nahG*). SA and ABA stimulate stomatal closure during pathogen attack and prevent entry. (d) Direct diffusion of dimethyl disulfide (DMDS) into the cells through the cell membrane, providing sulfur to the plant. Up and down arrows represent up-regulation and downregulation, respectively.

(100% at 0.27 mM) than commercial insecticide dimethyl disulfide (26–37% at 0.45 mM) after 12 h exposure (Xu et al., 2015). Volatiles produced by *Bacillus* sp., *Paenibacillus* sp. *and Xanthomonas* sp. are reported as lethal to rice root-knot nematode (*Meloidogyne graminicola*) and significantly reduce the infection of rice crop both in vitro and *in planta* under dual-chamber pot experiments (Bui et al., 2020). Further, the gall formation and J2 infection were reduced up to 60% during *in planta* experiments (Bui et al., 2020). Many VOCs produced from different genera of bacteria, have exhibited strong nematicidal activity The exposure of VOCs has lethal effect on nematodes growth by altering pharyngeal and epithelial tissues, inhibiting egg hatching, chemoattractant to trap nematodes and repellent. A concentration dependent effect was observed in above studies for contact nematicidal activity. The effective concentration of VOCs against tested nematodes are represented in Table 3.

2.4. Microbial VOCs interactions with insects

Role of bacterial VOCs has been investigated in mediating the olfactory responses in insects. Bacterial emitted VOCs may act as attractant or repellent for insects, promoting unusual behavior and disturbing physiological functions of insects (Davis et al., 2013; Sidorova et al., 2021; Song and Ryu, 2013). Therefore, microbial VOCs may help in reducing insect infestation. In a study by Song and Ryu (2013), VOCs 3-pentanol and 2-butanone induced resistance against sucking aphid *Myzus persicae* in cucumber under field conditions. Soil of cucumber plants were drenched with 1 mM of 3-pentanol and 0.1 μM of 2-butanone, that significantly reduced aphids infestation up to 100 folds, by controlling the development of nymphs and adults (Song and Ryu, 2013). Additionally, 3-pentanol and 2-butanone induced expression (2.5 folds) of jasmonic acid related defense gene *CsLOX1* in plants at concentration of 1 mM and 0.1 μM while these genes were downregulated at concentrations of 1 μM and 10 nM respectively (Song and Ryu, 2013). Chemosensory systems of insects are very receptive to VOCs. A study by Sidorova et al. (2021) demonstrated the action of VOCs (terpenes and ketones 2-octanone and 2-pentanone) on the fruit fly *Drosophila melanogaster*. Out of different ketones, alcohols and terpenes tested, 10 μM 2-octanone killed all the adults of *D. melanogaster* after 14 days of incubation. However, larvae and pupae were killed at 10 and 15 μM concentration after incubation of 9 to 14 days (Sidorova et al., 2021). At higher concentration (25 and 50 μM) all flies, larvae and pupae were dead within one day of incubation. Similarly, limonene showed strong effect at concentration of 50 to 400 μM leading to 100% mortality of flies, larvae and their pupae within a day (Sidorova et al., 2021). In another study, Reddy et al. (2014) studied endosymbionts belonging to genera *Bacillus, Enterobacter, Klebsiella* and *Stenotrophomonas* isolated from midgut of adult flies of *Bactrocera zonata* and used their filtrate as attractants against the fruit fly *B. zonata*. Among these, *E.*

cloacae and *K. pneumoniae* attracted maximum flies in olfactometer cage over other bacteria across all age groups of flies. The volatiles emitted by these bacteria can prove to be a good candidate for developing insect traps (Reddy et al., 2014). The Mexican fruit flies were attracted towards VOCs (2,5-dimethylpyrazine, 3-methylbutanol, 2-phenylethanol, 3-hydroxybutanone and trimethylpyrazine) produced by *Enterobacter agglomerans* (Robacker and Lauzon, 2002). It was also noticed that the bacterial strain, having uricase activity, strongly attracted the fruit fly as compared to uricase negative (Robacker and Lauzon, 2002). VOCs emitted by *P. chlororaphis* and *Serratia proteamaculans* showed killing effect against diverse genera of pathogens, pests and insects. 2-nonanone, 2-heptanone and dimethyl disulfide reduced viability of *D. melanogaster* at concentration of 5–10 μM (Popova et al., 2014). It might be due to their growth inhibitory effect on other organisms as reported in several studies as given in Table 4.

2.5. Bacterial VOCs affects the growth of protists

Protists play an important role in soil microbiota interactions, involved in shaping of microbial community in soil. Nevertheless, there is a limited information on mechanism involved in interaction of protists with bacterial VOCs in the soil environment. Bohm and coworkers (Bohm, 2017a) reported that bacterial volatiles are directly involved in bacteria-protists interactions. Bacterial volatiles act as chemoattractant as well as repellent for protozoan in direct trophic interactions (Schulz-Bohm et al., 2017a). For example, volatiles produced by *Dyella* reduced the growth of *Vermamoeba* and *Saccamoeba*, while VOCs produced by *Collimonas* stimulated the growth of *Vermamoeba* and *Tetramitus* (Schulz-Bohm et al., 2017a). The concentration of VOCs derived from *Burkholderia* and *Paenibacillus* played important role in affecting protozoan growth. Both of these bacteria reduced the growth of *Vermamoeba* and *Saccamoeba*, while populations of these protozoan increased when they directly preyed on *Burkholderia* and *Paenibacillus* (Schulz-Bohm et al., 2017a). Moreover, VOCs produced by *Pseudomonas* stimulated the growth of *Tetramitus* while these VOCs inhibited *Tetramitus* in direct tropic interaction (Schulz-Bohm et al., 2017a).Volatiles produced by *B. subtilis, P. fluorescens, Serratia odorifera* and *Xanthomonas campestris* negatively affected the growth of *Acanthamoeba castellanii* and *Paramecium caudatum* in partition plate assay. VOCs inhibited *A. castellanii* (60% - 95%) and *P. caudatum* (100%) growth after 4 days of co-inoculation. However, the lethal effect was directly correlated with the population density in the case of *A. castellanii* only (Kai et al., 2009).

2.6. Influence of bacterial VOCs on plant growth and development

A few studies have reported the stimulation of plant growth and health by bacterial VOCs (Table 5). VOCs produced by *E. cloacae, B. subtilis* and *B. pumilus* were shown to mediate growth promotion of *Brachypodium distachyon. B. subtilis*-derived VOCs were the most prominent, with significant enhancement of total biomass (81%), including adventitious root length (Delaplace et al., 2015). VOCs produced by these bacterial strains changed the root architecture by enhancing the development of adventitious and primary roots, leading to increase in plant biomass (Delaplace et al., 2015).

A *P. fluorescens* (Pf. SS101)-produced mixture of VOCs was shown to enhance tobacco plant growth (up to 9.5-fold) under in-vitro and in-vivo conditions (Park et al., 2015). The individual VOCs produced by this strain also enhanced plant growth 3-fold (13-tetradecadien-1-ol) and 2 fold (2-butanone and 2-methyl-n-1-tridecene) (Park et al., 2015). This study demonstrates the interaction of bacterial VOCs with plants and their direct effect on plant growth promotion under in vitro and *in planta* conditions (Park et al., 2015). Another study showed that *P. fluorescens* VOCs stimulated *Medicago truncatula* growth and significantly increased plant biomass and chlorophyll content in the leaves (Hernández-León et al., 2015). Similarly, another study, proved that *P. fluorescens* have significant difference in VOC profiles of wild and mutant *GacS* strain. Wild-type and mutant strains of *P. fluorescens* enhanced plant biomass and induced systemic resistance in *A. thaliana* (Cheng et al., 2016). However, a contradictory effect was observed in tobacco: while the wild-type strain inhibited tobacco plant growth, the mutant strain enhanced root biomass and lateral root formation. These findings suggest that these *P. fluorescens* VOCs affect plants in a species specific manner (Cheng et al., 2016).

B. amyloliquefaciens-produced VOCs significantly increased shoot biomass and enhanced plant growth in *Arabidopsis* (Asari et al., 2016). The commonly described plant growth promoters 2,3-butanedione and acetoin were detected through headspace analysis of a VOC mixture from this *B. amyloliquefaciens*. The effect of these VOCs on plant growth varied according the growth medium (LB, M9A and TSA) used for their cultivation (Asari et al., 2016). Surprisingly, bacterial VOCs exert leaves chlorosis and cell death when grown on LB and M9A media. A distant effect of bacterial VOCs was also observed when it was grown closer to the plant, chlorosis was observed in the plant (Asari et al., 2016). In a different study, the role of VOCs emitted by a *Bacillus* sp. in growth enhancement of *Lactuca sativa* was described (Fincheira et al., 2017). Exposure to 2-nonanone (50 ppm) and 2-undecanone (0.05 ppm), both detected in this *Bacillus* species' VOCs, increased lateral root length under controlled conditions. A concentration-dependent improvement in biomass and shoot length was also described (Fincheira et al., 2017).

A study by (Hernandez-Calderon et al., 2018) reported differential effect of VOCs produced by plant-beneficial strains *Bacillus methylotrophicus, Arthrobacter agilis* and the plant pathogen *Pseudomonas aeruginosa* on the growth of *Sorghum bicolor*. The plants changed the pattern of their metabolites, via elicitation of nutritional and defensive traits, in response to VOCs produced by the plant-beneficial and plant-pathogenic bacteria. The plants increased their biomass and chlorophyll content as a result of exposure to the VOCs produced by these strains (Hernandez-Calderon et al., 2018). Additionally, VOCs induced the accumulation of nutrients in root exudates through regulation of iron transporter genes. The exudates profile was distinct with respect to their chemical composition and their concentration, when plants were exposed to VOCs of different bacterium (Hernandez-Calderon et al., 2018).

VOCs produced by an endophytic *Microbacterium* sp. significantly increased shoot and root biomass of *Arabidopsis*, lettuce and tomato (Cordovez et al., 2017). Sulfur-containing compounds were abundant in the mixture of volatiles produced by this strain. A synthetic form of dimethyl trisulfide compounds, as detected in that mixture of VOCs, enhanced plant growth of *Arabidopsis* (Cordovez et al., 2017). Notably, the VOCs effect was tissue specific, as exposure of the root induced plant growth, while no effect noticed when shoot was exposure. In addition, the VOC mixture of this bacterium modulated nitrogen- and sulfur-metabolism pathways by upregulating genes involved in the assimilation and transport of nitrogen and sulfate (Cordovez et al., 2017).

Direct exposure to VOCs produced by *Paraburkholderia phytofirmans* enhanced the growth of *A. thaliana*, and exposure to specific VOCs from this bacterium (2-undecanone, hexanol, 3-methylbutanol and dimethyl disulfide) increased chlorophyll content, primary root length, leaf rosette diameter and plant fresh weight (Ledger et al., 2016). It was suggested that this VOCs effect on plant growth might be due to stimulation of phytohormones.

A study by Jiang et al. (2019) showed that VOCs emitted from a *Bacillus* sp. promoted growth in seedlings of *Arabidopsis* through the production of auxin and strigolactone. Exposure to these VOCs upregulated the genes involved in phytohormone biosynthesis and metabolism in the plant. Among all of the tested mixtures of this bacterium's VOCs, exposure to pure tetrahydrofuran-3-ol (1 μg/μL), 2-heptanone (10 ng/μL) and 2-ethyl-1-hexanol (1 μg/μL) significantly enhanced the growth of *Arabidopsis* (Jiang et al., 2019). An indole compound from another

bacterial genus, *Proteus vulgaris,* increased the fresh weight of *A. thaliana* (74–80%) by acting as a signaling molecule that stimulated the interaction between cytokinin, auxin and brassinosteroid pathways (Bhattacharyya et al., 2014). VOCs produced by *Staphylococcus hominis* increased the growth of *Nicotiana benthamiana* and those produced by *E. cloacae* increased lateral root number, and fresh root and shoot weight in both *A. thaliana* and *N. benthamiana* (Camarena-Pozos et al., 2019). Exposure to ethyl isovalerate, isoamyl acetate, 3-methyl-1-butanol, benzyl alcohol, 2-phenylethyl alcohol, and 3-(methylthio)-1-propanol (produced from different *Psychrobacillus* spp., *S. hominis, E. cloacae*, *B. pumilus, Bacillus megaterium* and *Micrococcus terreus*) promoted plant growth individually, as well as in a mixture (Camarena-Pozos et al., 2019). For example, the combination of 2-phenylethyl alcohol and benzyl alcohol increased the number of lateral roots up to 5-fold, whereas the individual compounds increased it up to 3-fold. Therefore, the authors concluded that there is a combined effect of VOCs, enhancing the number and density of lateral roots in the plant.

From these described publications, it can be concluded that bacterial VOCs often have concentration dependent and plant species-specific effect on plant growth. Examples of VOCs produced by many bacteria, and their effective concentration shown to induce plant growth are depicted in Table 4. However, far fewer studies have explored the effects of the individual identified compounds; this aspect needs to be better understood so that their application can serve agricultural sustainability.

2.7. Bacterial VOCs as plant-defense elicitors

Bacterial VOCs have been reported to induce multiple defense-response pathways in various plant species. However, researchers have mainly explored their major effects under controlled/laboratory conditions (Table 5). The long-chain (C13) alkane tridecane produced by a *Paenibacillus polymyxa* strain induced the expression of pathogenesis-related (PR) genes in *A. thaliana* and elicited the defense mechanism against the pathogen *Pseudomonas syringae* (Lee et al., 2012). In another study by (Song and Ryu, 2013), demonstrated that bacterium-produced 3-pentanol and 2-butanone inhibited different species of *Pseudomonas* and induced the plant defense-related gene *LOX* in cucumber, which developed resistance to bacterial angular leaf spot pathogen *Pseudomonas syringae* pv. *lachrymans*. In addition, these compounds controlled aphids infestation under field conditions by stimulating the oxylipin pathway in cucumber, which attracts the aphid's natural enemy *Coccinella septempunctata* (Song and Ryu, 2013). The authors suggests that such compounds can be used in agriculture fields to control plant diseases and pests through induction of plant defense genes (Song and Ryu, 2013). *B. amyloliquefaciens* VOC 3-pentanol induced expression of PR genes *PR2* and *PIN2* in *Capsicum annum*. Seed priming with 3-pentanol reduced the severity of disease caused by *Xanthomonas axonopodis* pv. *vesicatoria* under field conditions by stimulating salicylic acid (SA), jasmonic acid (JA) and ethylene-signaling pathways in plants (Choi et al., 2014). In another study, the role of acetoin and 2,3-butanediol derived from a different strain of *B. amyloliquifaciens* was explored in the induction of stomatal closure in *A. thaliana* and *N. banthamiana* (Wu et al., 2018). These compounds elicited the pathways of the plant signaling hormones abscisic acid (ABA) and SA, resulting in stomatal closure and restricting pathogen entry. In addition, they stimulated plant defense through accumulation of nitric oxide and hydrogen peroxide in leaves (Wu et al., 2018). Effect of 2,3-butanediol(1 mM) exposure on plant defense gene expression induced expression of acquired systemic resistance gene 8.2 (*CaSAR8.2*), phenylalaline ammonia (*CaPAL*) and β-1,3-glucanase (*CaPR2*) (Yi et al., 2016). In *B. subtilis*, benzaldehyde, 1,2-benzisothiazol-3(2H)-one and 1,3-butadiene induced expression of SA and defense-response genes in tobacco plants. They also suppressed virulence- and growth-associated genes in the bacterial pathogen *R. solanacearum*, resulting in reduced colony size, disruption of cell morphology and changes in chemotaxis (Tahir et al., 2017a). Many *Bacillus* species have been shown to produce biologically active VOCs; however, other bacterial genera that are closely associated with plant roots have also been reported as plant-beneficial agents. Such bacterial genera are of interest for the involvement of their potentially bioactive VOCs in plant defense and plant growth promotion. For example, *P. aeruginosa* produces 3-hydroxy-5-methoxybenzene methanol (HMB), which induced systemic resistance in tomato plants. The pure HMB elicited the metabolic pathway leading to resistance against the wilt-causing fungus *Fusarium oxysporum* in tomato (Fatima and Anjum, 2017). *Arthrobacter agilis* and its VOCs differentially induced the defense mechanism in *Sorghum bicolor* (Hernandez-Calderon et al., 2018). The mixture of VOCs produced by this strain induced only *PR1* genes, whereas the bacterium itself induced both *PR1* and *COI1* defense-response genes (Hernandez-Calderon et al., 2018). Observed effects of 2,3-butanediol produced by the endophytic bacterium *Enterobacter aerogenes* included enhanced plant growth, pathogen suppression and herbivore resistance in maize. Among other actions, this volatile also led to the development of plant resistance against north corn leaf blight fungus *Setosphaeria turcica* (D'Alessandro et al., 2014).

Several studies has described a concentration dependent effect of bacterial VOCs on plant growth and defense. For example, Huang et al. (2012) observed the higher plant defense response of dimethyl disulfide at 1 mM, while no significant response was noticed at 0.1 mM. 2,3-butanediol has been reported as a strong plant defense inducer as well as growth promoter (Wu et al., 2018). It was reported that 297.5 μM was an effective concentration to induce plant defense response in a pot experiment. In another study, 0.2 μg of 2,3-butanediol was found to be effective to induce ISR when seeds were exposed to this compound (Ryu et al., 2004). Many researchers have reported both bacterial and plant species-specific, as well as concentration dependent responses in VOC induction of plant defense genes. Additionally, VOCs production may be affected by the bacterial growth conditions. It is worth mentioning that due to the different concentrations needed to affect different plants, the concentration of compounds (synthesized specific compounds or mixtures of, or naturally produced mixtures) should be carefully controlled according to the compounds, plants of target and environmental conditions when applied.

2.8. Role of bacterial VOCs in plant tolerance to abiotic stress

VOCs may help plants survive under abiotic stresses, such as nutrient deficiency, drought, and salinity. *B. amyloliquefaciens* VOCs induced salt tolerance in *A. thaliana* via induction of genes related to sodium exporters, which regulate the sodium concentration in plant cells (Zhang et al., 2008). These volatiles also enhanced iron uptake via upregulation of the iron-acquisition machinery and triggered rhizospheric acidification for better establishment of plants, resulting in an overall increase in plant growth (Zhang et al., 2009a). The iron-uptake mechanism and ferric reductase activity were regulated by *Sinorhizobium meliloti* VOCs, which helped to establish plant–microbe symbiosis. In addition, the plants exposed to VOCs showed increased biomass, chlorophyll content and rhizospheric acidification under both iron-deficient and iron-enriched conditions (Orozco-Mosqueda Mdel et al., 2013).

Sulfur is also an essential nutrient for plant growth and development. Various bacterial species produce sulfur-containing VOCs in the plant rhizosphere. For example, *Bacillus* sp. endophytes enhanced *Nicotiana attenuata* growth by exposure to sulfur-containing VOCs and which increased sulfur content in the tobacco plants (Meldau et al., 2013). Compounds such as dimethyl disulfide and dimethyl trisulfide are produced in abundance by microorganisms, and provide sulfur to plants (tobacco and maize) (Kanchiswamy et al., 2015). Therefore, bacterial VOCs may induce the assimilation of sulfur in plant cells, which is an essential element for synthesis of cysteine and methionine that are

essential amino acids for protein synthesis. These compounds may therefore be used in agriculture to compensate for sulfur deficiency in soil.

Bacterial VOCs have been studied to increase salt tolerance under high salinity conditions and mimic plant salinity stress. In a study, *P. chlororaphis* volatile 2,3-butanediol elicited SA-dependent responsive genes, inducing drought tolerance in *Arabidopsis* (Cho et al., 2008). A strain of *Pseudomonas simiae* produced VOCs, which induced systemic salt tolerance to up to 100 mM/L NaCl in soybean seedlings. Furthermore, VOC exposure increased the cellular levels of proline and glycine, which protect the soybean against osmotic stress (Vaishnav et al., 2015). In another study, *Paraburkholderia phytofirmans* was shown to produce 2-undecanone, 7-hexanol, 3-methylbutanol and dimethyl disulfide, which improved *A. thaliana* salt tolerance (to up to 200 mM NaCl and 20 mM $CaCl_2$), via enhancement of the sodium-exclusion mechanism, enabling *A. thaliana* to survive under long-term salinity conditions (Ledger et al., 2016).

3. Approaches, challenges and perspectives for employment of bacterial VOCs in agriculture under field conditions

Application and transportation of bacterial volatiles in soil are affected by physical, chemical and biological characteristics of soil and structure of VOCs. Before employing the VOCs in field conditions, it is important to determine the volatility and diffusion rate of volatiles in different soils. Diffusion of VOCs in soil depends upon their water solubility and vapor pressure. Long chain hydrocarbons, aromatics and non-polar compounds translocate quickly over long distances through air filled pockets in soil due to their low water solubility and high volatility (Ehlers et al., 2020; Tang et al., 2019).

Methodologies for direct application of VOCs in agriculture fields and greenhouses are rarely explored and need further investigations. Only a few studies have tested the effect of VOCs on plant growth promotion and diseases suppression under field conditions through soil drench method, spray and seed treatment. For example, application of 3-pentanol and 2-butanone through soil drench method in cucumber, induced resistance against bacterial pathogens and protected the plants from aphids by controlling population of nymphs. Further, it induced the emission of plant volatiles to attract natural enemies against aphids (Song and Ryu, 2013). In another study, Goelen et al. (2021) observed that mixture of styrene and benzaldehyde significantly attracted the parasitoids (*Aphidius colemani*) in Y-tube olfactometer assay. Such bacterial VOCs can be used to attract and trap parasitoids under greenhouse and field conditions.

Bacterial VOC, 3-pentanol (1 mM) has been used for seed priming to control bacterial spot disease caused by *Xanthomonas axonopodis* pv. *vesicatoria* and induced resistance in pepper seedling significantly under pot and field conditions (Choi et al., 2014; Song and Ryu, 2013). Application of dimethyl disulfide via soil drench method elicited plant defense in tobacco and corn (Huang et al., 2012). However, ISR in plants was dependent on concentration of dimethyl disulfide produced by *Bacillus cereus* C1L. (Huang et al., 2012). The VOC, 2,3-butanediol has been observed as a plant growth promoter under in vitro conditions in many studies. However, studies on its application under field conditions are limited. In a study by Kong et al. (2018), soil drenching with 2,3-butanediol (1 mM) significantly induced systemic resistance against cucumber mosaic virus (CMV) and tobacco mosaic virus (TMV) in pepper under green house and field trials. Though soil drenching is user friendly but it requires subsequent field trials to study the stability and efficacy of VOCs under different environmental conditions.

These studies highlight the potential application of bacterial VOCs to control plant pathogens under field conditions. Mixture of bacterial VOCs has significantly reduced the growth of plant pathogens and induced systemic resistance in plants under controlled conditions (D'Alessandro et al., 2014; Fincheira et al., 2017; Heenan-Daly et al., 2021). Most of the studies have employed individual and mixture of synthetic VOCs to explore their efficacy for controlling pests and plant growth promotion (Chen et al., 2021; Fincheira et al., 2017; Heenan-Daly et al., 2021; Montes-Osuna et al., 2022; Sidorova et al., 2021). The effect of naturally produced bacterial VOCs under field conditions is relatively less prominent as compared to mixture of pure compounds. Because the effect of VOCs is concentration dependent, therefore, it requires a particular dose to induce the desired biological activity including plant growth promotion and induced systematic resistance. Hence, it is important to concentrate naturally produced bacterial VOCs and develop suitable formulations for their use in agriculture fields. Site-specific controlled release formulation is a suitable option for application of VOCs in agriculture. To overcome the limitation of bacterial volatiles in field applications, VOCs must be trapped or encapsulated with engineered eco-friendly material such as chitosan, alginate, gellan and gelatin or natural products like oil for their controlled release (Sharifi and Ryu, 2020). Porous eco-friendly materials like biochar, activated charcoal can also be used as suitable platform for sustained release of VOCs during agricultural application via spray drying directly on the plant surface or soil drench with trapped carbonaceous material. Despite all challenges in field conditions, VOCs can be effectively utilized after trials under protected cultivation of commercial organic farming as the required concentration of VOCs can be maintained in such enclosed environments. The potential VOCs can also be used under companion cropping system by enhancing the resistance of susceptible cultivars. However, it requires in-depth investigations for real time analysis of VOCs produced under natural conditions during plant-microorganisms interaction.

4. Detailed mechanisms of action of bacterial VOCs

The collective impact of bacterial VOCs on plant growth and development and pathogen suppression has been studied by several researchers (Table 4). Most studies were carried out on model plants, such as *A. thaliana, N. benthamiana, Solanum lycopersicum* and *Glycine* max. Studies have investigated the role of bacterial VOCs in phytohormones signaling pathways involved in plant growth and developmental. Zhang and co-workers described the impact of *B. subtilis* GB03 VOCs on gene expression in *Arabidopsis* plants under controlled conditions (Zhang et al., 2008; Zhang et al., 2007; Zhang et al., 2009a; Zhang et al., 2009b). VOCs produced by this *Bacillus* strain upregulated the expression of three nitrilases genes (*NIT1, NIT2, NIT3*), tryptophan synthase (*TSB2*) and anthranilate synthase (*ASA1*) that are involved in biosynthesis of indole acetic acid. Additionally, VOCs exposure downregulated the auxin efflux carrier gene and enhanced accumulation of flavonoids (negative regulators of auxin transport), increasing auxin concentration in roots (Zhang et al., 2007). High auxin level in roots favors lateral root formation and hence plant growth promotion. VOCs exposure also induced the expression of cell elongation gene expansin 5 (*EXP5)* and pectin related genes (pectin methylesterase, pectinase and pectin lyases) associated with cell wall loosening, that help in cell expansion in shoots and aerial parts (Zhang et al., 2007). Similarly, Hao et al. (2016) described the role of *B. amyloliquefaciens* FZB42 derived VOCs that downregulated the *AEC* gene in *Arabidopsis* roots, at seedling stage. VOCs exposure also downregulated the genes involved in flavonoids biosynthesis in leaves, while upregulated it in the roots, that helps to regulate the auxin level in different plant tissues (Hao et al., 2016). This leads to plant growth promotion via increasing auxin level in roots. However, no such effect was observed at maturity stage suggesting that VOCs response differ according the developmental stages in plant (Hao et al., 2016). Other *Bacillus* sp. JC03 derived VOCs upregulated the expression of auxin biosynthesis gene (*ARF1*) and downregulated the strigolactone biosynthesis gene (*CCD7*) in *Arabidopsis* (Jiang et al., 2019). In another study, role of *Bacillus* sp. VOCs has been observed to induce the expression of photosynthesis-related genes encod-

ing chlorophyll-binding proteins and photosynthate transport genes in tobacco (Kim et al., 2015).

In addition to the role of bacterial VOCs in plant development through regulation of phytohormones several studies described an additional function in induction of defense related genes. For example, *Bacillus* sp. derived acetoin and 2,3-butanediol regulated stomatal closure during pathogen attack in *A. thaliana* and *N. benthamiana* via induced expression of genes *nced1*, *ICS1* and *nahG* (Wu et al., 2018). These genes are responsive to biosynthesis of salicylic acid, abscisic acid and salicylate hydroxylase, respectively. 3-Hydroxy-5-methoxy benzenemethanol derived from *P. aeruginosa* elicited defense-response genes in tomato via upregulating phenylpropanoid and salicylic acid metabolic pathways (Fatima and Anjum, 2017) . Additionally, it upregulated the genes related to synthesis of tryptophan and the metabolites 4-hydroxybenzene and cinnamate in plants (Fatima and Anjum, 2017). Bacterial VOCs were also shown to induce the plant signaling hormone ethylene that regulates plant development and stress response. *Bacillus* GB03 VOCs were shown to regulate genes responsible for ethylene biosynthesis such as *SAM-2* (S-adenosylmethionine synthetase 2), *ACS4* (ACC synthase 4), *ACS12* (ACC synthase 12) and *ACO2* (ACC oxidase) and ethylene-signaling genes *ERF1* (Ethylene response factor 1), *GST2* (Glutathione S-transferase 2) and *CHIB* (Basic chitinase) in *Arabidopsis* (Kwon et al., 2010). Another study described the effect of *B. amyloliquefaciens* VOCs on upregulating ethylene biosynthesis and signaling related genes (*ACS7, AC03, ERS1* and *ERF2*) in *Arabidopsis* leaves (Hao et al., 2016).

Plants may sense the VOCs produced by both beneficial and harmful bacteria. The effect of VOCs produced by pathogenic bacteria (*Erwinia amylovora*, or *P. syringae)* has been reported (Cellini et al., 2018). VOCs produced by these bacterial strains elicited plant defense and growth in different plant tissues. For example, 2,3-butanediol produced by these bacteria acts in plant defense and plant growth promotion activity via induction of salicylic acid and signal transduction in apple plants (Cellini et al., 2018). Benzaldehyde 1,2-benzisothiazol-3(2H)-one and 1,3-butadiene, produced by *B. amyloliquefaciens* and *Bacillus atrophaeus*, developed wilt resistance and defense in tobacco, and directly reduced the pathogenicity of *R. solanacearum* (Tahir et al., 2017a). The activity of these VOCs in the plant was shown to be through elicitation of SA pathway via upregulation of defense-response genes *EDS1* and *NPR1*. The direct effect on *R. solanacearum* was through modulation of transcription levels of several pathogenicity-related genes (virulence regulator *phcA*, as well as *T3SS* and *T4SS* for type III and IV secretion systems, respectively) and genes involved in chemotaxis (Tahir et al., 2017a). The VOCs of *Bacillus* D13 were shown to affect motility and pathogenicity of *Xantomonas oryzae* via reduced expression of *motA*, *motB* and *rpfC* genes (Xie et al., 2018). Dimethyl disulfide produced by *P. fluorescens* inhibited bacterial quorum sensing through suppression of transcription of N-actylhomoserine lactone (AHL) synthase genes *phzl* and *csal* (Chernin et al., 2011). In the fungal pathogen *Thielaviopsis ethacetica, Pseudomonas* spp. VOCs reduced the expression of pathogenicity-related (PR) necrosis-inducing protein NPP1, and NLP proteins controlling the regulation of cytolytic toxin, which can cause cell death in plants (Gong et al., 2022). In addition, expression of DNA damage-response genes in this fungus suggested the possibility of DNA damage following exposure to these VOCs (Freitas et al., 2022). A study by (Gong et al., 2022), examined the mechanism of *Streptomyces setonii* VOCs action on *Ceratocystis fimbriata* was examined through transcriptome analysis. Exposure to VOCs produced by this bacterium downregulated the genes related to ribosomal synthesis (*MX1*), ergosterol biosynthesis (*ERG4, ERG5,* and *ARE2*), spore development (*VELC, wetA*), cell membrane biosynthesis (*OLE1* and *POT12*), cell wall biosynthesis (*azaE*, *OCH1* and *GUF1*) hydrolases and toxin synthesis (*ALB1*) and mitochondrial function (cytochrome *c*1 heme lyase, ATP-dependent RNA helicase) in *C. fimbriata* (Gong et al., 2022). The mechanisms of action of bacterial VOCs to induce plant resistance and down-regulation of growth and pathogenicity responsive genes in microorganisms is depicted in Fig. 2.

Bacterial VOCs were shown to have the ability to control nematodes growth but the mechanism of action is scanty. In a study by Ayaz et al. (2021), tomato protection against nematodes was reported in the presence of *Bacillus* GBSC56 VOCs. The protection mechanism involved the enhanced production of antioxidant enzymes (*SOD, CAT, POD* and *APX*) and defense related genes (such as *PR1, PR5*, and *SlLOX1*) responsible for induced systemic resistance (ISR) in tomato (Ayaz et al., 2021). Expression of plant growth promotion genes (*SlCKX1, SlIAA1*, and *Exp18*) were also upregulated (Ayaz et al., 2021). In another study, *B. amyloliquefaciens* VOCs altered the expression of several genes related to metabolic pathways that improved defense response against nematodes in *Arabidopsis* (Hao et al., 2016).

A few bacterial VOCs has also been reported to inhibit plant growth in some cases. For example, VOCs derived from *Serratia plymuthica* and *Stenotrophomonas maltophilia* reduced *Arabidopsis* growth and downregulated the transcription of regulatory genes involved in mitochondrial electron transport chain, photosystem, plant stress tolerance and defense (Wenke et al., 2012). VOCs downregulated W-motif proteins and *WRKY* gene associated transcription factors, resulting in altered plant phenotypic pattern through chlorosis and decreased growth of cotyledons and primary roots. Therefore, VOCs play an important role in plant defense regulatory pathways (Wenke et al., 2012).

Bacterial VOCs also regulate the expression of genes to assist plants under abiotic stress conditions. For example, *B. subtilis* VOCs was shown to induce salt tolerance in plants via downregulated expression of sodium-transporter gene *HKT1* (regulators of sodium ions entry into plant root cells) (Zhang et al., 2008). An additional mechanism for salt tolerance in plant through VOCs exposure was described by Bhattacharya and coworkers (Bhattacharyya et al., 2015). *Alcaligenes faecalis* derived VOCs upregulated sodium/hydrogen exchanger 1 transporters (*NHX1*) (which translocate excess sodium ions into the vacuole). In addition, these VOCs upregulated the expression of the antiporter *SOS1* (salt overly sensitive 1) that removes excess salts from the plant cells (Bhattacharyya et al., 2015; Vaishnav et al., 2015). VOCs exposure also upregulates *gai1* expression, increasing the content of the osmoprotectant proline in *Arabidopsis.* Similarly, *Pseudomonas simiae* VOCs exposure was also shown to induce salt tolerance in *Glycine* max through upregulation of transporters genes and increased the proline and glycine content (Vaishnav et al., 2015).

Iron is a limiting growth factor for the plants. Role of VOCs has also been reported to regulate iron transporters under iron limited conditions: *B. subtilis* GB03 VOCs induced expression of iron-transcription factor genes to stimulate expression of iron-transporter genes (ferric reductase *FRO2* and the iron transporter *IRT1*) (Zhang et al., 2009a). *B. subtilis* GB03 VOCs enhanced plant iron acquisition mechanism by inducing iron homeostasis transcription factor 1 (*FIT1*), that regulates gene expression of *FRO2* (3 folds) and *IRT1* (20 folds). *FRO2* is a ferric reductase, which reduces the ferric iron (Fe^{3+}) to ferrous (Fe^{2+}) and *IRT1* is a high affinity Fe^{2+} transporter to shuttle the iron (Fe^{2+}) inside the plant cell. VOCs exposure also increased the rhizosphere acidification by inducing root proton release capacity upto 3 folds that leads to solubility of iron in soil. Overall, VOCs exposed *Arabidopsis* plants exhibited higher accumulation of iron, more green in colour, increased chlorophyll content (84%) and enhanced photosynthetic efficiency (Zhang et al., 2009b). Similarly, in another study, VOCs produced by *B. amyloliquefaciens* enhanced the iron acquisition in *Arabidopsis* via upregulating the expression of *FIT1*, *FRO2* and *IRT1* gene up to 6 folds under iron limiting conditions in soil (Wang et al., 2017). Additionally, VOCs exposure increased chlorophyll content upto 28% and significantly enhanced photosynthetic rate in *Arabidopsis* (Wang et al., 2017). Role of VOCs produced by bacterial species (*Rahnella aquatilis* and *Sinorhizobium meliloti)* has been introduced in mobilization and absorption of iron limited conditions via induced expression of genes H^+ AT-

Pase (*AHA2*) upto 25 folds, *FRO2* (1.8 fold) and *IRT1* (1.3 fold) in *A. thaliana* (Kong et al., 2021) and *Medicago truncatula* (Orozco-Mosqueda Mdel et al., 2013). These genes play a major role in rhizospheric acidification via release of protons (Kong et al., 2021; Orozco-Mosqueda Mdel et al., 2013).

These described studies have highlighted the role of bacterial VOCs in regulation of plant defense-related genes and other metabolic pathways involved in the induction of plant growth and development, and alleviating abiotic stress. Inhibitory and killing effects of bacterial VOCs on plant pathogens have also been studied by different research groups. Still, the detailed mechanisms of action of bacterial VOCs on plants and their pathogens still needs further exploration, especially in agriculture crops and related pathogens. The mechanisms of action of bacterial VOCs associated with biotic and abiotic stress tolerance to plant are schematically presented in Fig. 3.

5. Conclusion and future perspectives

Bacteria emit an enormous array of VOCs, some of which directly or indirectly affect other organisms in their vicinity. This review focuses on the far less studied modes of action and effects of bacterial VOCs on neighboring bacteria, fungi, nematodes and plants. This includes fungicidal and bactericidal effects, as well as modulation of metabolic pathways, which enhance plant growth and induce systemic resistance to pathogens and abiotic stresses. Bacterial VOCs demonstrate a strong biological effect, even at very low concentrations (nanomolar to micromolar) and their diffusibility at ambient temperature, simple structure and absence of toxic residues make some of these VOCs attractive for use in agriculture. In addition, VOCs can be used to control spoilage of postharvest crops due to their dispersal in the environment and long-distance effects. The application of such bacterial VOCs may be economically beneficial to farmers and thus offer a sustainable alternative to toxic agrochemicals.

However, identification and quantification of VOCs in a mixture are challenging. Identification of the individual bioactive molecules present in VOCs mixture is very tedious, mainly because the bacteria usually release a complex set of VOCs, some of which have synergistic effects. The mechanism of interaction among microbial communities, insects, pests, nematodes and plants requires an in-depth investigation to explore the potential application of these VOCs as a sustainable solution for emerging agricultural challenges (e.g., plant disease management, food spoilage, pathogen control, crop productivity, abiotic stress management). The major limitations to the use of bacterial VOCs in the agricultural sector under field and greenhouse conditions include their rapid dispersal and high volatility, even at ambient temperature, and low solubility in water. Future studies might target the fate and structural aspects of bacterial VOCs, towards their formulation and controlled release, better efficiency and sustainable use. Furthermore, environmental parameters and management practices that influence VOC effectiveness and fate must also be explored.

Credit author statement

Annu Rani: Data curation, analysis, and writing the original draft under supervision AR **Anuj Rana**: Conceptualization, designing, data analyzing, visualization, software, writing the original draft and editing. **Rahul Kumar**: Conceptualization, visualization, writing, reviewing and editing **Arvind Kumar:** Writing, reviewing and editing **Madhvi Chahar:** Writing, reviewing and editing **Surender Singh:** Writing, reviewing and editing **Lata Nain:** Designing, visualization, reviewing and editing **Krishan Pal Singh:** Conceptualization, reviewing and editing **Dror Minz**: Conceptualization, Supervision, Funding acquisition, data authentication, writing, reviewing and editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationship that could have appeared to influence the work reported in this paper.

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