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Review

Effects of discrete bioactive microbial volatiles on plants and fungi

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ABSTRACT

Plants live in association with microorganisms, which are well known as a rich source of specialized metabolites, including volatile compounds. The increasing numbers of described plant microbiomes allowed manifold phylogenetic tree deductions, but less emphasis is presently put on the metabolic capacities of plant-associated microorganisms. With the focus on small volatile metabolites we summarize (i) the knowledge of prominent bacteria of plant microbiomes; (ii) present the state-of-the-art of individual (discrete) microbial organic and inorganic volatiles affecting plants and fungi; and (iii) emphasize the high potential of microbial volatiles in mediating microbe–plant interactions. So far, 94 discrete organic and five inorganic compounds were investigated, most of them trigger alterations of the growth, physiology and defence responses in plants and fungi but little is known about the specific molecular and cellular targets. Large overlaps in emission profiles of the emitters and receivers render specific volatile organic compound-mediated interactions highly unlikely for most bioactive mVOCs identified so far.

Key-words: plant-associated microorganisms; plant-microbe interaction; ammonia; bioactive compounds; carbon dioxide; hydrogen cyanide; hydrogen sulfide; microbial volatile organic compounds; nitrogen oxide; secondary metabolism; VOCs.

INTRODUCTION

Plants are well-known producers of scents, because flowers, leaves and also roots release a wealth of volatile organic compounds (VOCs). It is estimated that collectively plants produce close to 30 000 different VOCs using as much as 20% of their fixed CO_2 (Baldwin 2010). The prominent feature of volatiles is their potential to act in short as well as long distances, which was well documented for plant–insect and plant–plant bi-trophic and tri-trophic interactions belowground and aboveground (Rasmann *et al.* 2005; Baldwin *et al.* 2006; Heil and Silva Bueno 2007; Dicke and Baldwin 2010; Insam and Seewald 2010, summarized in Delory *et al.* 2016). Although many volatiles were assigned to be synthesized and released by plants, one has to take into account that natural habitats are not sterile but are more or less colonized by microorganisms. The application of new technologies such as fast sequencing methods and culture independent species determinations highlighted the incredible complexity of the microbial populations and communities. To underline this ubiquitous appearance in most ecosystems, for example, there are more than 10^{11} bacterial cells and 5×10^6 bacterial species in 1 g soil, or 10^7 bacterial cells per square cm^2 leaf area (summarized in Farré-Armengol *et al.* 2016). Given the estimated 10^9 km^2 of the phyllosphere worldwide, the dominance of microorganisms on plants becomes obvious. Subsequently, the wealth of microbial metabolic activities is also witnessed. Particularly, rich in structural complexity and diversity are compounds of specialized metabolism (antibiotics, toxins, siderophores, etc.), which have the potential to influence the neighbouring organisms and the community(ies). In the past decade, it was also documented that beside diffusible compounds, microorganisms are an outstanding source of VOCs, characterized by their high vapour pressure, low boiling point and a molecular mass of below 300 Da (summarized in Schulz and Dickschat 2007; Effmert *et al.* 2012; Lemfack *et al.* 2014; Dickschat 2017).

Compared with ~2500 known flower scent compounds (Knudsen *et al.* 2006; http://www2.botany.gu.se/SCENTbase.html), already ~1300 microbial VOCs (mVOCs) from only ~600 microorganisms are presently registered in the mVOC database (Lemfack *et al.* 2014; http://bioinformatics.charite.de/mvoc/). Overall, relatively little thought has been given to the microbial sources of odour, and limited information of biological/ecological roles and mode of actions of these compounds are available, despite the ubiquitous and often massive appearance of microorganisms. It is commonplace that microorganisms, bacteria and fungi, are responsible for the production of aromas of foodstuff, for example, cheese, wine, beer and yoghurt, which have been selected for human preferences. Attention was given to mVOCs as indicators for contaminations and pollutants with potential consequences for human health (Korpi *et al.* 2009). Beside diverse medical applications of mVOCs new approaches in agriculture and biotechnology are also envisioned (summarized in Piechulla and Lemfack 2016). Altogether, studies on fungal and bacterial VOCs lag behind the knowledge on plant-derived VOCs. This shortcoming is particularly pronounced when considering that 10^{16} microbial species are suspected to exist on Earth (Farre-Armengol *et al.* 2016). Consequently, responses and reactions to mVOCs in receiver organisms are more frequent than previously recognized or estimated. Therefore special impetus is needed to explore the effects of mVOCs in receiver organisms.

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Urgent and interesting questions are as follows: What are the roles of mVOCs in habitats/ecosystems? Which discrete microbial volatiles are bioactive? Which targets are affected in the receiver organism? What are the reactions of the receiver organisms to these volatiles? Can the responses in the receiver be generalized, or are the signals receiver-specific? Do generalized mVOC signatures/fingerprints exist? Furthermore, little is known about the evolution of mVOC-dependent microbe-receiver interactions.

The potential of mVOCs was indicated in the past decade. In various experimental co-cultivation set ups, the effects of mVOCs on/in organisms were explored, such as alterations in plants (Chung *et al.* 2015; Kai *et al.* 2016), insects (Davis *et al.* 2013), soil fauna, bacteria and fungi (De Vrieze *et al.* 2015; Schmidt *et al.* 2015; Werner *et al.* 2016). Regarding plants, observations and results obtained from various experiments, range from, for example, strong growth inhibitions to significant growth promotions. Such heterogeneous results may occur because interactions of microbes with receiver organisms are complex; they can be disparate, diffuse and seemingly independent. Moreover, mVOCs act as multitrophic signals in ecologically complex systems, which are not well studied or defined to date. It is also critical whether the plants perceive cues from a discrete (individual, single) or a mixture of mVOCs. To date, most effects mediated by mVOCs were obtained from co-cultivation experiments, where plants were exposed to the complex mixtures of inorganic and organic volatiles emitted by the microbes. It also has to be taken into account that the compositions of the bacterial blends depend very much on the substrate availability and metabolic activities of the microorganisms (Fiddaman and Rossall 1994). To substantiate and provide functional evidence for the mVOC action potential, it is necessary to identify discrete bioactive compounds and test them individually or in defined mixtures. As a first step, we analysed plant microbiomes to identify prominent plant-associated bacteria, which might be relevant in volatile-mediated microbe–plant interactions. Secondly, the actual knowledge of discrete bioactive mVOCs is summarized and presented here. This systematic exploration gives an overview of respective compounds/compound classes affecting plants and fungi and summarizes the processes that are influenced, including those critical to plant health. This will offer tangible practical benefits in addressing agricultural and environmental problems. In addition, the question regarding specificity is addressed by comparing the microbial volatilomes with the plant volatilomes.

THE POTENTIAL OF PLANT MICROBIOMES

It is well accepted that plant microbiomes greatly promote or compromise plant health and productivity (Hartmann *et al.* 2008). Over the past years, studies to describe these plant microbiomes substantially increased and the use of direct sequencing of the environmental samples provided further valuable insight into the phylogenetic diversity of microbes associated with plants or presence in different micro-habitats like flowers, roots, leaves and rhizospheres (Bakker *et al.* 2013; Bulgarelli *et al.* 2013; Knief *et al.* 2012; Philippot *et al.* 2013; Turner *et al.* 2013; Knief 2014; Guttman *et al.* 2015). The analysis of the most prominent and recent studies on plant microbiomes by metagenomic sequencing indicated bacteria as the dominant taxa within the microorganisms. *Actinobacteria*, *Bacteroidetes*, *Firmicutes* and *Proteobacteria* are the most prominent phyla of bacteria associated with plants (Bai *et al.* 2015). This review summarized almost 700 bacterial genera that inhabit diverse plant micro-habitats (Fig. S1), and the 30 most listed genera are presented in Fig. 1. In plant microbiomes, the *Flavobacterium* (90.9%), *Pseudomonas* (90.9%), *Rhizobium* (90.9%) and *Sphingomonas* (81.8%) are most frequently found, while the presence of *Acidovorax, Bacillus, Bradyrhizobium, Cryseobacterium, Devosia, Mesorhizobium, Methylobacterium, Massilia, Microbacterium, Nocardioides, Pedobacter, Phenylobacterium, Rhodococcus, Streptomyces and Variovorax* range from 55 to 75%.

It is well established that microorganisms including plant-associated bacteria produce a wealth of small volatile compounds with the potential to act as infochemicals and to play an important role in mediating plant–microbe interactions (Kai *et al.* 2009; Wenke *et al.* 2010; Peñuelas *et al.* 2014). So far, volatilomes of 112 bacterial genera have been analysed and are consigned in mVOC database (Lemfack *et al.* 2014). From a comparison of the genera appearing in plant microbiomes and those present in mVOC database, it is summed up that the volatile emission of ~10% of the plant microbiomes were so far analysed (Fig. S1). Albeit the volatile profiles of plant-associated bacteria like *Bacillus, Burkholderia* and *Pseudomonas* that were commonly studied (Table 1), this present analysis also highlights the potential of the unknown volatilomes of plant-associated microbes. To fill this lack of knowledge and to better understand the network that governs plant–microbe interactions, much emphasis has to be put on this research field in the future.

BIOLOGICAL EFFECTS OF DISCRETE MICROBIAL ORGANIC VOLATILE COMPOUNDS ON PLANTS AND FUNGI – STATE-OF-THE-ART

Test system and compound classes

In the past decade many microbe–plant co-cultivation experiments were performed showing volatile-mediated reactions in plants (summarized in Kai *et al.* 2016). The rational for using these co-cultivations is that in nature, microorganisms appear in the same habitat as plants and subsequently volatiles released from microorganisms might affect plants under natural conditions and *vice versa*. However, the dual co-cultivations as they usually were performed have several drawbacks: (i) in nature microbial communities rather than one bacterial species colonizes a habitat; (ii) bacterial cell densities on Petri dishes of one particular species easily reaches 10^{11} CFU, which in average is much higher than reached in natural communities; (iii) in nature, the bacterial metabolism depends on the different and variable plant exudates; and (iv) microorganisms usually live under harsh environmental conditions, for example, substrate limitation and sub-optimal temperatures rather than under comfortable laboratory conditions (exceptions from this rule are, for example, the rhizosphere, which is rich in

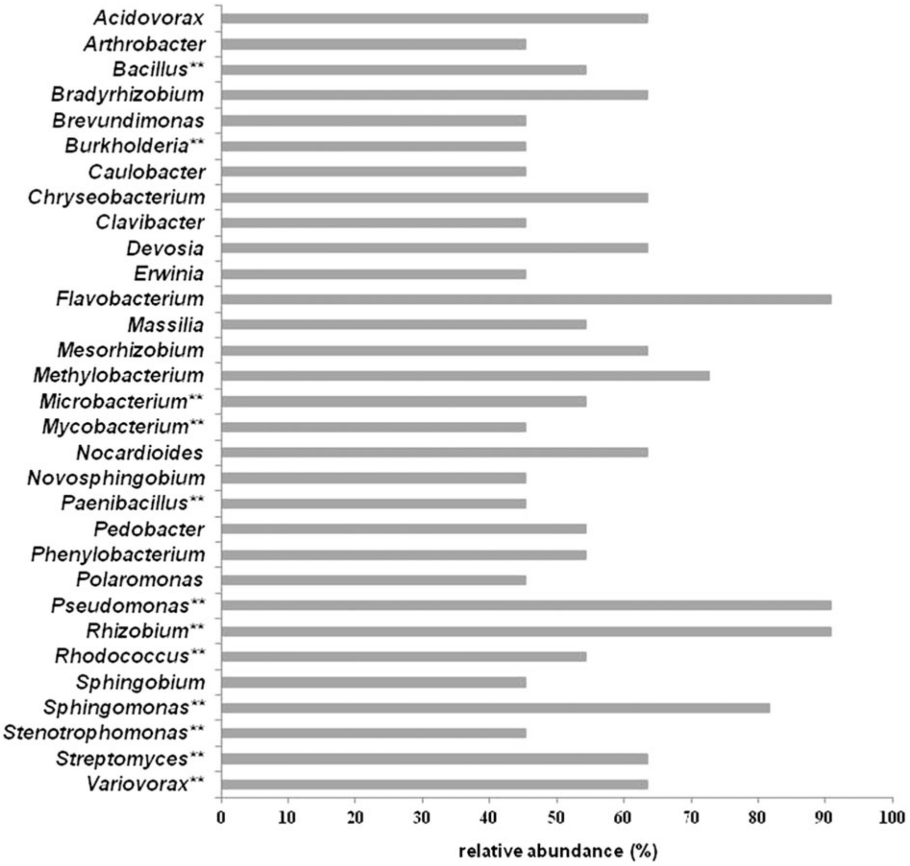

Figure 1. Relative abundance of dominant bacterial genera in plant microbiomes. The data represent the relative occurrence (%) of the 31 most dominant genera of plant microbiomes (analysis based on Table S1). Bacterial genera marked with (**) are also present in the mVOC database.

exudates, and the presence of carcass or soil enriched with manure and whey). It will be a challenge in the future to design laboratory experiments that allow to unravel the genuine ecological and biological roles of the microbial volatiles that appear under real and nature-simulated conditions. To acquire a first idea about the biological functions of these mVOCs, reductionist approaches similar as in plant–insect interactions (via electroantennograms) and in plant–plant interactions (via application of individual compounds) are supportive. Therefore, single mVOCs or reconstituted mVOC mixtures should be investigated to identify and explore bioactive mVOCs and decipher their underlying mechanisms of action. As there is a great need regarding this knowledge, an initial step was to screen the existing literature and summarize the effects of discrete mVOCs on plants and fungi. These mVOCs were organized according to compound classes (Table 1). Presently, 94 discrete mVOCs (less than 10% of the listed compounds in mVOC database) with bioactivity were described, and 50 and 57 affect plants and fungi, respectively. Alcohols and ketones were most frequently tested, followed by S- and N-containing compounds. This comes not as a surprise because alcohols and ketones contribute with 16% and 13%, respectively, to the diversity of microbial volatiles (Schenkel *et al.* 2015). Although aromatic compounds (14%) and terpenes (11%) are substantially present in microbial volatilomes, so far, only nine terpenes and three aromatic compounds were investigated, indicating a gap of knowledge.

Investigated plants and bacteria

In more than 50% of the experiments (43 of 77), the model plant *Arabidopsis thaliana* was selected as a receiver organism, while *Lactuca sativa, Nicotiana tabacum, Lycopersicon* sp., *Brassica oleracea, Capsicum annum, Glycine max, Citrus* sp., *Atractylodes* sp., *Zea mays, Malus* sp., *Medicago* sp., *Cistus* sp., *Amaranthus* sp. and *Populus niger*, each were only investigated a few times. *Phytophthora, Sclerotinia, Rhizoctonia, Fusarium, Alternaria* and *Botrytis* were the most frequently phytopathogenic fungi tested. The 12 individual mVOCs mostly used in assays are dimethyl disulfide, butanediol, 1-octen-3-ol, 2-undecanone, indole, 2-nonanone, 1-undecene, 1-hexanol, dimethyl trisulfide, benzaldehyde, 2-aminoacetophenone, and acetophenone (Fig. S2). Only one example of a defined mixture of four ketones was successfully applied, which affected the growth of the phytopathogenic fungi *Rhizoctonia solani* (Table 1). The most frequently mVOC producers investigated are bacteria such as *Pseudomonas* sp., *Bacillus* sp., *Burkholderia* sp., *Serratia* sp., *Stenotrophomonas* sp., *Collimonas* sp. and *Streptomyces* sp. and fungi like *Aspergillus* sp., *Fusarium* sp., *Muscodor* sp., and *Alternaria* sp.

Table 1. Discrete microbial organic volatile compounds effecting plants and fungi

Compound class/discrete mVOC	Emitter	Receiver: plant	Receiver: fungi	Reference
Acids – derivatives				
Acetic acid	*Pseudomonas* sp., *Bacillus* sp.		*Sclerotinia sclerotiorum*, inhibition of mycel growth and sclerotia formation; mic 4.2, 9.2 mg, respectively	Giorgio *et al.* 2015
Ethyl octanoate	*Saccharomyces cerevisiae* CR-1		*Phyollostricta citricarpa* inhibition of germination and appressoria formation (1 *u*L mL^{-1})	Toffano *et al.* 2017
Isoamyl acetate	*Muscodor albus*		inhibition of phytopathogenic fungi	Strobel *et al.* 2001
Isovaleric acid	*Pseudomonas* sp.		*Phytophthora infestans*, inhibition of sporangia germination (min. 30% inhibition)	De Vrieze *et al.* 2015
N-acyl-homoserine lactones (AHLs)	Gram negative bacteria	*Hordeum vulgare*, root morphology		summarized in Schulz, Dickschat 2017
6-Pentyl-pyrone	*Trichoderma viridae, Trichoderma harzianum*	Seedling deformation, seedling blight suppression		El-Hasan and Buchenauer 2009
	Trichoderma asperellum	*Arabidopsis thaliana*, ISR		Kottb *et al.* 2015
	Trichoderma atroviridae	*A. thaliana*, root morphogenesis, auxin responsive gene expression, 50–200 *u*M		Garnica-Vergara *et al.* 2015
Alcohol				
2R,3R butandiol 2S,3S butandiol	*Bacillus subtilis* GB03, *Bacillus amyloliquefaciens* IN937a	*A. thaliana* resistance against *Erwinia carotovora*, 10 ng—1000 mg; tobacco, PR genes and defence priming upregulated		Ryu *et al.* 2003 Ryu *et al.* 2004 Han *et al.* 2006
	Pseudomonas chlororaphis O6	*tobacco*, enhanced growth, ISR against *Erwinia carotovora* but not against *Pseudomonas syringae*		Han *et al.* 2006 Ryu *et al.* 2003 Spencer *et al.* 2003
		A. thaliana drought survival, stomata closure and aperture, 100 *u*M		Cho *et al.* 2008
	Enterobacter aerogenes	*Zea mays* resistant against Northern corn leaf blight fungus *Setosphaeria turcica*		D'Alessandro *et al.* 2014
	Bacillus badius M12	Apple pieces, polyphenol oxidase		Gopinath *et al.* 2015
Chokol K	*Epicloe* sp.		inhibition of growth and spore germination of fungi	Steinebrunner *et al.* 2008
m-Cresol	*Ampelomyces, Cladosporium*	*A. thaliana*, suppression of symptoms, ISR, 0.001–100 mM		Naznin *et al.* 2014
cyclohexanol	several *Pseudomonas* sp.		*S. sclerotiorum* mycel growth, sclerotial germination	Fernando *et al.* 2005
2-Dodecanol	*Schewanella algae* YM8		*Aspergillus flavus*, mycelia and conidia inhibition, 5-200ug L^{-1}	Gong *et al.* 2015
2-Ethyl-1-hexanol	several *Pseudomonas* spp.		*S. sclerotiorum* mycel growth inhibition, sclerotial germination reduced	Fernando *et al.* 2005
Furfuryl alcohol	*Pseudomonas* sp.		*P. infestans*, inhibition of sporangia germination (min. 30% inhibition)	De Vrieze *et al.* 2015
1-Hexanol	*Tuber melanosporum, Tuber indicum, Tuber borchii*	*A. thaliana* growth inhibition, bleaching, 130 ppm		Splivallo *et al.* 2007

(*Continues*)

Table 1. (Continued)

Compound class/discrete mVOC	Emitter	Receiver: plant	Receiver: fungi	Reference
	Burkholderia sp., *Cellulomonas uda*, *Chromobacterium violaceum* CVO, *Escherichia coli* OP50, *Pseudomonas* sp. *Serratia* sp.	*A. thaliana*, MAMP response, flg-22 induced ethylene production; flg22 induced ROS production inhibited, 1 ng–1 mg		Blom *et al.* 2011a
	Pseudomonas simiae	*Glycine max*, seed germination inhibition, 50–100 *u*g		Vaishnav *et al.* 2016
1-Heptanol	*Paraburkholderia phytofirmans*	*A. thaliana*, growth promotion, salinity tolerance, 100 ng		Ledger *et al.* 2016
2-Methyl-1-butanol	*Xylaria* sp. PB3f3 (endophyte of *Haematoxylon brasiletto*)	*Amaranthus hypochondriacus, Solanum lycopersicon*, 4–160 *u*g mL^{-1}		Sánchez-Ortiz *et al.* 2016
	S. cerevisiae CR-1		*P. citricarpa* inhibition of germination and appressoria formation (1 *u*L mL^{-1})	Toffano *et al.* 2017
2-Methyl-1-propanol	*Xylaria sp.* PB3f3 (endophyte of *H. brasiletto*)	*A. hypochondriacus, S. lycopersicon*, 4–160 *u*g mL^{-1}		Sánchez-Ortiz *et al.* 2016
3-Methyl-butanol	*P. phytofirmans*	*A. thaliana*, growth promotion, salinity tolerance, 100 ng		Ledger *et al.* 2016
	S. cerevisiae CR-1		*P. citricarpa* inhibition of germination and appressoria formation (1 *u*L mL^{-1})	Toffano *et al.* 2017
3-Octanol	*T. melanosporum*, *T. indicum, T. borchii*	*A. thaliana* growth inhibition, bleaching, 13 and 130 ppm		Splivallo *et al.* 2007
	Trichoderma sp.		controlling conidiation, concentration dependent	Nemcovic *et al.* 2008
1-Octen-2-ol	Mould fungi	*A. thaliana*, enhanced JA/ET dependent, wounding-dependent plant gene expression, resistance against *Botrytis cinerea*		Kishimoto *et al.* 2007
1-Octen-3-ol	*Penicillium paneum*		*Penicillium paneum*, germination self inhibitor	Chitarra *et al.* 2004
	T. melanosporum, *T. indicum, T. borchii*	*A. thaliana* growth inhibition, bleaching, 13 and 130 ppm		Splivallo *et al.* 2007
	Trichoderma sp.		controlling conidiation, concentration dependent	Nemcovic *et al.* 2008
	many fungi		inhibition of fungal spore production, insect attractant	Berendsen *et al.* 2013, Chitarra *et al.* 2004, Davis *et al.* 2013
	Agarius bisporus		*Lecanicillium fungicola* germination inhibition, 1.25% *w*/*v*	Berendsen *et al.* 2013
	Bacillus pumilus (S32), *Paenibacillus* sp (S19)		*Phaeomoniella chlamydospora* antifungal activity, 41–410 mg L^{-1}	Haidar *et al.* 2016
1-Pentanol	*Bacillus* sp.	pathogen infection reduced in pepper		reviewed in Chung *et al.* 2015
3-Pentanol	Many bacteria, fungi	*Capsicum annum* ISR, resistance against *Xanthomonas axonopodis* and cucumber		Choi *et al.* 2014

(*Continues*)

Table 1. (Continued)

Compound class/discrete mVOC	Emitter	Receiver: plant	Receiver: fungi	Reference
		mosaic virus; SA and JA signalling; field experiment		
β-Phenyl-ethanol	*Serratia plymuthica* HRO C48	*A. thaliana*, growth reduction, 16.8 and 168 *µ*mol		Wenke *et al.* 2012
2-Phenyl-ethanol	*Pseudomonas* sp.		*P. infestans*, inhibition of mycelial growth (min. 30% inhibition)	De Vrieze *et al.* 2015
Phenyl-ethyl-alcohol	*Hypoxylon anthochroum* Blaci (endophyte of *Bursera lancifolia*)	*A. hypochondriacus, Panicum miliaceum, Trifolium pratense, Medicago sativa*, inhibition of germination, root elongation, seedling respiration, 12.5–500 *u*g mL^{-1}		Ulloa-Benitez *et al.* 2016
13-tetradecadiene-1-ol	*Pseudomonas fluorescens SS101*	*Nicotiana tabaccum* cv, Xanthi-nc, fresh weight increased at 50 ng		Park *et al.* 2015
Aldehydes				
Benzaldehyde	Alcaligenaceae, Bacillales, Micrococcaceae, Rhizobiaceae, Xanthomonadaceae		*Pochonia chlamydosporia, Paecilomyces lilacinus*, spore growth inhibition 4–6 g L^{-1}; mycelium growth inhibition, 16–40 g L^{-1}	Zou *et al.* 2007
	rhizobacteria	*A. thaliana,* root architecture		Gutiérrez-Luna *et al.* 2010
	P. fluorescens ALEB7B	*Atractylodes lancea*, increase of leaf net photosynthetic rate, superoxide dismutase, catalase, phenylalanine ammonia lyase, polyphenol oxidase		Zhou *et al.* 2016
Nonanal	Several *Pseudomonas* sp.		*S. sclerotiorum* mycel growth and sclerotial germination inhibited	Fernando *et al.* 2005
trans-2-Octenal	*T. melanosporum*, *T. indicum, T. borchii*	*A. thaliana* growth inhibition, bleaching, 13–130 ppm		Splivallo *et al.* 2007
5-Pentyl-2-furaldehyde	*Irpex lacteus*		Antifungal activity against *Blumeria graminis, Fusarium oxysporum, Colletotrichum fragarie, B. cinerea*	Hayashi *et al.* 1981
Phenyl-acetaldehyde	Alcaligenaceae, Bacillales, Micrococcaceae, Rhizobiaceae, Xanthomonadaceae		*P. chlamydosporia, P. lilacinus*, spore growth inhibition 6–8 g L^{-1}; mycelium growth inhibition, 17–34 g L^{-1}	Zou *et al.* 2007
Tetradecanal	Rhizobacteria	*A. thaliana,* root system architecture		Gutiérrez-Luna *et al.* 2010
Undecanal	*Pseudomonas* sp.		*P. infestans*, inhibition of mycelial growth (min. 30% inhibition)	De Vrieze *et al.* 2015
Aliphatic compounds				
1-Decene	Alcaligenaceae, Bacillales, Micrococcaceae, Rhizobiaceae, Xanthomonadaceae		*P. chlamydosporia, P. lilacinus*, spore growth inhibition 6 g L^{-1}; mycelium growth inhibition, 22–37 g L^{-1}	Zou *et al.* 2007
1-Dodecene	*Pseudomonas* sp.		*P. infestans*, inhibition of sporangia germination (min. 30% inhibition)	De Vrieze *et al.* 2015
Ethylene	*Tuber* sp.	*Cistus incanus, A. thaliana*, root morphology altered		Splivallo *et al.* 2009

(*Continues*)

Table 1. (Continued)

Compound class/discrete mVOC	Emitter	Receiver: plant	Receiver: fungi	Reference
2-Methyl-n-1-tridecene	*P. fluorescens* SS101	*N. tabaccum* cv Xanthi-nc, fresh weight improved with 5 ng		Park *et al.* 2015
Nonane	*S. algae* YM8		*A. flavus*, mycelia and conidia inhibition, 5–200 *u*g L^{-1}	Gong *et al.* 2015
Pentadecane	*Burkholderia sacchari* LMG 19450 *Serratia entomophilia* A1MO2	*A. thaliana*, MAMP response, 1 ng–1 mg		Blom *et al.* 2011a
Tridecane	*Paenibacillus polymyxa* E681	*A. thaliana,* ISR against *P. syringae*, priming gene expression PR1, ChiB, VSP2, 0.1 to 10 mM		Lee *et al.* 2012, Han *et al.* 2006
	P. simiae	*G. max*, seed germination, 50–100 *u*g		Vaishnav *et al.* 2016
1-Undecene	*Pseudomonas*		*Phytophthora infestans* growth inhibition	Hunziker *et al.* 2015
	Pseudomonas tolaasii	Broccoli and lettuce seed germination inhibition (50–500 *u*g)	*Agaricus bisporus* discoloration, 2.5 *u*g; *Pleurotus ostreatus* mycel growth inhibition, 2.5 *u*g	Lo Cantore *et al.* 2015
	Pseudomonas aeruginosa		*Aspergillus fumigatus*, dry mass reduction, 100 ppm	Briard *et al.* 2016
Ketones, – derivatives				
Acetoin	*Bacillus* sp. GB03, *Bacillus amyloliquefaciens* IN937a	*A. thaliana*, reduction of soft rot caused by *Erwinia carotovora*		Ryu *et al.* 2003 Ryu *et al.* 2004
	B. subtilis FB17	*A. thaliana*, ISR activated via SA/ET not JA pathway		Rudrappa *et al.* 2010
	B. subtilis, *B. amyloliquefaciens*	*Citrus*, reduction of post-harvest effects caused by *Penicillium digitatum, Penicillium italicum, Penicillium crustorum*		Arrebola *et al.* 2010
	B. amyloliquefaciens long C, *B. megaterium* SA1, *B. pumilus* I-6	*Lactuca sativa*, root length and number of lateral root increased, 0.1 *u*g–10 mg		Fincheira *et al.* 2016
Acetophenone	rhizobacteria	*A. thaliana,* root architecture		Gutiérrez-Luna *et al.* 2010
	Burkholderia ambifaria	*A. thaliana*, increase of plant biomass, 1 ng, 1 *u*g, 1 mg	growth reduction of *Rhizoctonia solani*, no growth reduction *Fusarium solani*, 1 ng, 1 ug, 1 mg	Groenhagen *et al.* 2013
	Pseudomonas sp.		*P. infestans*, inhibition of sporangia germination (min. 30% inhibition)	De Vrieze *et al.* 2015
2-Butanone	many bacteria and fungi *B. subtilis* GB03, *Bacillus amyloliquefaciens* IN937a	ISR, protection against *P. syringae*, induction oxylipin biosynthesis		Song and Ryu 2013
	P. fluorescens SS101	*N. tabaccum* cv Xanthi-nc, fresh weight, increase at 50 ng		Park *et al.* 2015
Decan-2-one	*Xanthomonas campestris* pv. *vesicatoria* 85–10		Mycel growth inhibiton *R. solani,* 0.01–100 *u*mol	Weise *et al.* 2012
2-Pentylfuran	*B. subtilis* GB03, *Bacillus amyloliquefaciens* IN937a, *Bacillus megaterium* XTBG34	*A. thaliana* growth promotion		Zou *et al.* 2010
3-Hexanone	*B. ambifaria*	*A. thaliana*, increase of plant biomass, 1 ng, 1 *u*g, 1 mg		Groenhagen *et al.* 2013

(*Continues*)

Table 1. (Continued)

Compound class/discrete mVOC	Emitter	Receiver: plant	Receiver: fungi	Reference
	Pseudomonas sp.		*P. infestans*, inhibition of sporangia germination (min. 30% inhibition)	De Vrieze *et al.* 2015
4-Methyl-thio-2-butanone	*B. ambifaria*	*A. thaliana*, reduction of plant biomass, no necrosis, no chlorosis, 1 ng, 1 *u*g, 1 mg		Groenhagen *et al.* 2013
1-Methyl-thio-3-pentanone	*B. ambifaria*	*A. thaliana*, reduction of plant biomass, no necrosis, no chlorosis, 1 ng, 1 *u*g, 1 mg		Groenhagen *et al.* 2013
2-Nonanone	*B. ambifaria*		growth reduction *R. solani, Alternaria alternata,* no growth reduction *F. solani*, 1 ng, 1 *u*g, 1 mg	Groenhagen *et al.* 2013
	P. chlororaphis 449		*R. solani*, growth inhibition, 10–100 *u*mol	Popova *et al.* 2014
	Pseudomonas sp., *Bacillus* sp.		*S. sclerotiorum*, inhibition of mycel growth and sclerotia formation; mic 4.9, 16.4 mg, respectively	Giorgio *et al.* 2015
	P. aeruginosa		*A. fumigatus*, dry mass reduction, 100 ppm	Briard *et al.* 2016
2-Octanone	*Pseudomonas* sp.		*P. infestans*, inhibition of mycelial growth (min. 30% inhibition)	De Vrieze *et al.* 2015
3-Octanone	*T. melanosporum, T. indicum, T. borchii*	*A. thaliana* growth inhibition, 13 and 130 ppm		Splivallo *et al.* 2007
	Trichoderma sp.		controlling conidiation, concentration dependent	Nemcovic *et al.* 2008
4-Octanone	*B. ambifaria*		growth reduction *R. solani*, no growth reduction *F. solani* 1 ng, 1 *u*g, 1 mg	Groenhagen *et al.* 2013
	Pseudomonas sp.		*P. infestans*, inhibition of mycelial growth (min. 30% inhibition)	De Vrieze *et al.* 2015
Phenyl acetone	*Pseudomonas* sp.		*P. infestans*, inhibition of mycelial growth (min. 30% inhibition)	De Vrieze *et al.* 2015
1-Phenyl-3-pentanone	*Mycoleptodonoides aitchionii*		*A. alternata, Alternaria brassicicola, Alternaria brassicae, Colletotrichum orbiculare, Corynespora cassicola*, inhibition of mycelial growth, spore germination, lesion formation, 35 ppm	Nishino *et al.* 2013
Phenyl propanedione	*Pseudomonas* sp.		*P. infestans*, inhibition of mycelial growth (min. 30% inhibition)	De Vrieze *et al.* 2015
1-Phenyl propane-1-one	*B. ambifaria*		growth reduction *R. solani*, no growth reduction *F. solani,* 1 ng, 1 *u*g, 1 mg	Groenhagen *et al.* 2013
Propiophenone	*Pseudomonas* sp.		*P. infestans*, inhibition of mycelial growth (min. 30% inhibition)	De Vrieze *et al.* 2015
6,10,14-Trimethyl-2-pentadecanone	rhizobacteria	*A. thaliana*, root system architecture		Gutiérrez-Luna *et al.* 2010
2-Undecanone	*X. campestris* pv. *vesicatoria* 85–10		mycel growth promotion *R. solani,* 0.01–100 *u*mol	Weise *et al.* 2012
	B. ambifaria		growth reduction *R. solani, A. alternata*, no growth reduction *F. solani*, 1 ng, 1 *u*g, 1 mg	Groenhagen *et al.* 2013
	P. chlororaphis 449		*R. solani*, growth inhibition, 10–100 *u*mol	Popova *et al.* 2014
	Pseudomonas sp., *Bacillus* sp.		*S. sclerotiorum*, inhibition of mycel growth and sclerotia formation; mic 14.8, 16.5 mg, respectively	Giorgio *et al.* 2015

(*Continues*)

Table 1. (Continued)

Compound class/discrete mVOC	Emitter	Receiver: plant	Receiver: fungi	Reference
	P. phytofirmans	*A. thaliana*, growth promotion, salinity tolerance, 100 ng		Ledger *et al.* 2016
	P. aeroginosa		*A. fumigatus*, dry mass reduction, 100 ppm	Briard *et al.* 2016
Terpenoids				
δ-Cadinene	*Trichoderma virens*	*A. thaliana* growth promotion, defence against *B. cinerea*		Zhang *et al.* 2007
β-Caryophyllene	*T. virens*	*A. thaliana* growth promotion, defence against *B. cinerea*		Zhang *et al.* 2007
	Fusarium oxysporum MSA35	Lettuce seedlings growth promotion		Minerdi *et al.* 2011
m-Cymene	*Pseudomonas* sp., *Bacillus* sp.		*S. sclerotiorum*, inhibition of mycel growth and sclerotia formation; mic 13.8, 17.2 mg, respectively	Giorgio *et al.* 2015
β-Elemene	*T. virens*	*A. thaliana* growth promotion, defence against *B. cinerea*		Zhang *et al.* 2007
Eucalyptol	*Hypoxylon anthochroum* Blaci (endophyte of *Bursera lancifolia*)	*A. hypochondriacus, Panicum miliaceum, Trifolium pratense, Medicago sativa*, inhibition of germination, root elongation, seedling respiration, 12.5–500 *u*g mL^{-1}		Ulloa-Benitez *et al.* 2016
Farnesol	*Candida albicans*		*Candida albicans*, self inhibition	Hornby *et al.* 2001
Germacrene D	*T. virens*	*A. thaliana* growth promotion, defence against *B. cinerea*		Zhang *et al.* 2007
Limonene	*Pseudomonas* sp., *Bacillus* sp.		*S. sclerotiorum*, inhibition of mycel growth and sclerotia formation; mic 17.2, 30.1 mg, respectively	Giorgio *et al.* 2015
(−)-Thujopsene	*Laccaria bicolor*	*Populus, A. thaliana* lateral root formation, 6.4 pmol		Ditengou *et al.* 2015
Aromatic compounds				
Butylated hydoxytoluene	*S. algae* YM8		*A. flavus*, mycelia and conidia inhibition, 5–200 *u*g L^{-1}	Gong *et al.* 2015
2,4-Bis(1,1-dimethylethyl)-phenol	*S. algae* YM8		*A. flavus*, mycelia and conidia inhibition, 5–200 *u*g L^{-1}	Gong *et al.* 2015
Methyl-benzoate	*Ampelomyces, Cladosporium*	*A. thaliana* supression of symptoms, ISR, 1 *u*M–100 mM		Naznin *et al.* 2014
N-containing compounds				
Acetamide	Alcaligenaceae, Bacillales, Micrococcaceae, Rhizobiaceae, Xanthomonadaceae		*P. chlamydosporia*, *P. lilacinus*, spore growth inhibition 2–4 g L^{-1}; mycelium growth inhibition, 53–67 g L^{-1}	Zou *et al.* 2007
1-Butanamine	Alcaligenaceae, Bacillales, Micrococcaceae, Rhizobiaceae, Xanthomonadaceae		*P. chlamydosporia, P. lilacinus*, spore growth inhibition 20–21 g L^{-1}; mycelium growth inhibition, 32–44 g L^{-1}	Zou *et al.* 2007
	Arthrobacter agilis UMCV2	*Medicago sativa*, growth, development, 8 mM		Velazquez-Bererra *et al.* 2011

(*Continues*)

Table 1. (Continued)

Compound class/discrete mVOC	Emitter	Receiver: plant	Receiver: fungi	Reference
N,*N*-dimethylhexadecanamine (related to QS signal)				
2,4-Dimethyloxazole	*S. algae* YM8		*A. flavus*, mycelia and conidia inhibition, 5–200 *u*g L^{-1}	Gong *et al.* 2015
2,5-Dimethylpyrazine	*P. aeruginosa*		*A. fumigatus*, dry mass reduction, 100 ppm	Briard *et al.* 2016
	Bacillus pumilus (S32), *Paenibacillus* sp. (S19)		*Phaeomoniella chlamydospora* antifungal activity, 100–2000 mg L^{-1}	Haidar *et al.* 2016
Indole	*Burkholderia* sp., *C. uda*, *C. violaceum* CVO, *E. coli* OP50, *Pseudomonas* sp. *Serratia* sp., *Stenotrophomonas rhizophila* ep10-p69	*A. thaliana*, block of ethylene production, high indole: increase of oxidative burst, 1 ng–1 mg		Blom *et al.* 2011a
	soil borne bacteria	*A. thaliana*, root growth		Bailly *et al.* 2014
Methanamine	Alcaligenaceae, Bacillales, Micrococcaceae, Rhizobiaceae, Xanthomonadaceae		*P. chlamydosporia, P. lilacinus*, spore growth inhibition 7–9 g L^{-1}; mycelium growth inhibition, 21–33 g L^{-1}	Zou *et al.* 2007
N-methyl-*N*-nitrosoisobutyramide	*M. albus*		*Trichoderma* sp., *Colletotrichum* sp., *Fusarium* sp., *Aspergillus* sp., *Geotrichum* sp. inhibition of radial growth, 0–1 mg; DNA alkylation	Hutchings *et al.* 2017
4-Nitroguaiacol	*P. simiae*	*G. max*, seed germination, 50–100 *u*g		Vaishnav *et al.* 2016
Nitropentane	*Pseudomonas* sp.		*P. infestans*, inhibition of mycelial growth (min. 30% inhibition)	De Vrieze *et al.* 2015
Phenanzine	*P. chlororaphis* O6	ISR		Han *et al.* 2006 Ryu *et al.* 2003 Spencer *et al.* 2003
Quinoline	*P. simiae*	*G. max,* seed germination reduced, 50–100 *u*g		Vaishnav *et al.* 2016
Trimethyl amine	*Geotrichum candidum*		*G. candidum*, self inhibiton	Robinson et al. 1997
S-containing compounds				
2-acetyl thiazole	*Pseudomonas* sp.		*P. infestans*, inhibition of sporangia germination (min. 30% inhibition)	De Vrieze *et al.* 2015
Benzothiazole	several *Pseudomonas* sp.		*S. sclerotiorum* mycel growth, sclerotial germination	Fernando *et al.* 2005
	Alcaligenaceae, Bacillales, Micrococcaceae, Rhizobiaceae, Xanthomonadaceae		*P. chlamydosporia, P. lilacinus*, mycelium growth inhibition, 29–158 g L^{-1}	Zou *et al.* 2007
	P. simiae	*G. max*, seed germination, 50–100 *u*g		Vaishnav *et al.* 2016
DMS	*P. aeruginosa*		*A. fumigatus*, dry mass reduction, 100 ppm	Briard *et al.* 2016
DMDS	*S. plymuthica* 4Rx13	*A. thaliana*, growth reduction, 0.5 *u*mol–0.5 mmol		Kai *et al.* 2010

(*Continues*)

Table 1. (Continued)

Compound class/discrete mVOC	Emitter	Receiver: plant	Receiver: fungi	Reference
	Bacillus cereus C1L	ISR in tobacco and maize against *B. cinerea, Cochliobolus heterostrophus*, 0.1 to 10 mM		Huang *et al.* 2012
	Bacillus sp. B55	*A. thaliana* growth promotion, 0–1 mM		Meldau *et al.* 2013
	B. ambifaria	*A. thaliana*, increase of plant biomass, 1 ng, 1 *u*g, 1 mg	growth reduction *R. solani*, no growth reduction *F. solani*, 1 ng, 1 *u*g, 1 mg	Groenhagen *et al.* 2013
	Pseudomonas sp., *Bacillus* sp.		*S. sclerotiorum*, inhibition of mycel growth and sclerotia formation; mic 31.4, 73.2 mg, respectively	Giorgio *et al.* 2015
	P. tolaasii	Broccoli and lettuce seed germination inhibition, 2.5 *u*g; growth stimulation, 0.312 and 0.625 *u*g	*A. bisporus* discoloration, 0.156 *u*g–20 *u*g; *P. ostreatus* mycel growth inhibition, 1.25–20 *u*g	Lo Cantore *et al.* 2015
	P. aeruginosa		*A. fumigatus*, dry mass reduction, 100 ppm	Briard *et al.* 2016
DMTS	several *Pseudomonas* spp.		*S. sclerotiorum* mycel growth, sclerotial germination	Fernando *et al.* 2005
	B. ambifaria		growth reduction *R. solani, A. alternata*; no growth reduction *F. solani*, 1 ng, 1 *u*g, 1 mg	Groenhagen *et al.* 2013
	S. algae YM8		*A. flavus*, mycelia and conidia inhibition, 5–200 *u*g L^{-1}	Gong *et al.* 2015
	Pseudomonas sp., *Bacillus* sp.		*S. sclerotiorum*, inhibition of mycel growth and sclerotia formation; mic 24 mg	Giorgio *et al.* 2015
Methanethiol	*P. tolaasii*	Broccoli and lettuce seed germination inhibition, 50–500 *u*g	*A. bisporus* discoloration,100 *u*g; *P. ostreatus* mycel growth inhibition, 50 *u*g	Lo Cantore *et al.* 2015
S-methyl-butanethioate	*Pseudomonas* sp.		*P. infestans*, inhibition of sporangia germination (min. 30% inhibition)	De Vrieze *et al.* 2015
S-methyl-methane-thiosulphonate	*B. ambifaria*		Growth reduction *R. solani,* no growth reduction *F. solani*, 1 ng, 1 *u*g, 1 mg	Groenhagen *et al.* 2013
	Pseudomonas sp.		*P. infestans*, inhibition of mycelial growth (min. 30% inhibition)	De Vrieze *et al.* 2015
Synthetic mixtures				
Decan-2-one, undecan-2-one, dodecan-2-one, 10-methylundecan-2-one	*X. campestris* pv. *vesicatoria* 85–10		Concentration dependent effect on mycel growth of *R. solani*, 0.09–9 *u*mol	Weise *et al.* 2012

Altogether, this overview shows that only a very limited number of mVOC producers and discrete mVOCs were so far in the focus of research interests. Therefore, more bacteria, fungi and individual compounds, contributing with small or large amounts to the VOC spectrum, need to be investigated in the future to decipher the microbial volatile language comprehensively.

Recorded parameters

In the past decade, the receiver organisms, plants and fungi, were explored by evaluating robust and easily recordable parameters, and so far only in a few cases less assessable molecular mechanisms, markers or targets were investigated (Table 2, Fig. 2). Changes in growth, biomass, morphology and seed/spore germination were the most obvious and frequently registered alterations that occurred after fumigation with discrete mVOCs. Effects on the physiology of plants such as photosynthesis or abiotic stresses (salinity and drought) were seldom explored. More emphasis was put on the investigation of plant defence mechanisms. The general observation of improved induced stress resistance (ISR) was underpinned by showing the involvement of characteristic features such as reactive oxygen species (ROS), microbial associated molecular patterns (MAMP), salicylic acid, jasmonic acid and ethylene signalling cascades, activation of pathogen related (PR) proteins and stress enzymes. It is also very likely that these response reactions include activations of gene expression via transcription factors, for example, WRKY18 (Wenke *et al.* 2012). Apparently, volatiles produced by microbes are able to help plants in the defence against potential intruders like pathogenic fungi or bacteria by inducing systemic resistance (e.g. Kottb *et al.* 2015). It is further interesting to note that all mVOC classes contribute to the reduction of fungal mycelium and spore growth, while mVOC alcohols, ketones and aliphatic compounds cause widespread effects in plants (Table 2). So far, no mVOC aldehyde and terpenoid was found/tested to induce ISR. Moreover, several mVOC compound classes have dual functions and cause growth promotion and growth reduction at certain experimental conditions (Table 2).

First steps elucidating the potential effects of discrete bioactive mVOCs were performed; however, more detailed and specific experiments are needed to unravel the respective targets and cellular and molecular reactions. For example, it has to be clarified (i) whether mVOCs interact with specific receptors and kicking-off special reactions and signal cascades in plants; (ii) whether general and global responses are dominantly addressed; or (iii) whether the signals are plant- or fungal-specific? Regarding the specificity, two aspects have to be considered. (a) Are the volatile compounds solely emitted by bacteria, fungi or plants or do the VOC profiles overlap? More than 70 compounds appear in common in the volatilomes of the three organismal groups (Fig. 3, Table S2). Owing to this overlapping emission potential, it will be difficult to decide in the habitat from which source a bioactive compound originates; consequently, specific VOC-mediated interactions are highly unlikely for most bioactive mVOCs identified so far. Specificity can be reached by sole phyla-emission, genus-emission or species-emission of distinct VOCs. At the present stage of knowledge, 13-tetradecadien-1-ol, 2-methyl-n-1-tridecene, 1-phenylpropane-1-one, *N*,*N*-dimethyl hexadecanamine and 2.4-dimethyloxazole are solely emitted by bacteria (not by fungi and plants), while 6-pentyl-pyrone, chokol K and 5-pentyl-2-furaldehyde are only released by fungi (Table S2). These compounds have the potential to mediate specific interactions. (b) Do mVOCs trigger specific/individual effects in the receiver organism? At present, it appears that dimethyl disufide, butanediol, 1-octen-3-ol and 2-undecanone have a rather broad spectrum of cellular targets. Dimethyl disulfide altered phenomena range from plant growth reduction, ISR, reduced seed germination, fungal discoloration, mycelium growth reduction and also include contradictory results such as seedling and plant growth promotions (Table 1& 2). A similar wide array of physiological parameters were addressed by 2,3-butanediol (ISR, PR gene activation, improved drought survival, stomata closure and aperture affected and growth promotion) and by 2-undecanone (growth promotion, salinity tolerance, fungal mycelium growth promotion as well as inhibition, reduced sclerotia formation). These results would support the conclusion that many discrete bioactive mVOCs generate pleiotropic effects rather than interacting with specific targets (molecules and/or pathways) in the plant. At this stage of knowledge, only one single mVOC (*N*-methyl-*N*-nitrosoisobutyramide) is known which specifically and singularly affects a defined feature (DNA alkylation) in fungi (Table 1). A receiver (plant)-specific mVOC was so far not detected, and its identification has to be postponed until adequate analyses demonstrate its existence. To increase the chances to detect such specific mVOCs, more compounds of the complex volatile spectra of the microorganisms, particularly including those compounds with minor contributions in a blend, need to be investigated in the future. This approach is expected to be successful in plant research because individual mVOCs specifically affecting vertebrates, invertebrates and bacteria were already described (summarized by Piechulla, unpublished), although the ultimate targets also remain to be determined.

In summary, the results obtained must be taken as snap shots because comprehensive and systematic analysis and sets of data are still missing. Rather general and multiple effects instead of very specific and distinct functions of (discrete) mVOCs were observed in plants (Fig. 2), most likely due to the fact that studies glanced so far at the morphology and phenotype but did not identify specific targets.

BIOLOGICAL EFFECTS OF MICROBIAL INORGANIC VOLATILE COMPOUNDS ON PLANTS – STATE-OF-THE-ART

Beside VOCs, the bacterial volatile bouquet also includes molecules of inorganic nature, for example, ammonia, hydrogen cyanide, carbon dioxide, hydrogen sulfide and nitric oxide. Although it is known for a long time that bacteria emit inorganic volatiles (Emerson *et al.* 1913; Clawson and Young 1913; and others), investigations reporting on volatile-mediated interactions between plants and bacteria often did not consider the

Table 2. Correlation of effects in plants and fungi with mVOC compound classes

Organisms		Chemical classes								
PLANT	Parameters	Acids	Alcohols	Aldehydes	Aliphatic compounds	Ketones	Terpenoids	Aromatic compounds	N-containing compounds	S-containing compounds
Growth	Biomass/growth		↑↓		↑↓	↑↓	↑			↑↓
	Seed germination/growth	↑	↑		↑				↑	↑↓
	Altered root morphology/growth	+	+	+	+	+	+			
Defence response	Induced systemic resistance	↑	↑		↑	↑		↑	↑	↑
	Phytopathogenic fungi		↓			↓	↓			
	SA, JA, ET dependent signalling		↑			↑				
	PR genes/ priming		↑		↑					
	ROS		↑							
	Ethylene production		↑							
	Stress enzymes			↑						
	MAMP dependent response		↑		↑					
	Post-harvest effects					↑				
Physiology	Photosynthesis				↑					
	Altered stomata closure/aperture		+							
	Salinity tolerance		↑							
	Drought survival		↑							
	Auxin dependent gene expression	↑								
FUNGHI										
	Mycel growth	↑	↑	↑	↑	↑	↑	↑	↑	↑
	Spore germination	↓	↓	↓	↓	↓				↓
	Spore growth		↓	↓	↓	↓	↓	↓	↓	↓
	Sclerotinia formation	↑								
	Discoloration									+
	Fungal growth					↑				
	DNA alkylation								↑	

↑, increase; ↓, decrease; +, altered phenotype; ROS, reactive oxygen species; PR, pathogen related, SA, salicylic acid; JA, jasmonic acid; ET, ethylene; dep, dependent.

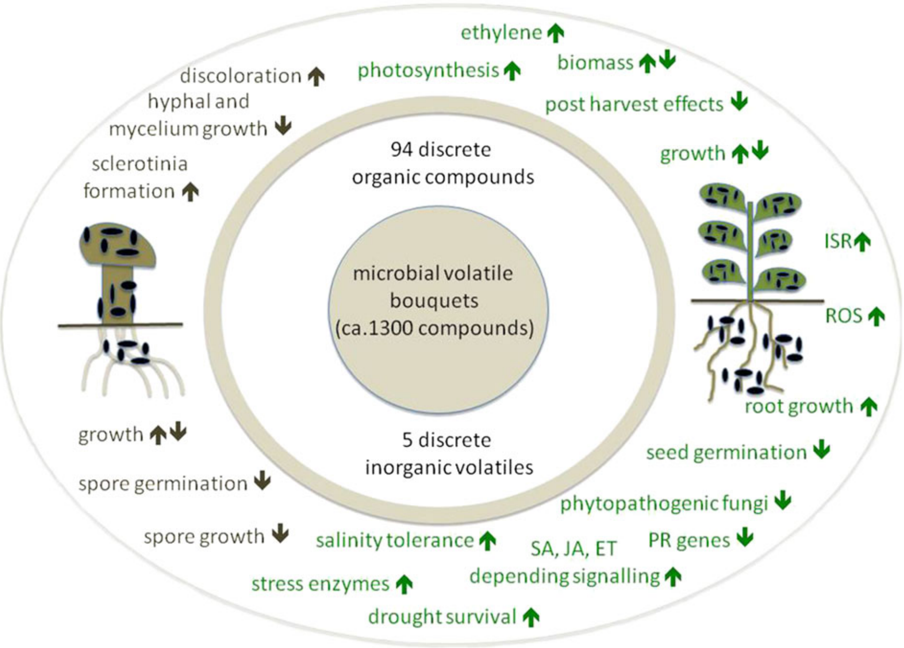

Figure 2. Overview of effects in plants and fungi due to distinct microbial volatiles. Presentation is extracted from Table 1. Colour code: green – altered parameters in plants, brown – altered parameters in fungi, dark blue – bacteria.

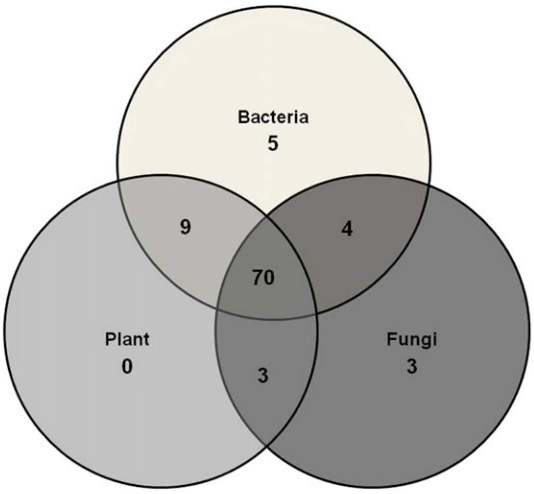

Figure 3. Overlap of emission of discrete mVOCs of bacteria, fungi and plants. Numbers are deduced from Table S2.

inorganic compounds as potential active agents. In fact, out of 32 selected research articles describing direct effects of volatiles on plant growth (starting 2003 with the article of Ryu *et al.* 2003, Table S3), 20 at least mentioned inorganic volatiles. However, the features of the inorganic volatiles are important to consider in organismal interactions because the action potential of these compounds range from plant growth promotion owing to, for example, carbon dioxide to killing due to, for example, HCN (Table 3). Furthermore, indirect actions via affecting phytopathogenic fungi or bacteria also have to be considered.

Carbon dioxide

Bacteria generally emit carbon dioxide (CO_2) due to respiration (e.g. tricarboxylic acid cycle) or fermentation processes. Because plants assimilate CO_2 via photosynthesis, it is conceivable that also bacterial CO_2 can be incorporated by plants. Researchers in the past years discussed that the emission of bacterial CO_2 is effective in certain co-cultivation bioassays (Kai and Piechulla 2009; Kai *et al.* 2016; Piechulla and Schnitzler 2016). Particularly, in test systems that were sealed with Parafilm® to prevent the escape of volatile compounds, researchers observed significant plant growth promotions. In such cases, it was underestimated that sealing of the test system not only inhibits the diffusion of VOCs but simultaneously results in an accumulation of CO_2. Kai and Piechulla (2009) reported that within 24 h of cultivation, the CO_2 level in the sealed growth containers rose from 390 to 3000 ppm. In correlation with the elevated CO_2 levels, strong growth promotion of *A. thaliana* plants was observed. This effect could be neutralized in the same sealed system by trapping the CO_2 with barium hydroxide ($Ba(OH)_2$). Similar results were shown for the sealed co-cultivation of bacteria and *Physcomitrella patens* (Kai and Piechulla 2010).

Plants increase their growth and biomass, shift their flowering time and enhance their photosynthetic activity owing to elevated CO_2 levels (reviewed in Jin *et al.* 2015; Becklin *et al.* 2016). Therefore, it is no surprise that CO_2 released from bacteria co-cultivated with plants can support plant growth (Table 3). Researchers are aware of this phenomenon (Table S3), Ledger *et al.* (2016), for instance, explored the potential influence of CO_2 on plant growth promotion by comparing sealed system with non-sealed systems and observed no difference in plant growth. To clarify the role and

Table 3. Discrete microbial inorganic volatile compounds effecting plants and fungi

Compound class/ inorganic volatile	Emitter	Receiver: Plant	Receiver: Fungi	Receiver: Bacteria	Reference
HCN	*Chromobacterium violaceum* CV0, *Pseudomonas protegens* CHA0, *Pseudomonas aeruginosa* (strains PA01a, PA01b, TBCF10839, PA14, TB, PUPa3), *Pseudomonas chlororaphis* subsp. *aureofaciens* ATCC13985, *Serratia plymuthica* IC14	Killing of *Arabidopsis thaliana*			Blom *et al.* 2011b
	P. protegens CHAO, *P. aeruginosa* (strains PAO1, PA14)	Inhibition of primary root growth of *Arabidopsis thaliana*		Suppression of *Bacillus subtilis* biofilm formation and colonization on *Arabidopsis*	Rudrappa *et al.* 2008
	50% of Potato – and wheat rhizosphere isolated Pseudomonads	Inhibition of cytochrome oxidase respiration in potato roots			Bakker and Schippers 1987
	P. fluorescens WSM3455	Deleterious effects on wild radish weed root (*Raphanus raphanistrum*) and subterranean clover root (*Trifolium subterraneum*)			Flores-Vargas and O'Hara 2006
	P. fluorescens P11	Inhibition of bean (*Phaseolus vulgaris* var. Saxa)			Piotrowska-Seget 1995
	P. fluorescens A112	Inhibition of lettuce (*Lactuca sativa* L. cv. Salad Bowl and Montana) root elongation			Aström 1991
	P. fluorescens S241	Reduction of bean (*Phaseolus vulgaris* cv. *Bonita*) and lettuce (*L. sativa* L. var. *Sativa* cv. Montana or Market Favourite) dry weight			Alström and Burns 1989
	Pseudomonas kilonensis/ *brassicancearum*	Reduction of aboveground biomass of *Echinochola crus-galli*			Zeller *et al.* 2007
	Pseudomonas putida ATH1RI/9, Acidovorax delafieldii ATH2-2RS/1	Reduced the growth of Velvetleaf (*Abutilon theophrasti*)			Owen and Zdor 2001
	P. fluorescens CC13	Induced necrosis on the rootlets of spinach			De Bellis and Ercolani 2001
	32% of 2000 tested isolates including *Pseudomonas* sp. (strains 42, 74, 473), *P. fluorescens* (strains 297, 126, 672), *P. aeruginosa* 136	Growth inhibition of lettuce and Barnyard grass			Kremer and Souissi 2001
	P. aeruginosa isolates			Promotion of competitiveness and suppression of *Burkholderia cenocepacia* K56–2	Smalley *et al.* 2015
	P. aeruginosa			Toxicity to *Burkholderia multivorans*	Bernier *et al.* 2016

(*Continues*)

Table 3. (Continued)

Compound class/ inorganic volatile	Emitter	Receiver: Plant	Receiver: Fungi	Receiver: Bacteria	Reference
	Pseudomonas sp. LBUM300			Repression of growth of *Clavibacter michiganensis* subsp. *michiganensis*	Lanteigne *et al.* 2012
	Pseudomonas corrugata		Antagonize growth of *Gaeumannomyces graminis* var. *tritici*		Ross and Ryder 1994
	P. chlororaphis PA23		Inhibition of *Sclerotinia sclerotiorum*		Athukorala *et al.* 2010
	P. protegens CHA0		Suppression of *Thielaviopsis basicola*		Ahl *et al.* 1986, Keel *et al.* 1989, Voisard *et al.* 1989
	P. protegens CHA0		Inhibition of vegetative growth of *Magnaporthe oryzae*		Spence *et al.* 2014
	P. fluorescens In5		Inhibition of growth of hyphae of *Rhizoctonia solani* and *Pythium aphanidermatum*		Michelsen and Stougaard 2012
	P. putida BK861 (HCN overproducing strain)		Suppression of *Septoria tritici* and *Puccinia recondita* f. sp. *tritici*		Flaishman *et al.* 1996
Ammonia	*B. subtilis* UB1 (strain has not been characterized)		Inhibition of *Neurospora crassa* strains	Stimulation of growth of *B. subtilis* UB2 (strain has not been characterized)	Ryan and Schneider 1947
	microbial degradation (bacteria not determined)		Increased mycelial growth and melanization of *R. solani* strains R118–11, R182		Lewis 1976
	S. plymuthica 4Rx13	Inhibition of *A. thaliana*			Kai *et al.* 2010
	Serratia odorifera 4Rx13, *S. plymuthica* HRO-C48, *S. plymuthica* 3Re4–18, *P. fluorescens* L13–6-12, *P. fluorescens* 3Re2–7, *B. subtilis* B2g, *Stenotrophomonas maltophilia* R3089, *Stenotrophomonas rhizophila* P69, *Staphylococcus epidermidis* 2P3-18a	Inhibition of *A. thaliana*			Weise *et al.* 2013
	Bacillus cereus YMF3 00019, *Bacillus amyloliquefaciens* YMF3 00061, *Proteus penneri* YMF3 00016, *Staphylococcus saprophyticus* YMF3 00594, *Pseudochrobactrum asaccharolyticum* YMF3 00201, *Proteus vulgaris* YMF3 00140, *Leucobacter komaqatae* YMF3 00179, *P. aeruginosa*		Induction of trap formation in *Arthrobotrys oligospora* YMF1 01883		Su *et al.* 2016

(*Continues*)

Table 3. (Continued)

Compound class/ inorganic volatile	Emitter	Receiver: Plant	Receiver: Fungi	Receiver: Bacteria	Reference
	YMF3 00188, *Alcaligenes faecalis* YMF3 00172, *Providencia rettgeri* YMF3 00150, *Brevibacterium epidermidis* YMF3 00155				
	B. subtilis, Bacillus licheniformis, Micrococcus luteus, *Escherichia coli*			Induction of biofilm formation in *B. licheniformis*	Nijland and Burgess 2010
	E. coli K12		Modification of antibiotic resistance in *E. coli* BL21, *P. aeruginosa*, *Staphylococcus aureus*, *B. subtilis*		Bernier *et al.* 2011
CO_2	*S. plymuthica* 4Rx13	Promoted the growth of *A. thaliana*			Kai and Piechulla 2009
	S. plymuthica 4Rx13	Promoted the growth of *Physcomitrella patens*			Kai and Piechulla 2010
H_2S	Sulfate reducing bacteria			Direct and reversible toxicity effect on sulfate-reducing bacteria	Reis *et al.* 1992
	Bacillus anthracis, P. aeruginosa, S. aureus, and *E. coli*			Mediate resistance to antibiotics	Shatalin *et al.* 2011
NO	*Azospirillum brasilense* Sp245	Mediate root branching of tomato (*Solanum lycopersicum* Mill.)			Molina-Favero *et al.* 2008
	B. anthracis			Lose their virulence and exhibit severely compromised survival	Shatalin *et al.* 2007
	B. subtilis			Protects bacterial cells from reactive oxygen species	Gusarov and Nudler 2005
	Streptomyces coelicolor			Regulation of production of antibiotics	Sasaki *et al.* 2016

determine the extent of incorporation of bacterial CO_2 in plant growth in co-cultivations, two lines of experiments can be performed, (i) tracing isotope labelled CO_2 of bacteria in plants and (ii) online monitoring of CO_2 levels in respective growth containers. Nevertheless, it is still very challenging to differentiate between plant growth promoting effects caused by CO_2 with the effects caused by other volatile (organic) compounds.

Hydrogen cyanide

The best studied bacterial inorganic volatile is HCN released from the *Pseudomonas* strains *Pseudomonas protegens*, *Pseudomonas fluorescens*, *Pseudomonas aeruginosa*, *Pseudomonas chlororaphis*, *Pseudomonas corrugata* and *Pseudomonas putida*, *Chromobacterium violaceum, Rhizobium* strains and *Serratia plymuthica* IC14 (Castric 1981; Antoun *et al.* 1998; Blumer and Haas 2000; Blom *et al.* 2011b). In ~1/3 of research articles reporting on direct effects of bacterial volatiles on plant growth have either performed experiments with HCN or discussed a possible role of HCN to explain their observation (Tables 3 and S3). Plants, fungi and bacteria experience growth reduction, inhibitions or are killed by HCN. In one case, an improved competitiveness was observed.

Hydrogen cyanide derives from amino acid degradation, for example, glycine is oxidized to HCN by the hydrogen cyanide synthase (Laville *et al.* 1992). In case of some cyanobacteria, other amino acids (e.g. L-histidine) can be converted to HCN by L-amino acid oxidases (Vennesland *et al.* 1981). HCN interferes with the respiratory electron transport by inhibiting the cytochrome *c* oxidase. By this toxic activity bacterial hydrogen cyanide was shown to negatively influence directly the growth of different plants, for example, *Arabidopsis*, potato, wild radish, subterranean clover, beans, lettuce, spinach and Barnyard grass (Bakker and Schippers 1987; Kremer and Souissi 2001; De Bellis and Ercolani 2001; Flores-Vargas and O'Hara 2006; Rudrappa *et al.* 2008; Blom *et al.* 2011b). Besides these deleterious effects on plants, bacterial HCN was also found to suppress the growth of various fungi including *Gaeumannomyces* var. *tritici*, *Sclerotinia sclerotiorum*, *Thielavopsis basicola*, *Magnaporthe oryzae*, *Rhizoctonia solani* and *Septoria tritici* and the oomycete *Phytium aphanidermatum* (Ross and Ryder 1994; Athukorala *et al.* 2010; Ahl *et al.* 1986; Michelsen and Stougaard 2012; Spence *et al.* 2014). The inhibition of phytopathogenic fungi was correlated with plant growth promotions, and subsequently, HCN producer strains seemed to be very attractive biocontrol agents (Voisard *et al.* 1989). A very recent study, however, showed *in vitro* that rhizobacterial HCN did not correlate with the biocontrol effect but instead acted via sequestration of metal ions and indirectly caused an increase of phosphate availability (Rijavec and Lapanje 2016).

It was further demonstrated that bacterial HCN influenced the competiveness of bacterial strains in microbial communities. By killing and suppression, the HCN producer dominated co-cultures of certain bacteria (Smalley *et al.* 2015; Bernier *et al.* 2016). Although this was only tested for human associated bacteria, it is very likely that this principle can also play a role in plant-associated bacterial communities and consequently indirectly influences plant growth. Initial results that support this assumption are presented by Lanteigne *et al.* (2012) who showed that *in planta*, the *Pseudomonas* strain LBUM300 significantly reduced the disease development of bacterial canker of tomato by growth inhibition of *Clavibacter michiganensis* subsp. *michiganensis* in the rhizospheric population.

Ammonia

Ammonia is a nitrogen-containing gas produced by bacteria via degradation of amino acids (Hills 1940), by nitrite ammonification (Simon 2002), by urease-mediated hydrolytic degradation of urea (Kleiner *et al.* 1998) and by decarboxylation of amino acids (Özugul and Özugul 2007). Plants can only tolerate low levels (less than 0.1 mmol) of ammonia, because accumulation of ammonia leads to chlorosis in leaves, lowered root/shoot ratios, reduced mycorrhizal associations and inhibited seed germination and seedling establishment (Britto and Kronzucker 2002).

The role that ammonia might play in bacterial–plant interactions (Table 3) is still poorly understood and not often considered or investigated (Table S3). Kai *et al.* (2010) and Weise *et al.* (2013) clearly demonstrated that ammonia as a component of the bacterial volatile mixture led, via alkalization of the growth medium, to drastic phytotoxic effects on *A. thaliana*. This negative effect was mostly observed when bacterial isolates were grown on peptide-rich medium suggesting that degradation of amino acids was the source of ammonia formation. Because amino acids are typical root exudates, it is assumed that rhizobacteria metabolize these amino acids in their natural habitat generating ammonia and therewith affecting plant roots. In addition, indirect effects of bacterial ammonia on plant growth by influencing phytopathogens have to be considered. In a very early experiment by Ryan and Schneider (1947), it was shown that ammonia emitted from *Bacillus subtilis* UB1 inhibited the growth of the fungus *Neurospora crassa*. In contrast, ammonia as main volatile degradation product of decomposing plant tissue increased the mycelial growth of *Rhizoctonia solani* strains by supplying an additional nitrogen source and inducing melanization by raising the medium pH (Lewis 1976). Besides these effects, ammonia was also described to influence bacterial growth. Ammonia emitted from *B. subtilis*, *B. licheniformis*, *Micrococcus luteus* and *E. coli* induced biofilm formation in *B. licheniformis* (Nijland and Burgess 2010). Using *E. coli* K12 as a model organism, Bernier *et al.* (2011) demonstrated that exposure to ammonia increased resistance to tetracycline in *E. coli* BL21, *P. aeruginosa*, *Staphylococcus aureus* and *B. subtilis*. Similarly, the ampicillin-sensitive strains *Serratia rubidaea* and *Serratia marcescens* grew unhindered on ampicillin-containing media when exposed to bacterial volatiles (Čepl *et al.* 2014). However, Čepl and coworkers did not relate this effect to an increased resistance of the bacterial strains but rather to an inactivation of ampicillin owing to the alkalized pH of the medium. While the ability to form biofilms is an important parameter for bacterial strains to colonize plant roots, an increased resistance or inactivation of antibiotics can shape bacterial communities in different plant habitats. In order to thoroughly investigate ammonia-mediated direct or indirect interferences between bacteria and plants as well as the relevance in interorganismic ecology, more research has to consider ammonia as a constituent of the bacterial volatile cocktail.

Hydrogen sulfide

Hydrogen sulfide (H_2S) is an inorganic gaseous molecule that is discussed as a phytotoxic agent causing detrimental effects in plant tissues but also as a signalling compound (Lisjak *et al.* 2013). Similar to HCN toxicity, hydrogen sulfide inhibits cytochrome *c* oxidase (Nicolls and Kim 1982; Dorman *et al.* 2002). Detrimental effects include the inhibition of oxygen release and phosphorous uptake in rice seedlings (Joshi *et al.* 1975) and lesions on leaves, defoliation and reduced growth of other plants, for example, *Medicago*, lettuce, grapes, sugar beets, pine and fir (Thompson and Kats 1978). These toxic effects of H_2S emerged at high concentrations (ppm range). Because most likely such high levels are not emitted under natural conditions, H_2S was recently considered *in planta* to be a signalling compound (Lisjak *et al.* 2013), playing a role in stomatal apertures and improvement of drought resistance (Garcia-Mata and Lamattina 2010; Jin *et al.* 2011), controlling root system development (Jia *et al.* 2015), altering enzyme activities and influencing NO and H_2O_2 metabolism (Lisjak *et al.* 2013). Thompson and Kats (1978) even showed that low concentrations of H_2S positively affect the growth of *Medicago*, lettuce and sugar beets. Furthermore, the exposition of roots or seeds of pea and bean plants to very low concentrations of H_2S led to an increased biomass and higher crop yield (Dooley *et al.* 2013). Beside direct effects on plant growth H_2S can also act indirectly by inhibition of fungal pathogens, for example, *Rhizopus nigricans*, *Mucor rouxianus*, *Geotrichum candidum, Aspergillus niger* and *Penicillium italicum* and thereby reduce fungal infections or post-harvest decay, respectively (Tang *et al.* 2014; Fu *et al.* 2014).

Plants are themselves H_2S emitters (Wilson *et al.* 1978; Winner *et al.* 1981; Sekiya *et al.* 1982; Rennenberg 1983, 1984; Rennenberg *et al.* 1990) and are therefore prominent sources regarding H_2S-mediated effects in plants. Although it is well known that bacteria produce hydrogen sulfide either from cysteine (Shatalin *et al.* 2011; Luhachack and Nudler 2014) or via sulfate reduction (sulfate-reducing bacteria, see review Barton *et al.* 2014), the role of bacterial derived hydrogen sulfide in plant growth development is so far not understood. Because there is accumulating evidence that H_2S released from bacteria play a role in homeostasis of the circulatory systems in mammals (Tomasova *et al.* 2016), it is most likely that also bacteria can regulate developmental processes in plants via H_2S emission. H_2S is rarely considered as putative component of bacterial volatile mixtures that directly influence plant growth (Table 3). So far, only two of 32 articles discussed a potential role of bacterial released H_2S as bioaction component in the volatile mixtures (Groenhagen *et al.* 2013; Delaplace *et al.* 2015), while Shatalin *et al.* (2011) demonstrated that a suppressed H_2S production by bacteria led to a higher sensitivity of bacterial pathogens to a multitude of antibiotics. Furthermore, Reis *et al.* (1992) found that hydrogen sulfide produced from sulfate reduction caused negative, direct and reversible effects on sulfate-reducing bacteria. The increase of antibiotic sensitivity and direct toxicity due to bacterial H_2S might play important roles in establishing and maintaining bacterial communities on plant bacteria interfaces. H_2S has also be shown to inhibit fungal phytopathogens (*R. nigricans*, *M. rouxianus* and *G. candidum*) and to reduce fungal infections of sweet potato when potato slices were H_2S fumigated (Hu *et al.* 2014). Thus, it is also conceivable that bacterial H_2S indirectly promotes plant growth by antagonizing fungal phytopathogens.

Nitric oxide

Nitric oxide (NO) is a nitrogen-containing gaseous lipophilic highly stable free radical (half-life from seconds to minutes) that can thus freely and easily diffuse over several cell layers or longer distances (Stöhr and Ullrich 2002). These characteristics enable NO as perfect signalling molecule in plants but also bacteria and animals (Stöhr and Ullrich 2002). In plants, via metal nitrosylation, *S*-nitrosylation and tyrosine nitration, NO influences physiological key processes including growth and development, seed dormancy/germination, photosynthesis, flowering and stomatal movement (see reviews Besson-Bard *et al.* 2008; Koul *et al.* 2014). Furthermore, NO can also affect the growth of bacteria by manipulating their antibiotic resistance, promoting their antibiotic production, representing a developmental regulatory element and/or leading to an adaption to oxidative stress; all these features can indirectly influence the interference between bacteria and plants (Table 3) (Gusarov and Nudler 2005; Gusarov *et al.* 2008; Chater 2016; Sasaki *et al.* 2016). For instance, low concentrations of NO lead to dispersal of biofilm, increased cell motility or biofilm enhancement, features, which play an important role in plant root colonization (Barraud *et al.* 2009; Liu *et al.* 2012; Arruebarrena Di Palma *et al.* 2013; Henares *et al.* 2013).

Although a broad range of bacteria can produce NO via nitrification, denitrification (Firestone and Davidson 1989) and nitric oxide synthesis using arginine as the substrate (Chen and Rosazza 1994), research concerning the direct or indirect impact of bacterial NO on plant growth and development is still in its infancy (Table 3). One example is the plant growth promoting bacteria *Azospirillum brasilense,* which modulates lateral and adventitious root formation of tomato through NO emission (Molina-Favero *et al.* 2008). Zamioudis *et al.* (2015) reported that plants exposed to bacterial volatiles accumulated NO in the maturation zone and the root tip, while Cho *et al.* (2008) found NO to be present in guard cells of *A. thaliana*. Both authors conclude that this NO is plant-derived; however, NO might also be produced by plant-associated bacteria and diffused into the respective plant tissues. The emission of NO can be measured using mid-infrared absorption-based detection technique (Cristescu *et al.* 2008). Real-time monitoring using this absorption-based technique revealed that *S. plymuthica* 4Rx13 did not emit NO during growth suggesting that volatile-mediated effects of *S. plymuthica* 4Rx13 on plant growth were not based on NO emission (Kai *et al.* 2010). In order to clarify the presence of NO in bacterial headspaces and in turn to elucidate a putative role in plant growth and development, the analysis of bacterial NO emission or NO scavenging experiments should be routinely performed.

CRITICAL ISSUES

This survey demonstrates clearly that the application of discrete bioactive mVOCs is a helpful tool to study and decipher the underlying cellular and molecular reactions and mechanism occurring in mVOC-mediated interactions. Understanding those will be a prerequisite for the development of strategies for applying mVOCs in plant and human health in the future. To be sustainably successful, it will be indispensible to explore mVOC effects under 'natural simulating conditions' in the lab and to define the important parameters that influence mVOC synthesis and emission, such as nutrient supply for the microorganisms, temperature and multifaceted environmental cues. Another challenge for the future is to determine the volatile production capacities of the microorganisms living in single or multi-species communities, during biofilm formation or colonization of habitats and so on, because concentrations and doses matter in applied research experiments dealing with discrete mVOCs or defined mVOC mixtures. Because microorganisms continuously synthesize or release mVOCs in a growth-dependent manner, laboratory experiments also need to mimic and simulate these emission profiles. This could be relevant because, for example, slow emission of a compound might initiate adaptation processes in the receiving plant, which subsequently results in plants that, for example, can cope with higher mVOC concentrations or need higher levels of the mVOCs to elevate their defence or resistance reactions.

CONCLUDING REMARKS

In the past, microorganisms have demonstrated their metabolic potential by producing extraordinary compounds with bioactivity. Many of these compounds (e.g. antibiotics) are urgently needed and applied to sustain and improve the health of humans, animals and plants. However, small volatile metabolites of microbes have been overlooked in the past. Since up to now, the volatilomes of only ~600 microbes have been investigated, the high potential becomes apparent considering the large number of microbial species existing on Earth. Parnell *et al.* (2016) recently argued that '… microbes will certainly play a role in revolutionizing agriculture over the next several decades to help to meet the demands of a growing population' and '… the application of microbial products is now considered a valuable addition to precision agriculture'. As carved out in this review, the potential of mVOCs cannot be neglected anymore but rather play key roles in plant growth promotions and developments, and mVOC-mediated biocontrol will become more important in the future as more bioactive compounds are discovered (Fig. 2). Elucidation of novel structures of volatile natural products and determination of the specific molecular targets of mVOCs will be the prerequisite for the application of mVOCs in greenhouses and field trials. As the efficacy of the laboratory experiments often does not translate into field success, a challenge of the future is also to integrate mVOCs or mVOC producers appropriately. Promising field trials were demonstrated by Choi *et al.* (2014), who successfully triggered induced resistance in pepper by the application of 3-pentanol, and in the VALORAM project (http://valoram.ucc.ie), *Pseudomonas* sp., *Bacillus* spp., *Paenibacillus* sp. increased the yield of potato in Bolivia, Peru and Equador (Velivelli *et al.* 2015).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Figure S1. Overlap of bacterial species of plant microbiomes and registered species of mVOC database item.
Figure S2. Abundance of discrete mVOCs.
Table S1. Analysis of plant microbiome literature
Table S2. Comparison of the emission of discrete VOCs of bacteria, fungi and plants.
Table S3. Investigations considering inorganic volatile-mediated interactions between plants and bacteria.