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Uta Effmert, Janine Kalderás, René Warnke & Birgit Piechulla

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Volatile Mediated Interactions Between Bacteria and Fungi in the Soil

Uta Effmert · Janine Kalderás · René Warnke ·
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Abstract Soil is one of the major habitats of bacteria and fungi. In this arena their interactions are part of a communication network that keeps microhabitats in balance. Prominent mediator molecules of these inter- and intraorganismic relationships are inorganic and organic microbial volatile compounds (mVOCs). In this review the state of the art regarding the wealth of mVOC emission is presented. To date, ca. 300 bacteria and fungi were described as VOC producers and approximately 800 mVOCs were compiled in DOVE-MO (database of volatiles emitted by microorganisms). Furthermore, this paper summarizes morphological and phenotypical alterations and reactions that occur in the organisms due to the presence of mVOCs. These effects might provide clues for elucidating the biological and ecological significance of mVOC emissions and will help to unravel the entirety of belowground, volatile-wired' interactions.

Keywords Bacteria · Fungi · Soil · Volatiles · Volatile mediated interactions

Introduction

Inter- and intra-organismal communication strategies are symbolized by the three monkeys: the deaf, the mute, and the blind. Interestingly, one major communication path was not featured: the sense of smell. This is surprising since the sense of smell is well-established in many animals and plants. Vertebrates and invertebrates are able to detect minute

amounts of volatiles even over very long distances; plants use volatiles to communicate with their pollinators as well as with plants of the same species or other plants (Baldwin et al., 2006; Dobson, 2006; Heil and Walters, 2009) (Fig. 1). The infochemicals used for these inter- and intra-organismal interactions are low molecular mass compounds with high vapor pressures, low boiling points, and a lipophilic character. All of these features facilitate evaporation. Consequently, these compounds disperse easily in the atmosphere and thus play essential biological/ecological roles in aboveground habitats. It was only recently recognized that belowground organisms are also opulent volatile producers and emitters. Therefore, a new research area focuses on volatile-based interactions in the soil. Here, we first describe the habitat soil with its characteristic structural prerequisites in relation to volatile-based communications. Then, we present a summary of volatile emissions of microbes (bacteria and fungi). In the final section, we discuss volatile-based bacterial and fungal interactions.

The Habitat Soil

The tremendous diversity of the bacterial and fungal kingdoms is paralleled by the heterogeneity of habitats these organisms are able to occupy. They appear ubiquitously around the world, successfully colonizing ecological niches and microhabitats (Dighton, 2003; Hawksworth and Mueller, 2005; Gasch, 2007). One of the major habitats for fungi and bacteria is soil, where they occur as free living organisms on the soil surface, in the soil core, or in association with belowground parts of living plants or organic material derived from dead plants and animals (Forster, 1988). Soil itself is a complex blend of weathered minerals and organic material mixed with biota. Fungi and bacteria hereby play a substantial role in the

U. Effmert · J. Kalderás · R. Warnke · B. Piechulla (✉)
Institute of Biological Sciences, University of Rostock,
Albert-Einstein-Str. 3,
18059 Rostock, Germany
e-mail: birgit.piechulla@uni-rostock.de

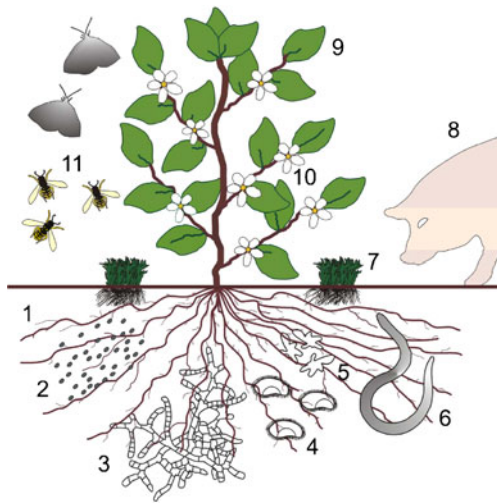


Fig. 1 Schematic presentation of organisms involved in volatile interactions above- and belowground (drawn by Marco Kai). 1 plant root, 2 bacteria, 3 fungi, 4 ciliates, 5 amoeba, 6 nematodes, 7 moos, 8 wild boar, 9 plant leaves, 10 plant flowers, 11 insects

decomposition and breakdown of organic as well as inorganic materials, respectively (Dighton, 2003). These biomineralization processes contribute substantially to soil production, generating a continuous flow of nutrients for plant primary production. Therefore, functional soils should be regarded as a balanced complement of abiotic (mineral and organic) and biotic components (Nakas and Klein, 1980; Dighton, 2003). As part of the microbiotic soil community, fungi and bacteria form dynamic and enduring communities that are integrated into even more complex microecosystems, or they arise as transient communities to secondarily colonize substrates as long as degradable nutrients are available.

Soil Properties Influence Microenvironments Belowground

Microbial colonization of soil is determined mainly by its physicochemical properties (Dequiedt et al., 2011). These properties are influenced by texture, carbon content, and microstructure, which in turn affect the formation of macroaggregates and subsequently soil parameters such as porosity or air and water content. Soil texture is determined by its inorganic components and describes the proportional distribution of mineral particle sizes: sand (0.05–2 mm), silt (2–50 μm), and clay (<2 μm) (Cehnu and Stotzky, 2002; Brown, 2003; Conklin, 2005; Schafer, 2006). Texture, mineral composition, and particle shape give rise to certain particle arrangements (microaggregates) that determine soil microstructures (Cehnu and Stotzky, 2002; Alekseeva, 2007). These microstructures and the presence of organic matter contribute to the assembly and stabilization of macroaggregates >0.25 mm in size (Forster, 1988; Ranjard and

Richaume, 2001). As a result, a complex network of void spaces is formed in soil, i.e., soil pores that can account for up to 50 % of the total soil volume (Ranjard and Richaume, 2001; Conklin, 2005; Standing and Killham, 2007). Their ability to retain water varies with their size and shape, so they are filled with different amounts of water and air. Depending on the air and water content, the chemical composition of aggregates, and the circulation within the pore network, numerous heterogenic microenvironments for microbial life are created. These vary in nutrient supply, aeration, availability of water, ionic composition, minerals, pH, redox potential, and surface composition (Forster, 1988; Ranjard and Richaume, 2001; Nannipieri et al., 2003).

Microhabitats Belowground

Microorganisms congregate in soil pores that provide a suitable microenvironment. Bacteria rely on the presence of organic and inorganic solutes in the aqueous phase of pores and on particle surfaces. The heterogeneity of these various microhabitats is probably the reason for the huge bacterial diversity in soil. Although the number of bacterial cells per gram of soil can easily exceed 10^{10} and estimates of the numbers of different species range from 10^3 to 10^5 , only a rather small proportion of soils is actually colonized by bacteria (Gans et al. 2005; Roesch et al. 2007; citations in Heuer and Smalla 2012). Bacteria may occur as free living organisms, but are usually attached to solid surfaces as scattered individual cells, microcolonies, or biofilms. Fungi inhabit the same locations but other pore sizes. Water saturated micropores ($\varnothing < 10 \mu\text{m}$) are reserved for bacterial communities, where they escape predation and the effects of fungal antibiotics. Because of their size, fungi settle in macropores ($\varnothing > 10 \mu\text{m}$) found between and within macroaggregates. In addition, fungal hyphae can extend through aerated water-unsaturated pores to reach new pores and exploit new nutrient resources (Forster, 1988; Cehnu and Stotzky, 2002). The latter is especially important since soil in its entirety represents a nutrient-depleted habitat for microorganisms. Consequently, microorganisms aggregate near any suitable nutrient source, which creates colonization hotspots. Therefore, bacteria and fungi have to compete for the same resources and undergo interspecies interactions. On the macroscale, plant litter like dead leaves, stems, roots, wood, and bark as well as animal remains and fecal material are important sources of biodegradable organic material, while on the microscale cell-wall remains, lipids, polysaccharides, proteins, DNA and RNA, and metabolites contribute to temporary microhabitats (Forster, 1988; Nannipieri et al., 2003). The most lively and enduring microhabitat is the living plant root, which releases a wide variety of soluble, insoluble, or volatile metabolites that attract an exceptionally

dense and diverse population of microbiota, including bacteria and fungi (Koske and Gemma, 1992; Chen et al., 2004; Gregory, 2006; Brimecombe et al., 2007; Nannipieri et al., 2007; Hussain and Hasnain, 2011). Bacteria adhere to the root surface itself (rhizoplane) and colonize a narrow soil zone around the plant root (rhizosphere) (Lenc et al., 2011). They benefit from a constant flow of organic substrates, but in return promote plant growth by providing soluble inorganic nutrients and producing growth-promoting factors (Brimecombe et al., 2007; Nannipieri et al., 2007; Compant et al., 2010). A special role is attributed to antagonistic bacteria, which are able to suppress the growth of various plant pathogenic fungi (Bhattacharyya and Jha, 2011). Mycorrhizal fungi (see Jung et al., 2012, this issue) also benefit from nutrients supplied by the plant root. More than 95 % of short roots of most terrestrial plants are colonized by symbiotic fungi, and these mycorrhizal fungi are surrounded by complex microbial communities. So called mycorrhiza helper bacteria (MHB) support mycorrhiza formation (Frey-Klett et al., 2007; Bonfante and Anca, 2009; Rigamonte et al., 2010). In addition, plant roots not only host beneficial but also attract detrimental organisms such as phytopathogens, which may harm plants and microbiota as well. Therefore, mycorrhizal fungi, their associated bacteria as well as rhizobacteria have to deal with a very complex and competitive rhizomicrobial milieu (Anderson, 1992; Bianciotto et al., 1996; Miransari, 2011). Bacteria and fungi closely intermingle in the mycorrhizosphere and mutually influence survival and colonization success as well as pathogenesis and virulence (Wargo and Hogan, 2006; Minerdi et al., 2008).

Volatiles as Medium for Interactions Belowground

Factors that regulate the dynamics and balance of symbiosis, cooperation, competition, and also coexistence in microbial communities have been investigated intensively. Phenomena like quorum-sensing and quorum-quenching (see Hartmann and Schikora, 2012, this issue), the impact of rhizobacterial and fungal antibiotics, effector molecules, and excreted enzymes have been recognized as effective regulatory principles (Walker et al., 2003, 2004; Chernin et al., 2011). The possible role of volatiles in bacterial-fungal interactions has been neglected for many years despite earlier reports on effective microbial volatiles (Stotzky and Schenk, 1976; Koske and Gemma, 1992). Prerequisite for volatile effectiveness is their release, emanation and distribution, and their perception by a target organism. This is ensured by the physicochemical properties of volatiles (low molecular weight, high vapor pressure, low boiling point), which facilitate distribution even over long distances (Farmer, 2001; Baldwin et al., 2006; Heil and Ton, 2008). However, does this also occur in soils? Yes, it does. Volatile distribution belowground takes

place by diffusion and advection (Minnich and Schumacher, 1993). Volatiles can move through the network of soil pores since they are active in both gas and liquid phases and capable of revolatization after passing through water-saturated pores (Koske and Gemma, 1992; Aochi and Farmer, 2005; Asensio et al., 2008). However, due to their high vapor pressure, volatiles move primarily by vapor diffusion (Minnich and Schumacher, 1993). These processes are all influenced by inherent chemical properties of the volatile itself and physicochemical properties of the surrounding soil, which affect adsorption, desorption, and degradation. Adsorption/desorption depends on the polarity of the compound, the soil texture and spatial architecture, and the presence of water. On the microscale, increasing humidity reduces the adsorption of nonpolar volatiles to mineral surfaces; on the macroscale, nonpolar volatiles are increasingly sorbed by organic matter in moist or wet soils (Minnich and Schumacher, 1993; Ruiz et al., 1998; Aochi and Farmer, 2005; Insam and Seewald, 2010). Volatile compounds also are amenable to biodegradation. Owen et al. (2007) found rapid degradation of geraniol in the rhizosphere of *Populus tremula*, an observation they attributed to the activity of soil microorganisms. However, compared to compounds solely soluble in water, volatiles are less likely to be quickly biodegraded (Koske and Gemma, 1992). Mineral surfaces may serve as catalysts for chemical reactions that contribute to abiotic degradation. Highly specific clay surfaces react with volatiles that carry polar functional groups. Furthermore, volatiles also may be exposed to free-radical oxidation (Minnich and Schumacher, 1993; Insam and Seewald, 2010). Measurements of volatile exchange rates have revealed low volatile emission from soil, supporting the assumption that soil acts as a volatile sink (Stotzky and Schenck, 1976; Asensio et al., 2007).

Microbial Volatile Emission

A large number of bacterial species presently are known, and it is estimated that this number could reach a million (10^6). While many microorganisms have been isolated from aboveground habitats (i.e., plants, human skin and intestines, animals, and refuse, sewage, and aquatic habitats), a rich source of bacteria is the terrestrial and belowground biotope. Metagenomic approaches have demonstrated that the microbial diversity is larger in soils than in marine sediments or aquatic habitats (Will et al., 2010; Daniel, 2011). The capacity of bacteria and fungi to decompose, mineralize, and accumulate organic matter is extraordinary and has a significant impact on the carbon, nitrogen, phosphate and sulfur biogeochemical cycles (Naeem, 1997). Some of the metabolized compounds are emitted as volatile products that are readily utilized by other organisms of the microbial food chain or released into the underground

Table 1 Producers and users of microbial volatiles

Producer/emitters →	compound	→ user/receiver	function
Inorganic			
No microorganism known	CO	Carboxydophilic bacteria (<i>Hydrogenomonas carboxydovorans</i> , <i>Selberia carboxyhydrogena</i> , <i>Oligotropha carboxydovorans</i> , <i>Carboxydotherrmus hydrogenoformans</i>)	Electron donor, carbon source
Heterotrophic microbes	CO ₂	Chemolitho (hydrogen-, sulfur-, ammonia-, nitrite-, Fe ²⁺ -oxidizing)- and oxygenic (cyanobacteria) and anoxygenic (Rhodospirillaceae, Chromatiaceae, Chlorobiaceae, Chloroflexaceae) photoautotrophic bacteria	Carbon source
Facultative and obligate anaerobic bacteria (clostridia, enterobacteria)	H ₂	Methanogenic archaea (<i>Methanobacterium ruminantium</i> , <i>M. thermoautotrophicum</i>) and homoacetogenic bacteria (<i>Clostridium acetivum</i> , <i>C. ljungdahlii</i>) Chemolitho (hydrogen-oxidizing)- and anoxygenic (Rhodospirillaceae, Chromatiaceae, Chlorobiaceae, Chloroflexaceae) photoautotrophic bacteria Methanogenic archaea (<i>Methanobacterium ruminantium</i> , <i>M. thermoautotrophicum</i>) and homoacetogenic bacteria (<i>Clostridium acetivum</i> , <i>C. ljungdahlii</i>)	Electron acceptor (methane or acetate production) Electron donor
Cyanobacteria (<i>Synechococcus</i> , <i>Synechocystis</i>)	O ₂	Aerobic microorganisms	Electron acceptor
Proteolytic clostridia and some aerobic chemoorganotrophic proteobacteria (<i>Serratia odorifera</i> 4Rx13, <i>Serratia plymuthica</i> HRO C48, <i>Pseudomonas fluorescens</i> L13-6-12, <i>Pseudomonas trivialis</i> 3Re2-7, <i>Stenotrophomonas rhizophila</i> P69, <i>Xanthomonas campestris</i> pv. <i>vesicatoria</i> 85-10)	NH ₃ (NH ₄ ⁺)	Many microorganisms Ammonia-oxidizing bacteria (Nitrosomonas, Nitrospira, Nitrosococcus)	Nitrogen source, olfaction, antibiotic resistance, toxic compound, electron donor
Ammonia-oxidizing bacteria (<i>Nitrosomonas</i> , <i>Nitrospira</i> , <i>Nitrosococcus</i>)	NO ₂ ⁻	Nitrite-oxidizing bacteria (<i>Nitrobacter</i> , <i>Nitrospina</i> , <i>Nitrococcus</i>)	Electron donor, nitrogen source
Denitrifying bacteria (<i>Alcaligenes faecalis</i> , <i>Bacillus licheniformis</i> , <i>Paracoccus denitrificans</i> , <i>Pseudomonas stutzeri</i> , <i>Thiobacillus denitrificans</i>)	N ₂	Nitrogen-fixing bacteria and archaea (<i>Rhizobium</i> , <i>Bradyrhizobium</i> , <i>Azorhizobium</i> , <i>Frankia</i> , <i>Klebsiella</i> , <i>Clostridium</i> , <i>Methanospirillum</i>)	Nitrogen source
Some proteobacteria (<i>Pseudomonas fluorescens</i> , <i>P. trivialis</i> , <i>Chromobacterium</i> , <i>Rhizobium</i>)	HCN	Chemolitho (sulfur-oxidizing)- and anoxygenic (Chromatiaceae, Chlorobiaceae) photoautotrophic bacteria	Defense compound, quorum sensing
Sulfate-reducing bacteria (<i>Desulfovibrio</i> , <i>Desulfomonas</i> , <i>Desulfotomaculum</i>)	H ₂ S/S/SO ₃ ²⁻		Electron donor, amino acid biosynthesis, defense compound
Organic			
Methanogenic archaea	CH ₄	Obligate methylophilic bacteria	Electron donor, carbon source
Many bacteria, see Table 2	Alkanes, alkenes	Aerobic microorganisms	Carbon source
<i>Clostridium</i> spp., <i>Pseudomonas</i> spp., <i>Streptomyces</i> spp.	ethylene		
Yeast; several bacteria, see Table 2	CH ₃ OH		

Table 1 (continued)

Producer/emitters →	compound	→ user/receiver	function
Yeast, facultative and obligate anaerobic bacteria (e.g. clostridia, enterobacteria, lactic acid bacteria); several bacteria and fungi, see Tables 2 and 3	C ₂ H ₅ OH	Obligate and facultative methylotrophic bacteria	Electron donor, carbon source, electron acceptor
<i>Clostridium</i> spp., <i>Bacillus</i> spp., <i>Lactobacillus</i> spp., <i>Salmonella</i> spp., <i>Shigella</i> spp., <i>Streptomyces</i> spp.; many other bacteria and fungi, see Tables 2 and 3	Butanol	Heterotrophic bacteria (acetic acid bacteria, <i>Clostridium kluyveri</i>)	Electron donor, carbon source
Many bacteria and fungi, see Tables 2 and 3	Low molecular mass alcohols	Heterotrophic bacteria	Electron donor, carbon source
Enterobacteria, bacilli, clostridia	Acetoin, 2,3-butanediol	Heterotrophic bacteria	Carbon source
Many bacteria and fungi, see Tables 2 and 3	CH ₂ O	Heterotrophic bacteria	Electron donor, carbon source
Many bacteria and fungi, see Tables 2 and 3	Low molecular mass aldehydes and ketones	obligate and facultative methylotrophic bacteria	electron donor, carbon source
Clostridia and other bacteria, see Table 2; fungi see Table 2	Acetone	Heterotrophic bacteria	Carbon source
Facultative and obligate anaerobic bacteria (clostridia, enterobacteria, lactic acid bacteria), many bacteria and fungi, see Tables 2 and 3	CHOOH, CH ₃ COOH, CH ₃ CH ₂ COOH, CH ₃ CH ₂ CH ₂ COOH, low molecular mass acids	Heterotrophic bacteria	Electron donor, carbon source
<i>Alcaligenes</i> spp., <i>Bacillus</i> spp., <i>Pseudomonas</i> spp., <i>Serratia</i> spp.; many other bacteria see Table 2, few fungi see Table 3	Methylamine and other amines	obligate and facultative methylotrophic bacteria	Electron donor, carbon source
<i>Streptomyces</i> spp.; see Table 2	Geosmin	methanogenic archaea	Electron donor, carbon source
<i>Alcaligenes</i> spp., <i>Chondromyces</i> spp., <i>Paenibacillus</i> spp., <i>Serratia</i> spp.; many other bacteria see Table 2	Pyrazines		
Enterobacteria, <i>Pseudomonas</i> spp.	Indole		Signaling (indirect?)
<i>Streptomyces</i> spp., <i>Bacillus</i> spp., <i>Pseudomonas</i> spp., <i>Tuber</i> spp.; many other bacteria and fungi, see Tables 2 and 3	Dimethyl/disulfide, trimethyl/disulfide	Marine sulfur-oxidizing bacteria (<i>Thiobacillus thioautotrophicus</i>) obligate and facultative methylotrophic bacteria (<i>Hyphomicrobium</i>)	Carbon and energy source
Gram negative bacteria (<i>Pseudomonas fluorescens</i> , <i>Serratia liquefaciens</i>)	N-acyl-l-homoserine lactones (AHL) (e.g. C4-HSL, C6-HSL, C10-HSL)	Gram negative bacteria (<i>Pseudomonas aeruginosa</i> , <i>Agrobacterium tumefaciens</i>)	Quorum sensing signal > biofilm formation
Gram positive bacteria <i>Streptomyces</i>	Gamma-butyrolactones	Gram positive bacteria	Quorum sensing signal
<i>Condromyces</i> spp., <i>Leuconostoc</i> spp., <i>Roseobacter</i> spp., <i>Lactobacillus</i> spp., <i>Serratia</i> spp.; many other bacteria, see Table 2	β-phenylethanol		
<i>Serratia odorifera</i> 4Rx13, <i>S. phymuthica</i> HRO-C48	Aromatic compounds	Aerobic and anaerobic bacteria	Carbon source
	Sodorifen		

The table presents examples of microorganisms that synthesize or use inorganic or organic volatile compounds. Summarized from G. Gottschalk, 1986; Fuchs, 2007; and DOVE-MO (Kalderas, 2011)

habitat (Table 1). Soil microorganisms produce large quantities of highly diverse volatiles (Stotzky and Schenck, 1976; Linton and Wright, 1993; Leff and Fierer, 2008; Insam and Seewald, 2010 and citations therein). Volatile metabolites also are produced by the root system of plants, but in this review these sources will not be considered. Instead, the focus lies on bacterial and fungal volatile emissions and uptakes (Kesselmeier and Staudt, 1999; Wenke et al., 2009). The volatile compounds can be of organic (volatile organic compounds, VOCs) or inorganic nature, both presumably important for this habitat and capable of influencing organismic communities (McNeal and Herbert, 2009). The functions of the volatiles are diverse, e.g., i) they play a role in the food chain of the microbial loop because they are assimilated and incorporated into organic matter (bioconversion), ii) they influence physiological processes (e.g., laccase activity, nitrification, nitrogen mineralization), iii) they function as electron acceptors or donors to support metabolic reactions, iv) they play a role in quorum sensing/quenching, v) they act as defense compounds, vi) they are used as communication signals, or vii) their functions remain so far elusive (Table 1).

Volatiles Emitted from Bacteria

Inorganic Volatiles

Some producers and users of inorganic volatiles are summarized in Table 1, which is a brief extract from Gottschalk (1986) and Fuchs (2007). **Carbon dioxide** is a major inorganic volatile produced by all heterotrophic living organisms, and indeed much of the CO₂ in the atmosphere originates from the huge microbial populations on earth, in both soil and aquatic habitats. Atmospheric CO₂ is assimilated primarily by plants and oxygenic and anoxygenic phototrophic bacteria (cyanobacteria, *Rhodospirillaceae* [purple nonsulfur bacteria], *Chromatiaceae* [purple sulfur bacteria], *Chlorobiaceae* [green sulfur bacteria], and *Chloroflexaceae* [green nonsulfur bacteria]). The characteristic Calvin reactions and enzymes also are present in soil bacteria, such as *Rhodospirillum rubrum*, *Thiobacillus intermedius*, *Ralstonia eutrophus*, *Pseudomonas facilis*, to name a few. Chemolithotrophic microorganisms use ATP and the reducing power of inorganic substrates for the reduction of CO₂. CO₂ also is used by methanogenic bacteria such as *Methanobacterium ruminantium* and *Methanobacterium thermoautotrophicum* for CH₄ production (Gottschalk, 1986).

Anthropogenically released **carbon monoxide** results from incomplete reduction of wood and polymers of dead organic material, while microbial CO production is unknown. Aerobically grown *Hydrogenomonas carboxydovorans* and *Selberia carboxyhydrogena* can live on CO by oxidizing it to CO₂. Some bacteria (e.g., *Rhodospseudomonas sphaeroides*,

Methylosinus, *Methylocystis*) use the serine-isocitrate lyase pathway to form oxaloacetate from phosphoenol pyruvate (PEP) and CO₂ (PEP carboxylase). As a result of this pathway, acetyl-CoA and finally succinate are formed from CH₂O and CO₂. Chemolithotrophic and phototrophic bacteria have in common the formation of cell material via CO₂ reduction by using the reducing power from inorganic compounds. Energy sources can be H₂, sulfide, ammonia, or nitrite.

Hydrogen is formed under anaerobic conditions during the fermentation of carbohydrates to short-chain fatty acids by *Clostridium* spp., *Enterobacteriaceae* (e.g., *Escherichia*, *Salmonella*, *Shigella*) and others. A group of chemolithotrophic bacteria (hydrogen-oxidizing bacteria), anoxygenic phototrophic bacteria, as well as methanogenic archaea utilize H₂ as an electron donor.

Well-known volatile-dependent soil bacteria are the free-living and symbiotic **nitrogen**-fixing organisms. The latter are, for example, *Rhizobium* spp. and *Frankia* spp., and exist in partnerships with plants. These bacteria form bacteroids, and consequently, root nodules develop. The product of the nitrogenase is **ammonia**, which is usually not released but is efficiently incorporated into organic compounds by glutamate dehydrogenase, glutamine synthetase, and glutamate synthase. Soil-living clostridia (*Clostridium* spp.) and other bacteria (e.g., *Peptococcus anaerobicus*) ferment amino acids and nucleotides and live from these recycled carbon skeletons as well as ammonia. Recently, it was shown that *Serratia*, *Pseudomonas*, *Stenotrophomonas*, and *Xanthomonas*, when grown on complex media (NB or LB), emitted gaseous ammonia (or amines), which was detected in the headspace with Nessler's reagent (Kai et al., 2010; Weise et al., 2012; Weise and Piechulla unpublished). Gaseous ammonia released from bacteria can modify, e.g., the antibiotic resistance of *E. coli* to tetracycline (Bernier et al., 2011). Apparently, increased intracellular polyamine levels alter the membrane permeability to antibiotics as well as resistance to oxidative stress. Another recent publication showed that ammonia could be sensed by *Bacillus licheniformis*, which was considered to be a first indication of bacterial olfaction (Nijland and Burgess, 2010). Although the nitrogen supply is usually a limiting factor in soil, it cannot be excluded that NH₃ emission may occur in nature under confined protein-rich growth conditions (e.g., decomposition of carcasses, lysis of large microbial populations or plant materials, or land spreading of whey in agriculture). The amounts as well as the ecological consequences have not been investigated.

Denitrifying bacteria release nitrogen during respiration and reduction of nitrate (in some cases N₂O instead of N₂ is released). The group of nitrogen-evolving bacteria is quite diverse, including *Alcaligenes faecalis*, *Bacillus licheniformis*, *Paracoccus denitrificans*, and *Pseudomonas stutzeri*.

Most soil microorganisms use sulfate as their principal sulfur source, and the intrinsic enzyme system reduces

sulfate to sulfide (sulfate assimilation). However, in anaerobic regions in the soil, sulfate is used by *Desulfovibrio*, *Desulfomonas*, *Desulfuromonas*, and *Desulfotomaculum* as a terminal electron acceptor, and consequently **hydrogen sulfide** is formed and released (dissimilatory sulfate reduction). The toxic end product H_2S is used by chemolithotrophic bacteria as electron acceptor, e.g., *Thiobacilli*, and H_2S can also be incorporated into O-acetylserine, an intermediate of amino acid biosynthesis. Furthermore, it also has been shown that H_2S production in soil is due to the presence of cysteine (Morra and Dick, 1991). Only recently it was demonstrated that H_2S production acts as a defense mechanism that protects bacteria from antibiotics (Shatalin et al., 2011).

The release of **HCN** from bacteria varies in different species (Stotzky and Schenck, 1976). *Pseudomonas* spp. (e.g., CHA0), *Chromobacterium* and *Rhizobium* typically emit this toxic inorganic volatile, while defective mutants (e.g., CHA207) do not (Blumer and Haas, 2000; Pessi and Haas, 2000; Kai et al., 2010; Blom et al., 2011b). Hydrogen cyanide inhibits several metal-containing enzymes, most significantly the cytochrome c oxidase of the respiratory chain. Therefore, this volatile can be toxic for most aerobic organisms living in the same habitat as *Pseudomonades*. It was reported that both the RHI/R- as well as the AHL-based quorum sensing system regulate HCN biosynthesis (Winson et al., 1995; Pessi and Haas, 2000). Consequently, bacterial population densities can be controlled by HCN levels.

The distribution and appearance of inorganic gaseous compounds in the soil determine the localization of other soil organisms, e.g., the oxidizers (nitrification) of ammonium occur in the upper sediment layers, followed by nitrate and sulfide oxidizers. In the deeper anaerobic layers, methanogenic and acetogenic bacteria reside. Many of the gaseous compounds are quickly recycled (e.g., H_2) because producers and utilizers appear in nearby soil zones. Compounds emitted in excess are released into the atmosphere, for example, CO_2 , N_2 , and in some regions H_2S .

Organic Volatiles (VOCs) (<120 D)

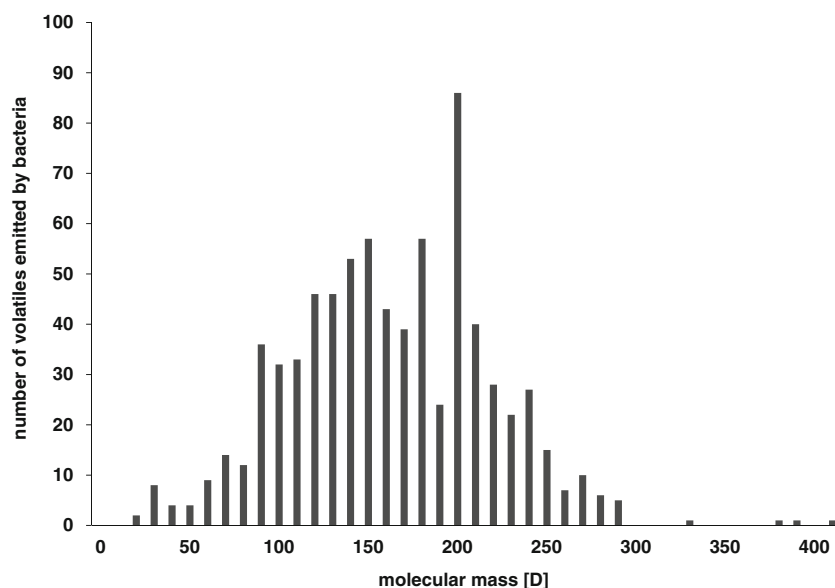
The smallest organic volatile compound is **methane**, the most reduced compound. Its formation is the terminal step in the food chain of methanogenic archaea (Gottschalk, 1986). They utilize CO_2 , CH_2O , HCOOH , or CH_3OH and H_2 to synthesize methane. This soil-based methane production is of global importance; for example, tundra and rice fields contribute 40 % of atmospheric methane. In the soil, CH_4 is a good substrate for obligate and facultative methylotrophs, which are often anaerobic organisms that grow in deeper soil layers. Bacterial production of the C_1 volatile **methanol** has been described in *Enterobacteriaceae* such as *Escherichia coli*, *Shigella flexneri*, and *Salmonella enterica* (Bunge et al.,

2008) and in *Xanthomonas campestris* (Weise et al., 2012). Methanol can be metabolized by methylotrophic bacteria including *Hyphomicrobium* species, some *Pseudomonas* species (*P. oxalaticus*), and *Protaminobacter* (Gottschalk, 1986). After an initial conversion into formaldehyde, a condensation with ribulose-5-phosphate forms dihydroxyacetone phosphate in the so-called ribulose-monophosphate cycle in *Methylococcus* and *Methylomonas* species. Yeasts, *Zymomonas mobilis*, lactic acid bacteria, and clostridia form **ethanol** (Gottschalk, 1986). Ethanol together with acetate is a good substrate for *Clostridium kluyveri*. **Butanol** and **acetone** are emitted e.g., by *Clostridium acetobutylicum* when enzymes of this pathway are activated under low pH conditions (Lütke-Eversloh and Bahl, 2011). Butanol also is formed by various microorganisms, and is considered a volatile organic compound (VOC). In the presence of butyrate and e.g., during glucose depletion butanol is a preferred product of butyrate metabolism. Many clostridia reduce acetone to isopropanol. **Acetoin** and **2,3-butanediol** typically are produced during incomplete oxidation by *Bacillus* spp. (Gottschalk, 1986). Formed from pyruvate via α -acetolactate, both compounds are released under glucose abundance and taken up when glucose is depleted. Acetoin and 2,3-butanediol then can serve as a source for ATP production needed during the sporulation process. Butanediol production also is carried out by *Enterobacteriaceae* e.g., *Serratia*, *Enterobacter*, and *Erwinia*. Small molecular weight acids such as formate, acetate, propionate and butyrate are typical mixed acid fermentation products synthesized by *Enterobacteriaceae*, *Clostridia*, *Propionibacteria*, and e.g., *Megasphaera elsdenii* (Gottschalk, 1986). Small organic acids are utilized by many heterotrophic soil microorganisms.

Volatile Organic Compounds (>120 D) Emitted from Bacteria and Fungi

It is well-known that bacteria emit small molecular weight organic volatiles (<120 D, see above), but the frequent release of other compounds (120 to ca. 300 D) by microorganisms has only recently attracted attention. A literature search allowed the compilation of around 800 VOCs emitted by bacteria and fungi. Most compounds are in the range from 130 to 210 D (Fig. 2). In the 'database of volatiles emitted by microorganisms (DOVE-MO),' all VOC emitting microorganisms were compiled, including those in soil (literature search till December 2010, Kalderas, 2011). Since the origin of the microbes often was not well-documented, or it was difficult to assign microorganisms to a single habitat, we compiled all VOC emitting microorganisms in DOVE-MO (Database of volatiles emitted by microorganisms) and present them in alphabetical order (bacteria: Table 2, fungi: Table 3). In total, 671 different VOCs are emitted by 212 bacterial species, and

Fig. 2 Distribution of molecular masses of bacterial volatile organic compounds (VOCs)



335 VOCs from 96 fungal species are known. It is expected that future investigations in this new and developing research area will rapidly add organisms and VOCs to this database.

The volatile spectra of the microbes can be simple (<10 VOCs) as well as very complex (>50 VOCs) (e.g., Kai et al., 2007, 2010). Approximately 50 bacterial and ca. 30 fungal species presently are known that emit complex volatile mixtures. The number of detectable volatiles in a species blend increases when various techniques are applied (e.g., dynamic headspace volatile capture in open and closed airflow systems, different trapping materials, solid phase microextraction (SPME), gas chromatography combined with mass spectrometry (GC/MS), proton transfer reaction/mass spectrometry (PTR-MS), selected ion flow tube/mass spectrometry (SIFT-MS), secondary electron spray ionization/mass spectroscopy (SESI-MS), as well as analytical chemistry) (summarized in Wenke et al., 2012). Furthermore, the effects of growth media and conditions on the emission spectra have to be considered (Fiddaman and Rossall, 1994; Kai et al., 2010; Blom et al., 2011a).

The compiled information of volatile-producing microorganisms and their emission profiles was used to search for characteristic VOCs emitted by certain bacterial or fungal genera. The dominant classes of compounds emitted by fungi are alcohols (e.g., isomers of butanol, pentanol, octanol), hydrocarbons, ketones, terpenes, alkanes, and alkenes (Chiron and Michelot, 2005, Table 3). Prominently emitted VOCs from bacteria are alcohols, alkanes, alkenes, and ketones, followed by esters and pyrazines, lactones, and sulfides (Wenke et al., 2012, Table 2). Some examples are given. *Streptomyces* species are especially rich in sesquiterpenes (Citron et al. 2012) and preferentially emit methylated short-chain alcohols and acids, while *Pseudomonas* species release C9–C16 alkanes/alkenes (Table 2). The product

profiles of *Bacteroides* spp. and *Lactobacillus* spp. are rich in various C4 to C16 methylated carboxylic acids, C4 to C14 carboxylic acids, and small methylated alcohols (Table 2). Short-chain and long-chain acids are well-known carbon sources for many microorganisms, but the role of low molecular mass ketones and alcohols in the metabolic food chain is less clear (Table 1). N-acyl-L-homoserine lactones (AHL) are preferentially used as infochemicals (Ryan and Dow, 2008; Dickschat, 2009). Methylamine and other amines serve as good electron donors and carbon sources for many methylotrophic bacteria and methanogenic bacteria. The emission of indole from enterobacteria is well-known, but its ecological relevance is still speculative; an effect in indirect signaling has been indicated (Ryan and Dow, 2008). The sulfur containing compounds dimethyldisulfide (DMDS) and dimethyltrisulfide (DMTS) are often emitted from bacteria and fungi (Tables 2 and 3). While the organic sulfur compounds dimethylsulfide (DMS) and dimethylpropionate (DMSP) play central roles in the global sulfur cycles. This is apparently not the case for DMDS and DMTS (Schäfer et al., 2010). A clear picture on the biological or ecological relevance of the latter compounds is still missing since contrasting results have been obtained. DMDS had inhibitory effects on *Arabidopsis thaliana* in dual culture assays (IC₅₀: 2.5 μmol) (Kai et al., 2010), while in another study it was shown that it could protect plants against fungal pathogens due to the induction of systemic resistance (Huang et al., 2012).

Prominent in bacterial emission profiles are pyrazines and β-phenylethanol. However, their biological functions are presently elusive. Even less understood is the biological and ecological relevance of the emission of extraordinary structures such as the terpene geosmin and sordorifen (Gerber and Lechevalier, 1965; Dickschat et al.,

Table 2 Compilation of VOC producing bacteria

Species	Tax ID (NCBI)	Volatile Synonym	References
<i>Acinetobacter calcoaceticus</i>	471	Sulfoacetaldehyde	Schulz and Dickschat, 2007
<i>Actinobacillus actinomycetemcomitans</i>	714	Acetic acid	Kurita-Ochiai et al., 1995
<i>Aeromonas veronii</i>	654	Dimethylselenide, Dimethyldisulfide, Methaneselenol, Dimethylselenenylsulfide	Schulz and Dickschat, 2007
<i>Alcaligenes faecalis</i>	511	Acetamide, Benzaldehyde, Phenylacetaldehyde, Methanamine, Benzothiazole, Methylpyrazine, 1-Butanamine, Dodecane, Dimethyldisulfide, Nonadecane, 1-Decene, 2,5-Dimethylpyrazine	Zou et al., 2007
<i>Alcaligenes</i> spp.	507	Methanethiol, Dimethylsulfide	Schulz and Dickschat, 2007
<i>Alteromonas</i> spp.	226	3-(Methylsulfonyl)propan-1-ol, Dimethyldisulfide, 2-Methylmercaptethanol	
<i>Anabaena</i> spp.	1163	Methyl iodide	
<i>Arctic sea ice associated bacterium ARK10141</i>	196850	Geosmin	
<i>Arctic sea ice associated bacterium ARK10146</i>	196852	Tridecan-2-one, Dimethyldisulfide, Dimethyltrisulfide, Trimethylpyrazine, Hexadecan-2-one, 2,5-Dimethylpyrazine, Pentadecan-2-one, 13-Methyltetradecan-2-one, 13-Methyltridecan-3-one	Dickschat et al., 2005c
<i>Arctic sea ice bacterium ARK10044</i>	196844	Tridecan-2-one, Hexadecyl acetate, Trimethylpyrazine, Hexadecan-2-one, 2,5-Dimethylpyrazine, Pentadecan-2-one, Tetradecan-2-one, 13-Methyltetradecan-2-one	
<i>Arctic sea ice bacterium ARK10063</i>	196865	Benzaldehyde, Menthol, Camphor, Clovene, para-Menth-1-en-4-ol, alpha-Terpineol, Trimethylpyrazine, Dihydroactinidiolide, 2,5-Dimethylpyrazine, Pentadecan-2-one, Borneol, Isolongifolene, beta-Ionone 5,6-epoxide, beta-Caryophyllene, 13-Methyltetradecan-2-one	
<i>Arctic sea ice bacterium ARK10223</i>	196854	Benzaldehyde, Tridecan-2-one, Trimethylpyrazine, 2,5-Dimethylpyrazine, Pentadecan-2-one, Tetradecan-2-one, 13-Methyltetradecan-2-one	
<i>Arctic sea ice bacterium ARK10267</i>	196855	Benzaldehyde, Benzyl alcohol, Phenol, Camphor, 2-Phenylethanol, Furfural, Acetophenone, Methylpyrazine, Clovene, Calamenene, para-Menth-1-en-4-ol Tridecan-2-one, Tetramethylpyrazine, alpha-Terpineol, Dodecan-2-one, 3-Ethyl-2,5-dimethylpyrazine, 2-Ethyl-3,5-dimethylpyrazine, Trimethylpyrazine, Ethyltrimethylpyrazine, Hexadecan-2-one, 2,5-Dimethylpyrazine, Tetradecan-2-one, Isolongifolene, Cadina-1(10),6,8-triene, Geranylacetone, beta-Caryophyllene, 2,5-Diethyl-3,6-dimethylpyrazine, 13-Methyltetradecan-2-one, 11-Methyltetradecan-2-one, 2,6-Diethyl-3,5-dimethylpyrazine	
<i>Arthrobacter globiformis</i>	1665	Phenylacetaldehyde, 2-Phenylethylamine	Schulz and Dickschat, 2007
<i>Arthrobacter nitroguajacolicus</i>	211146	Acetamide, Benzaldehyde, Phenylacetaldehyde, Methanamine, Benzothiazole, Methylpyrazine, 1-Butanamine, Dodecane, Dimethyldisulfide Nonadecane, 1-Decene, 2,5-Dimethylpyrazine	Zou et al., 2007
<i>Azoarcus evansii</i>	59406	Phenylacetate	Schulz and Dickschat, 2007
<i>Bacillus amyloliquefaciens</i>	1390	Acetoin, 2,3-Butanediol	Ryu et al., 2003; Farag et al., 2006
		Acetone Benzaldehyde, 1-Butanol, 2,3-Butanedione, Ethanol, Glyoxylic acid, Methanethiol, 1-Pentanol, Acetylene, Isoprene, 2-Methyl-1-propanol, 2-Butanone, Diethylacetic acid, 2-Methylbutanal, Cyclohexane, Dodecane, 2-Methyl-1-butanol, Ethyl acetate, 3-Methylbutanoic acid, 2-Methylfuran, Hexadecane, 3-Methylbutanal, Dimethyldisulfide, 1-Undecene, Tetrahydro-2,5-dimethylfuran, Undecane, 2-Ethylfuran, Dimethyltrisulfide, 2-Pentylfuran, 3-Methyl-1-butanol, Acetic acid butyl ester, Butanol-3-methyl acetate, 1-Methoxy-3-methylbutane, 2-Hydroxy-3-pentanone, 2,4-Hexadienal	Farag et al., 2006
<i>Bacillus popilliae</i>	78057	N-3-Methylbutylidene-3-methylbutylamine, N-Phenylmethylene-2-methylpropylamine, N-Phenylmethylene-3-methylbutylamine	Schulz and Dickschat, 2007
<i>Bacillus pumilus</i>	1408	N-Isopentylideneisopentylamine n-Hexadecanoic acid, Diethylphthalate, 3-Methyl-1-butanol, oleic acid, 8-Methyl-1-decene, 3,4-Dimethyl-5-hexen-3-ol, (E)-2-Octenal, 2,4-Decadienal, (Z)-2-Heptenal	Dickschat et al., 2005b Wei-wei et al., 2008

Table 2 (continued)

Species	Tax ID (NCBI)	Volatile Synonym	References
<i>Bacillus simplex</i>	1478	Propanone, Benzaldehyde, Phenol, Benzenacetaldehyde, Propionic acid, 1-Hexadecanol, Phenylethanol, Cyclohexene, Benzene ethanol, Nonane, 2-Undecanone, Decanal, Dodecane, Hexadecane, Dimethyl disulfide, Tetradecane, 2-Nonanone, Terpineol, 2-Octanol, Trimethylpyrazine	Gu et al., 2007
<i>Bacillus</i> spp.	1386	Acetic acid, Acetoin, Isoprene, 3-(N-methylsulfonyl)propan-1-ol, Dimethyl disulfide, 2,3,5,6-Tetramethylpyrazine, 2-Methylmercaptoethanol, (2R,3R)-Butane-2,3-diol Acetamide, Phenylacetaldehyde, Methanamine, Benzothiazole, Methylpyrazine, 1-Butanamine, Dodecane, Nonadecane, 1-Decene, 2,5-Dimethylpyrazine 2,3-Butanediol, Acetoin	Schulz and Dickschat, 2007 Zou et al., 2007 Ryu et al., 2003 Wei-wei et al., 2008
		Octanal, n-Hexadecanoic acid, Diethylphthalate, Octadecanoic acid, Heptanol, 2-Pentylfuran, Nonanal, 2-Methyl-7-oxabicyclo[2.2.1] heptane, Oleic acid, (E)-2-Octenal, (E)-2-Nonenal, (E)-2-Decenal, 2,4-Decadienal, 2-Undecenal, (Z)-2-Heptenal	Farag et al., 2006
		Acetone, 2,3-Butanedione, Ethanol, Glyoxylic acid, Methanethiol, 1-Pentanol, Acetylene, Isoprene, 2-Methyl-1-propanol, 2-Butanone, Diethylacetic acid, 2-Methylbutanal, Benzaldehyde, 1-Butanol, 2,3-Butanediol, Acetoin, Cyclohexene, Dodecane, 2-Methyl-1-butanol, Ethyl acetate, 3-Methylbutanoic acid, 2-Methylfuran, Hexadecane, 3-Methylbutanal, Dimethyl disulfide, 1-Undecene, Tetrahydro-2,5-dimethylfuran, Dimethyltrisulfide, 2-Pentylfuran, 3-Methyl-1-butanol, Acetic acid butyl ester, 3-Methylbutanol acetate, 2-Hydroxy-3-pentanone, 2,4-Hexadienal	Gu et al., 2007
		Benzaldehyde, Propanone, Phenol, 1-Hexadecanol, Benzenacetaldehyde, Propionic acid, Benzenethanol, Phenylethanol, Cyclohexene, Decanal, Dodecane, Hexadecane, Dimethyl disulfide, Tetradecane, Nonane, 2-Nonanone, 2-Undecanone, Terpineol, 2-Octanol, Trimethylpyrazine	
<i>Bacillus weihenstephanensis</i>	86662	Propanone, Benzaldehyde, Phenol, Benzenacetaldehyde, Propionic acid, 1-Hexadecanol, Benzenethanol, Phenylethanol, Cyclohexene, Nonane, 2-Undecanone, Decanal, Dodecane, Hexadecane, Dimethyl disulfide, Tetradecane, 2-Nonanone, Terpineol, 2-Octanol, Trimethylpyrazine	
<i>Bacteroides bivius</i>	28125	Acetic acid	Wiggins et al., 1985
<i>Bacteroides distasonis</i>	823	Acetic acid, Propionic acid, Isobutyric acid, Isovaleric acid	Hinton and Hume, 1995
<i>Bacteroides fragilis</i>	817	Acetate, Succinate, Isobutyrate, Isovalerate	Brondz and Olsen, 1991
		Hexadecanoic acid, Tetradecanoic acid, 12-Methyltetradecanoic acid, 13-Methyltetradecanoic acid, 3-Hydroxy-15-methylhexadecanoic acid, 3-Hydroxyhexadecanoic acid	
<i>Bacteroides gracilis</i>	824	Hexadecanoic acid, Dodecanoic acid, Octadecanoic acid, Tetradecanoic acid, 3-Hydroxytetradecanoic acid, 3-Hydroxyhexadecanoic acid, Hexadecenoic acid	Wiggins et al., 1985
<i>Bacteroides ovatus</i>	28116	Acetic acid, Propionic acid, Isovaleric acid	Brondz and Olsen, 1991
<i>Bacteroides</i>	818	Acetic acid, Propionic acid, Isobutyric acid, Isovaleric acid	Wiggins et al., 1985
<i>Bacteroides ureolyticus</i>	827	Hexadecanoic acid, Dodecanoic acid, Octadecanoic acid, Tetradecanoic acid, 3-Hydroxytetradecanoic acid, 3-Hydroxyhexadecanoic acid, Hexadecenoic acid	Schulz and Dickschat, 2007
<i>Bacteroides vulgatus</i>	821	Acetic acid, Propionic acid, Isobutyric acid, Isovaleric acid	Höckelmann and Jüttner, 2004
<i>Brevibacterium linens</i>	1703	Methanethiol, S-Methylthiobutyrate, S-Methylthio-2-methyl butyrate, S-Methyl thioacetate, S-Methyl thiocaproate, S-Methylthio-3-methyl butyrate, S-Methyl thiopropionate, S-Methylthio-2-methyl propionate, S-Methyl thiovalerate	Schulz and Dickschat, 2007
<i>Calothrix parietina</i>	32054	Octanal, Decanal, 6-Methyl-5-hepten-2-one, beta-Cyclocitral, Heptadecane, Limonene, Heptadecene, Nonanal, 2,6,6-Trimethylcyclo-hex-2-en-1-one, 8-Methylheptadecane, Dihydro-beta-ionone, beta-Ionone, beta-Ionone-5,6-epoxide	
<i>Calothrix</i> spp.	1186	Cresol, Skatole, Sulcatone, beta-Cyclocitral, 2,2,6-Trimethylcyclohexanone, Sulcatol, Dihydroactinidiolide, 2-Hydroxy-2,6,6-trimethylcyclohexan-1-one, Dihydro-beta-ionone, beta-Ionone, (Z)-5-Heptadecene, Geosmin, beta-Ionone-5,6-epoxide	Schulz and Dickschat, 2007
		Octanal, Decanal, Heptadecane, Limonene, Nonanal, Geosmin, beta-Ionone-5,6-epoxide	Höckelmann and Jüttner, 2004
<i>Campylobacter fetus</i>	196	Hexadecanoic acid, Dodecanoic acid, Octadecanoic acid, Tetradecanoic acid, 3-Hydroxytetradecanoic acid, 3-Hydroxyhexadecanoic acid, Hexadecenoic acid	Brondz and Olsen, 1991
<i>Campylobacterium ochraceum</i>	1018	Acetic acid, Propionic acid, Isovaleric acid	Kurita-Ochiai et al., 1995
<i>Campylobacterium divergens</i>	2748		Ercolini et al., 2009

Table 2 (continued)

Species	Tax ID (NCBI)	Volatile Synonym	References
<i>Carnobacterium maltaromaticum</i> <i>Chondromyces crocatus</i>	2751	Toluene, Menthol, Hexadecanol, Dibutylphthalate, Hexanal, Carbondisulfide, Isobornylacetate, Linalool, alpha-Pinene, 2-Ethylphenol, 4-Methylguaiacol, ortho-Dimethylbenzene, tert-Butylcyclohexanol, 2-Ethyl-1-hexanol, Ethyloctanoate, para-Dimethylbenzene, 4-Methylthiophenol, 1-Propanethiol, Decanal, 1-Undecanol, 1-Dodecanol, Citronellylacetate, 1-Hexadecene, Methoxybenzenethiol, 2-Nonanone, 1-Tetradecene, Decane, delta-Nonalactone, 1-Octen-3-ol, 2-Butyl-1-octanol, 2-Pentylthiophene, Limonene, 2-Ethylhexyl-2-ethyl hexanoate, 2-Dodecanol, 2-Ethylhexanal, Ethylhexanoate, Nonanal, Tetradecanal, Butylhydroxytoluene, Isotridecanol, Terbutylcyclohexyl acetate, Decenyl acetate, 2-Methyl-1-dodecanol, Hexyl formate, Ethenyl decanoate, Undecanthiol, 2-Methyl-1-undecanol, 1-Nonen-3-ol, Limoneneoxide, 9,12-Tetradecadien-1-ol acetate, 3-Hydroxydodecanoic acid, 2-Hexyl-1-decanol, 4-Methoxybenzhydrol, Tetradecen-1-ol, 5-Undecene, 5-Methyl-1,5-hexadien-3-ol, Dodecyl hexanoate, 5-Butyl-4-nonene, 2-Methyl-2-decene, 6-Methyl-1-octanol, Tetradecen-1-ol acetate, 4-Methylundecene, 8-Methyl-1-undecene, 2,3-Epoxygeranyl acetate, 2-Hexyl-1-octanol, 2-Ethylidodecanol, 2-Methyl-2-dodecene, 2-Buten-1-ol, Dodecanal, 2-Octen-1-ol, 5-Octadecene, 9-Octadecene, Tetradecenoic acid,	Schulz et al., 2004
	52	2-Ethyl-1-hexanol, 2-Nonanone, 2-Ethylhexanal, 2-Hexyl-1-octanol, 2-Buten-1-ol Benzylalcohol, 2-Phenylethanol, endo-Bornyl acetate, Benzothiazol, 1,4-Dimethoxybenzol., 2,5-Dimethylpyrazine, 2-Methoxy-3-(2-methylpropyl)pyrazine, 2-Methoxy-3-(1-methylethyl)pyrazine, (1-Methylethyl)pyrazine, beta-Copaene, 2-Methoxy-3-(1-methylpropyl)pyrazine, alpha-Elementene, Dimethyl-(1-methylethyl)pyrazine, 2-(1-Hydroxy-2-methylpropyl)-3-methoxypyrazine, Eremophilene, 1,4-Cadinadiene, Zonarene, Bicycloolemene, 2,5-bis-(1-Methylethyl)pyrazine, 2-(1-Methylethyl)-5-(1-methylethyl)pyrazine, 2,5-Bis(2-methylpropyl)pyrazine, (1R,6S,10S)-6,10-Dimethylbicyclo[4.4.0]decan-3-one, 2,6-bis-(1-Methylethyl)pyrazine, beta-Ylangene, Methyl salicylate, 1-Phenylethanol, Anisol, 2-Aminoacetophenone, Methyl 2-methoxy benzoate, 2-(Methoxymethyl)furan, alpha-Murolene, (-)-Germacrene D, (6S,10S)-6,10-Dimethylbicyclo[4.4.0]dec-1-en-3-one, (1R,6R,10R)-6,10-Dimethylbicyclo[4.4.0]decan-3-one, (1I0E,5E)-Germacadien-11-ol, Methyl anthranilate, Nonanal, 2-Methyl-3-methoxypyrazine, 2-Methyl-5-(1-methylethyl)pyrazine, Cubenol, 3-Methoxy-2,5-dimethylpyrazine, 3-Methoxy-2,6-dimethylpyrazine, 2-Methyl-6-(1-methylethyl)pyrazine, 6,10-Dimethylbicyclo[4.4.0]decan-3-ol, Geosmin Methyl salicylate, 1-Phenylethanol, Anisol, 2-Aminoacetophenone, Methyl 2-methoxy benzoate, 2-(Methoxymethyl)furan, alpha-Murolene, (-)-Germacrene D, (6S,10S)-6,10-Dimethylbicyclo[4.4.0]dec-1-en-3-one, (1R,6R,10R)-6,10-Dimethylbicyclo[4.4.0]decan-3-one, (1I0E,5E)-Germacadien-11-ol, Geosmin, 4-Methoxyacetophenone, Methyl 4-methoxy benzoate, Furfuryl 3-methyl butanoate, 2-Aminobenzaldehyde, Methyl anthranilate, Nonanal, 1,4-Dimethoxybenzene, 4-Phenylbutanone, Isopropylpyrazine, 2-Methyl-5-isopropylpyrazine, alpha-Eudesmol, 2-Methoxy-3-(1-hydroxy-2-methylpropyl)pyrazine, 2,5-Diisopropylpyrazine, 2-Isopropyl-5-isopropenylpyrazine, 2-Isopropyl-5-buten-2-yl-pyrazine, Eremophilene, 2,5-Diisobutylpyrazine, (1S,6R,10R)-6,10-Dimethylbicyclo[4.4.0]decan-3-one, 2-Methyl-6-isopropylpyrazine, 2,6-Diisopropylpyrazine 4-Phenyl-2-butanone, 2-Methoxy-3-methylpyrazine, 1-epi-Cubenol, alpha-Eudesmol, 5-Methyl-2-(1-methylethyl)pyrazine, 3-Methoxy-2,5-bis(1-methylpropyl)pyrazine, Methoxydi-(1-methylethyl)pyrazine, 3-Methoxy-2-(1-methylethylpropyl)-5-(2-methylpropyl)pyrazine, 2-Butan-2-yl-5-propan-2-yl-pyrazine, 3-Methoxy-5-(2-methylpropyl)-2-propan-2-yl-pyrazine, 3-Methoxy-2,5-bis(2-methylpropyl)pyrazine, 5-Butan-2-yl-3-methoxy-2-propan-2-yl-pyrazine, 5-Butan-2-yl-3-methoxy-2-methyl-pyrazine, 3-Methoxy-2-methyl-5-(2-methylpropyl)pyrazine, 6-Methyl-2-(1-methylethyl)pyrazine, (1S,6S,10S)-6,10-Dimethylbicyclo[4.4.0]decan-3-one, Methyl salicylate, 1-Phenylethanol, Anisol, 2-Aminoacetophenone, Methyl 2-methoxy benzoate, 2-(Methoxymethyl)furan, alpha-Murolene, (-)-Germacrene D, (6S,10S)-6,10-Dimethylbicyclo[4.4.0]dec-1-en-3-one, (1R,6R,10R)-6,10-Dimethylbicyclo[4.4.0]decan-3-one, (1I0E,5E)-Germacadien-11-ol, 4-Methoxyacetophenone, Methyl 4-methoxy benzoate, Furfuryl 3-methyl butanoate, 2-Aminobenzaldehyde, Benzothiazol, 1,4-Dimethoxybenzol., 2,5-Dimethylpyrazine, 2-Methoxy-3-(2-methylpropyl)pyrazine, 2-Methoxy-3-(1-methylethyl)pyrazine, (1-Methylethyl)pyrazine, beta-Copaene, 2-Methoxy-3-(1-methylpropyl)pyrazine, alpha-Elementene, Dimethyl-(1-methylethyl)pyrazine, 2-(1-Hydroxy-2-methylpropyl)-3-methoxypyrazine, Eremophilene, 1,4-Cadinadiene, Zonarene, Bicycloolemene, 2,5-bis-(1-Methylethyl)pyrazine, 2-(1-Methylethyl)-5-(1-methylethyl)pyrazine, 2,5-Bis(2-methylpropyl)pyrazine, (1R,6S,10S)-6,10-Dimethylbicyclo[4.4.0]decan-3-one, 2,6-bis-(1-Methylethyl)pyrazine, beta-Ylangene, Geosmin Alpha-Murolene, Cadin-1,4-diene, Geosmin	Schulz and Dickschat, 2007
		Dickschat et al., 2005e	Dickschat et al., 2005d

Table 2 (continued)

Species	Tax ID (NCBI)	Volatile Synonym	References
<i>Citrobacter freundii</i>	546	Methanethiol, Phenol, Dimethylselenenylsulfide	Schulz and Dickschat, 2007
<i>Citrobacter</i> spp.	544	2-Phenylethanol, 3-Methylbutyl propionate, 3-(Methylsulfanyl)propan-1-ol, Dimethyl(disulfide, 3-Methylbutyl) acetate, 2-Methylmercaptoethanol	
<i>Clostridium bifermians</i>	1490	Acetic acid, Propionic acid, Isovaleric acid, Isocaproic acid	Wiggins et al., 1985
<i>Clostridium butyricum</i>	1492	Acetic acid, Butyric acid	
<i>Clostridium cadaveris</i>	1529	Acetic acid, Butyric acid, Propionic acid	Michalke et al., 2000
<i>Clostridium collagenovorans</i>	29357	Dimethylselenium, Dimethyl(diselenium, Dimethyltellurium, Trimethylbismuth, Trimethylstibine, Trimethylarsine	Schulz and Dickschat, 2007
		Trimethylbismuth, Trimethylstibine, Trimethylarsine	Wiggins et al., 1985
<i>Clostridium fallax</i>	1533	Acetic acid, Butyric acid	
<i>Clostridium histolyticum</i>	1498	Acetic acid	
<i>Clostridium sporogenes</i>	1509	Acetic acid, Butyric acid, Propionic acid, Isobutyric acid, Valeric acid, Isovaleric acid, Isocaproic acid	
<i>Clostridium</i> spp.	1485	Acetic Acid, Acetoin, 2,3-Butanediol, Butyric acid, Formic acid, Ethanol, Methanol, Propionic Acid, Dimethylsulfide, Ethylene, Isobutanol, Acrylic acid, Isobutyric acid, Valeric acid, Caproic acid, Isovaleric acid, Isocaproic acid, Isopentanol, Crotonic acid, Acetic acid, Butyric acid	Stotzky and Schenck, 1976
<i>Clostridium tertium</i>	1559	Acetic acid, Butyric acid	Wiggins et al., 1985
<i>Cytophaga</i> spp.	978	3,3,7,7-Tetramethyl-1,2,5-trithiepane, 3,3,6,6-Tetramethyl-1,2,5-trithiepane, 4,4-Dimethyltrithiolane, 4,4,6,6-Tetramethyl-1,2,5-trithiepane, 3,3,8,8-Tetramethyl-1,2,5,6-tetrathioane, 2-Methylpropane-1,2-dithiol, 3,3,7,7-Tetramethyl-1,2,5,6-tetrathioane, 5,5-Dimethyltetraethane,	Sobik et al., 2007
<i>Desulfovibrio acrylicus</i>	41791	Methanethiol, Dimethylsulfide	Schulz and Dickschat, 2007
<i>Desulfovibrio gigas</i>	879	Dimethylselenium, Dimethyl(diselenium, Dimethyltellurium, Trimethylarsine	Michalke et al., 2000
		Trimethylarsine	Schulz and Dickschat, 2007
<i>Desulfovibrio vulgaris</i>	881	Dimethylselenium, Dimethyl(diselenium, Trimethylstibine, Trimethylarsine	Schulz and Dickschat, 2007
		Trimethylstibine, Trimethylarsine	Michalke et al., 2000
<i>Dinoroseobacter shibae</i>	215813	2-Phenylethanol, 4-Octanolide, 4-Nonanolide, 4-Undecanolide, 4-Heptanolide, Undecanal, Dodecanal, Butyl benzoate, Benzylcyanide, 1-Nonanol, 6-Methyl-5-hepten-2-one, 4-Hexanolide, 4-Decanolide, Tetramethylpyrazine, 4-Dodecanolide, S-Methylmethanethiosulfonate, 5-Nonanolide, Dimethyltrisulfide, 2-Methyl-4-pentanolate, 4-Methylquinazoline, 3-Methyl-1,4-pentanolate, 2-Butyl-3,6-dimethylpyrazine, 3-Butyl-2,5-dimethylpyrazine, Geranylacetone	Dickschat et al., 2005f
		S-Methylmethanethiosulfonate, S-Methylmethanethiosulfinate	Schulz and Dickschat, 2007
		2-Ethyl-5-methylpyrazine, 2-Ethyl-3,6-dimethylpyrazine, 3-Ethyl-2,5-dimethylpyrazine, 5-Methyl-2-(1-methylethyl)pyrazine, Methylmethanethiylsulfide	Dickschat et al., 2005e
<i>Dinoroseobacter</i> spp.	309512	4-Butanolide, Octan-4-olide, Nonan-4-olide, Undecan-4-olide, Heptan-4-olide, 4-Pentanolate, Butyl benzoate, Hexan-4-olide, Decan-4-olide, Dodecan-4-olide, 2-Methylpentan-4-olide, Tetradecan-4-olide, 3-Methylpentan-4-olide	Schulz and Dickschat, 2007
<i>Enterobacter agglomerans</i>	549	1-(2-Pyridinyl)ethanone	
<i>Enterobacter cloacae</i>	550	Dimethylselenide	
<i>Enterobacter</i> spp.	547	Acetoin, Indole, 2-Phenylethanol, Hydroxypropanone, 3-(Methylsulfanyl)propan-1-ol, Dimethyl(disulfide, 2-Methylmercaptoethanol	
		Acetic acid, Methanol, Acetaldehyde, Acetone, 1-Butanol, Methanethiol, 2-Methyl-1-butanol, Ethanol, Indole	Bunge et al., 2008
<i>Escherichia coli</i>	562	Acetoin, 2,3-Butanediol, 2,3-Butanedione, Glyoxylic acid, Acetylene, Isoprene, 1-Propanol-2-methyl, 2-Butanone, Diethylacetic acid, Dodecane, Ethyl acetate, 3-Methylbutanoic acid, 2-Methylfuran, Hexadecane, 3-Methylbutanal, Dimethyl(disulfide, 1-Undecene, Tetrahydro-2,5-dimethylfuran, 1-Undecane, Dimethyltrisulfide, 2-Pentylfuran, 3-Methyl-1-butanol, Acetic acid butyl ester, 3-Methylbutyl acetate, 2-Hydroxy-3-pentanone, 2,4-Hexadienal, Acetone, 1-Butanol, Methanethiol, 2-Methyl-1-butanol, Ethanol	Farag et al., 2006
		Ethanol, Indole, Acetonitrile	Zhu et al., 2010

Table 2 (continued)

Species	Tax ID (NCBI)	Volatile Synonym	References
Indole			
<i>Escherichia</i> spp.	561	2-Phenylethanol, Ethyl octanoate, 1-Decene	Schulz and Dickschat, 2007; Ryan and Dow, 2008
<i>Flavobacterium</i> spp.	237	Ethanol, Dimethyl disulfide	Schulz and Dickschat, 2007
<i>Fosfombronia pusilla</i>	34161	Geosmin	Freeman et al., 1976
<i>Fusobacterium nucleatum</i>	851	Acetic acid, Butyric acid, Propionic acid, Valeric acid, Isovaleric acid	Dickschat et al., 2005a
<i>Geobacillus stearothermophilus</i>	1422	Methanethiol, L-Methionine	Kurtita-Ochiai et al., 1995
<i>Halomonas venusta</i>	44935	Dimethylselenide, Dimethyltelluride, Dimethylditelluride, Methanetelluro	Schulz and Dickschat, 2007
<i>Jannaschia helgolandensis</i>	188906	(S)-2-Methoxy-3-(1-methylpropyl)pyrazine	Dickschat et al., 2005e
<i>Klebsiella oxytoca</i>	571	5-Methyl-2-(1-methylethyl)pyrazine	Schulz and Dickschat, 2007
<i>Klebsiella pneumoniae</i>	573	Dimethyl disulfide, Dimethyl trisulfide	
<i>Klebsiella</i> spp.	570	Phenol, 2-Methyl-5-isopropylpyrazine	
<i>Lactobacillus brevis</i>	1580	Acetoin, Indole, 2-Phenylethanol, 2-(Hydroxymethyl)furan, 1-Phenylpropan-2-one, Ethyl butanoate, 3-Methylbutyl butanoate, Methylpropyl acetate, 3-(Methylsulfonyl)propan-1-ol, Pentyl butanoate, Hexan-2-one, 2-Methylbutyl acetate, Dimethyl disulfide, 3-Methylbutyl acetate, 2-Methylmercaptoethanol	Tracey and Britz, 1989
<i>Lactobacillus casei</i>	1582	3-Methylthiopropionate, Methanethiol, 3-(Methylsulfonyl)propan-1-ol, Dimethyl disulfide, Methional	
<i>Lactobacillus fermentum</i>	1613	Acetic acid, Acetoin, Benzaldehyde, Benzenemethanol, Butanoic acid, Octanoic acid, Decanoic acid, Dodecanoic acid, 2-Phenylethanol, Isobutanol, Ethyl-2-hydroxy propionate, Pentanoic acid, Heptanoic acid, Nonanoic acid, Hexanoic acid, 3-(Methylthio)-1-propanol, Tetradecanoic acid, 3-Methyl-2-butanol, alpha, alpha-Dimethylbenzenemethanol, Isoamylalcohol	Schulz and Dickschat, 2007
<i>Lactobacillus hilgardii</i>	1588	L-Cystathionine	
<i>Lactobacillus lactis</i>	29397	3-Methylthiopropionate, Methanethiol, 3-(Methylsulfonyl)propan-1-ol, Dimethyl disulfide	
<i>Lactobacillus plantarum</i>	1590	alpha-keto-gamma-methylthiobutyric acid, Methanethiol, Methional, Methylmercaptoacetaldehyde	Tracey and Britz, 1989
		Acetic acid, Acetoin, Benzenemethanol, Butanoic acid, Octanoic acid, Decanoic acid, Dodecanoic acid, 2-Phenylethanol, Isobutanol, Ethyl-2-hydroxy propionate, Pentanoic acid, Heptanoic acid, Hexanoic acid, 3-(Methylthio)-1-propanol, Tetradecanoic acid, 3-Methyl-2-butanol, alpha, alpha-Dimethylbenzenemethanol, Isoamylalcohol, Benzaldehyde	
		3-Methylthiopropionate, Methanethiol, Phenylpyruvate, L-Phenylalanine, 3-(Methylsulfonyl)propan-1-ol, Dimethyl disulfide, Benzaldehyde	Schulz and Dickschat, 2007
<i>Lactobacillus</i> spp.	1578	Methanethiol, Dimethyl disulfide, Dimethyl trisulfide	
<i>Lactococcus lactis</i>	1358	Acetic acid, Acetoin, Benzaldehyde, Benzenemethanol, Butanoic acid, Octanoic acid, Decanoic acid, Dodecanoic acid, 2-Phenylethanol, Isobutanol, Ethyl-2-hydroxy propionate, Pentanoic acid, Heptanoic acid, Nonanoic acid, Hexanoic acid, 3-(Methylthio)-1-propanol, Tetradecanoic acid, 3-Methyl-2-butanol, alpha, alpha-Dimethylbenzenemethanol, Isoamylalcohol	Tracey and Britz, 1989
<i>Lactococcus</i> spp.	1357	L-Cystathionine, S-Methyl thiobutyrate, S-Methylthio-2-methyl butyrate, S-Methyl thioacetate, S-Methyl thiocaproate, S-Methyl thio-3-methyl butyrate, S-Methyl thiopropionate, S-Methylthio-2-methyl propionate, S-Methyl thiovalerate	Schulz and Dickschat, 2007
		Methanethiol, Phenyl pyruvate, Phenylacetaldehyde, Dimethyl disulfide, L-Phenylalanine, Dimethyl disulfide, Dimethyl trisulfide	
<i>Leuconostoc cremoris</i>	33965	Acetic acid, Acetoin, Benzaldehyde, Benzenemethanol, Butanoic acid, Octanoic acid, Decanoic acid, Dodecanoic acid, 2-Phenylethanol, Isobutanol, Ethyl-2-hydroxy propionate, Pentanoic acid, Heptanoic acid, Nonanoic acid, Hexanoic acid, 3-(Methylthio)-1-propanol, Tetradecanoic acid, 3-Methyl-2-butanol, alpha, alpha-Dimethylbenzenemethanol, Isoamylalcohol	Tracey and Britz, 1989
<i>Leuconostoc dextranum</i>	33966	Acetic acid, Acetoin, Benzaldehyde, Benzenemethanol, Butanoic acid, Octanoic acid, Decanoic acid, Dodecanoic acid, 2-Phenylethanol, Isobutanol, Ethyl-2-hydroxy propionate, Pentanoic acid, Heptanoic acid, Nonanoic acid, Hexanoic acid, 3-(Methylthio)-1-propanol, Tetradecanoic acid, 3-Methyl-2-butanol, alpha, alpha-Dimethylbenzenemethanol, Isoamylalcohol	

Table 2 (continued)

Species	Tax ID (NCBI)	Volatile Synonym	References
<i>Leuconostoc mesenteroides</i>	1245	Acetoin, Benzaldehyde, Benzenemethanol, Butanoic acid, Octanoic acid, Decanoic acid, Dodecanoic acid, 2-Phenylethanol, Isobutanol, Ethyl-2-hydroxy propionate, Pentanoic acid, Heptanoic acid, Nonanoic acid, Hexanoic acid, 3-(Methylthio)-1-propanol, Tetradecanoic acid, 3-Methyl-2-butanol, alpha, alpha-Dimethylbenzenemethanol, Isoamylalcohol	
<i>Leuconostoc oenos</i>	1247	Acetic acid, Acetoin, Benzaldehyde, Benzenemethanol, Butanoic acid, Octanoic acid, Decanoic acid, Dodecanoic acid, 2-Phenylethanol, Isobutanol, Ethyl-2-hydroxy propionate, Pentanoic acid, Heptanoic acid, Nonanoic acid, Hexanoic acid, 3-(Methylthio)-1-propanol, Tetradecanoic acid, 3-Methyl-2-butanol, alpha, alpha-Dimethylbenzenemethanol, Isoamylalcohol	
<i>Leuconostoc paramesenteroides</i>	1249	Acetoin, Benzaldehyde, Benzenemethanol, Butanoic acid, Octanoic acid, Decanoic acid, Dodecanoic acid, 2-Phenylethanol, Isobutanol, Pentanoic acid, Heptanoic acid, Nonanoic acid, Hexanoic acid, 3-(Methylthio)-1-propanol, Tetradecanoic acid, 3-Methyl-2-butanol, alpha, alpha-Dimethylbenzenemethanol, Isoamylalcohol	
<i>Loktanelia hongkongensis</i>	278132	Tetramethylpyrazine, 2-Ethyl-5-methylpyrazine, 3-Ethyl-2,5-dimethylpyrazine, 5-Methyl-2-(1-methylethyl)pyrazine, 2,5-Dimethyl-3-(3-methylbutyl)pyrazine, 3-Butyl-2,5-dimethylpyrazine	Dickschat et al., 2005e
<i>Loktanelia</i> spp.	245186	Indole, 4-Butanolide, Octan-4-olide, Nonan-4-olide, Undecan-4-olide, Heptan-4-olide, 4-Pentanolide, S-Methyl methanethiosulfonate, 4-(Methylsulfonyl)butan-2-one, S-Methylmethanethiosulfonate, Tetradecan-4-olide, Tropone, Methyl 2-furancarboxylate, 1-Phenylpropan-1,2-dione, Hexan-4-olide, Decan-4-olide, Dodecan-4-olide, 3-Methylbutan-4-olide, S-Methyl thiopropanone	Schulz and Dickschat, 2007
<i>Lyngbya</i> spp.	28073	Indole, 2-Phenylethanol, 4-Nonanolide, 4-Pentanolide, Undecanal, 1-Tetradecanol, Benzocyanide, 6-Methyl-5-hepten-2-one, Dimethyltrisulfide, 2-Ethyl-3,6-dimethylpyrazine, 4-Methylthio-2-butanone, Methylmethylthiomethylidithiolate, 4-Methylquinazoline, 2-Isopentyl-3,6-dimethylpyrazine, 2-Butyl-3,6-dimethylpyrazine, Tetramethylpyrazine, Geranylacetone, 1-Phenylpropan-1,2-dione, Hexan-4-olide, Decan-4-olide, Dodecan-4-olide, 3-Methylbutan-4-olide, S-Methyl thiopropanone	Dickschat et al., 2005f
<i>Lyobacter gummosus</i>	262324	Geosmin	Schulz and Dickschat, 2007 Zou et al., 2007
<i>Methanobacterium formicicum</i>	2162	Acetamide, Benzaldehyde, Phenylacetaldehyde, Methanamine, Benzothiazole, Methylpyrazine, 1-Butanamine, Dodecane, Dimethylidithiolate, Nonadecane, 1-Decene, 2,5-Dimethylpyrazine Stibine, Dimethylselenium, Trimethylbismuth, Trimethylstibine, Dimethyldiselenium, Dimethyltellurium, Trimethylarsine, Dimethylstibine, Monomethylstibine, Monomethylarsine, Dimethylarsine Trimethylbismuth, Monomethylarsine, Dimethylarsine	Michalke et al., 2000 Schulz and Dickschat, 2007 Siotzky and Schenck, 1976 Michalke et al., 2000
<i>Methanobacterium</i> spp.	2160	Trimethylarsine, Dimethylarsine	Schulz and Dickschat, 2007
<i>Methanobacterium thermoautotrophicum</i>	145262	Trimethylstibine	
<i>Methanosarcina barkeri</i>	2208	Dimethylselenium, Trimethylstibine, Dimethyldiselenium	Schulz and Dickschat, 2007 Gu et al., 2007
<i>Methylobacterium</i> spp.	407	Methyl iodide	
<i>Microbacterium oxydans</i>	82380	Propanone, Benzaldehyde, Phenol, Benzenacetaldehyde, Propionic acid, 1-Hexadecanol, Benzenethanol, Phenylethanol, Cyclohexene, Nonane, 2-Undecanone, Decanal, Dodecane, Hexadecane, Dimethyldisulfide, Tetradecane, 2-Nonanone, Terpeneol, 2-Octanol, Trimethylpyrazine	
<i>Microbacterium thermosphactum</i>	2756	Ethanol, Methanol	Freeman et al., 1976
<i>Myxococcus</i> spp.	32	5-Methylhexan-3-ol, 7-Methyloctan-3-one, 5-Methyl-4-hexen-3-one	Schulz and Dickschat, 2007
<i>Myxococcus xanthus</i>	34	2-Phenylethanol, Benzothiazole, Benzocyanide, 6-Methyl-5-hepten-2-one, Butyl propionate, 5-Methylhexan-3-ol, 5-Methylhexan-3-one, Tridecane, 2-Acetylfluran, Dimethyltrisulfide, Butyl acetate, 7-Methyloctan-3-one, 5-Methylhex-4-en-3-one, Cyanoisooquinoline, (3S)-Decan-3-ol, 4-Methylquinoline, 2-Aminoacetophenone, Decan-3-one, Nonan-3-one, Undecan-3-one, Dimethyltetrasulfide, Octan-3-one, Geranylacetone, Geosmin, (-)-Germaerene D, 9-Methyldecan-3-one, (1(10)E,5E)-Germacradien-11-ol	Dickschat et al., 2004
		Sulcatone, Undecan-3-ol, (S)-Decan-3-ol, Isopropidone, Octalinhydrocarbon, 4-Methylquinoline, 2-Aminoacetophenone, Decan-3-one, Nonan-3-one, Undecan-3-one, Dimethyltetrasulfide, Octan-3-one, Geranylacetone, Geosmin, (-)-Germaerene D, 9-Methyldecan-3-one, (1(10)E,5E)-Germacradien-11-ol	Schulz and Dickschat, 2007

Table 2 (continued)

Species	Tax ID (NCBI)	Volatile Synonym	References
<i>Nannocystis exedens</i>	54	Geosmin	Dickschat et al., 2005d
		(-)-Germacrene D, 9-Methyldecan-3-one, (1(10)E,5E)-Germacradien-11-ol	Dickschat et al., 2005a
		8,10-Dimethyl-1-octalin, (1(10)E,5E)-Germacradien-11-ol, Geosmin	Nawrath et al., 2008
		Benzylalcohol, Hexadecan-1-ol, 2-Phenylethanol, Isobornyl acetate, Benzothiazole, Ethyl 2-methyl propionate, Heptan-4-olide, 2-Butyl acetate, 4-Pentanolide, Ethyl-3-methyl butyrate, Dodecan-1-ol, Tetradecan-1-ol, Benzylnitrite, Pinanol, 2-Aminoacetophenone, Methyl-2-furan carboxylate, Hexan-4-olide, (-)-2-Methylisoborneol, Limonene, Ethyl-2-methyl butyrate, Diethyl succinate, Borneol, 1-Phenyldecan-1-one, 2-Methyldecan-1-one, 2-Methyl-2-bornene, 2,5-Dimethyl-3-(1-methylethyl)pyrazine, Germacrene D, (6S,10S)-6,10-Dimethylbicyclo[4.4.0]dec-1-en-3-one, 2,5-Di-(1-methylethyl)pyrazine, 2-(1-Methylethyl)-5-(1-methylethyl)pyrazine, 2,5-Di-(1-methylethyl)pyrazine, 5-(1-Methylethyl)-2-(1-methylpropyl)pyrazine, (1(10)E,5E)-Germacradien-11-ol, beta-Ylangene, Geosmin	Dickschat et al., 2007
		2-Furanmethanol, Geosmin	Schulz and Dickschat, 2007
		Geosmin	Schulz et al., 2004;
			Dickschat et al., 2005a, d
			Nawrath et al., 2008
			Dickschat et al., 2007
			Dickschat et al., 2005e
<i>Nannocystis exedens</i> subsp. <i>cinnabarina</i>	54	8,10-Dimethyl-1-octalin	Dickschat et al., 2005a
		2-Phenylethanol	Schulz and Dickschat, 2007
<i>Oceanibulbus indolifex</i>	225422	2-Ethyl-5-methylpyrazine, 3-Ethyl-2,5-dimethylpyrazine, 5-Methyl-2-(1-methylethyl)pyrazine	Wei-wei et al., 2008
		Benzaldehyde, 2-Acetylfuran, 2,5-Dimethylpyrazine, 4-(Methylsulfonyl)butan-2-one	Schulz and Dickschat, 2007
<i>Ocatdecabacter</i> spp.	53945	4-(Methylsulfonyl)butan-2-one, (R)-4-(Methylsulfonyl)butan-2-ol	Dickschat et al., 2005e
		3-Methylthiopropionate, Methanethiol, 3-(Methylsulfonyl)propan-1-ol, Dimethyldisulfide, Methional	Dickschat et al., 2005a
<i>Oenococcus oeni</i>	1247	2-Methylisoborneol	Schulz and Dickschat, 2007
		2-Methylisoborneol, Geosmin	
<i>Oscillatoria chalybea</i>	41313	n-Hexadecanoic acid, Octadecanoic acid, Diethylphthalate, Hexadecanoic acid methyl ester, Octadecanoic acid methyl ester, Azulene, Di-2-propenyltrisulfide, Diallyldisulfide, Tetradecanal, 1,3-Dithiole-2-thione, Oleic acid, (Z)-9-Hexadecenoic acid methyl ester, 2,4-Decadienal, 2-Undecenal	
		Isopropylpyrazine, 2-(2-Methylpropyl)pyrazine, 2-Methyl-5-isopropylpyrazine, 2,6-Diisobutylpyrazine, 2,5-Diisopropylpyrazine, 2-Isopropyl-5-buten-2-yl-pyrazine, 2,5-Diisobutylpyrazine, 2-Methyl-5-isobutylpyrazine, 2-Methyl-6-isopropylpyrazine, 2,6-Diisopropylpyrazine	
<i>Oscillatoria</i> spp.	1158	2,5-Dimethyl-3-(2-methylpropyl)pyrazine	
<i>Paenibacillus polymyxa</i>	1406	Methanethiol, Dimethylsulfide	
<i>Parasporobacterium paucivorans</i>	115544	Acetic acid, Acetoin, Benzaldehyde, Benzenemethanol, Butanoic acid, Octanoic acid, Decanoic acid, Dodecanoic acid, 2-Phenylethanol, Isobutanol, Ethyl-2-hydroxy propionate, Pentanoic acid, Heptanoic acid, Nonanoic acid, Hexanoic acid, 3-(Methylthio)-1-propanol, Tetradecanoic acid, 3-Methyl-2-butanol, alpha, alpha-Dimethylbenzenemethanol, Isoamylalcohol	
<i>Pediococcus dammosus</i>	51663	Octanal, alpha-Pinene, 2-Heptanone, Decanal, 6-Methyl-5-hepten-2-one, beta-Cyclocitral, 2-Tridecanone, Heptadecane, 2-Decanone, 6-Methylheptan-2-one, Limonene, Heptadecene, 7-Methylheptadecane, Nonanal, 1-Octen-3-one, 2,6,6-Trimethylcyclo-hex-2-en-1-one, 8-Methylheptadecane, 2-Decenal, Geosmin, Dihydro-beta-ionone, beta-Ionone, beta-Ionone-5,6-epoxide	
<i>Phormidium</i> spp.	1198	Sulcatone, Dihydroactinidiolide, 2-Hydroxy-2,6,6-trimethylcyclohexan-1-one, Tetrahydroionone, Dihydro-beta-ionol, 4-Oxodihydro-beta-ionone, Geosmin, Dihydro-beta-ionone, beta-Ionone, beta-Ionone-5,6-epoxide	
<i>Photobacterium</i> spp.	657	Methyl iodide	
<i>Planitibacter</i> spp.	190323	Methyl iodide	
<i>Plectonema</i> spp.	1183		

Table 2 (continued)

Species	Tax ID (NCBI)	Volatile Synonym	References
<i>Porphyromonas endodontalis</i>	28124	Octanal, Decanal, 6-Methyl-5-hepten-2-one, Heptadecane, Limonene, 7-Methylheptadecane, Nonanal, 2,6,6-Trimethylcyclo-hex-2-en-1-one, 8-Methylheptadecane, Beta-Cyclocitral, Dihydro-beta-ionone, beta-Ionone, 2,6-epoxide	Höckelmann and Jüttner, 2004
<i>Porphyromonas gingivalis</i>	837	Sulcatone, Beta-Cyclocitral, Dihydro-beta-ionone, beta-Ionone, beta-Ionone-5,6-epoxide, 2,2,6-Trimethylcyclohexanone, Sulcatol, Dihydroactinidiolide, 2-Hydroxy-2,6,6-trimethylcyclohexan-1-one, beta-Cyclogeraniol, Dihydro-beta-ionol	Schulz and Dickschat, 2007
		Hexadecanoic acid, Tetradecanoic acid, 12-Methyltetradecanoic acid, 11-Methyldecanoic acid, 13-Methyltetradecanoic acid, 3-Hydroxy-15-Methylhexadecanoic acid, 3-Hydroxypentadecanoic acid, 3-Hydroxyhexadecanoic acid	Brondz and Olsen, 1991
		Acetic acid, Butyric acid, Propionic acid, Isobutyric acid, Valeric acid, Isovaleric acid	Kurita-Ochiai et al., 1995
		Methanethiol	Schulz and Dickschat, 2007
<i>Prevotella buccae</i>	28126	Hexadecanoic acid, Tetradecanoic acid, 12-Methyltridecanoic acid, 12-Methyltetradecanoic acid, 14-Methylhexadecanoic acid, 11-Methyldecanoic acid, 14-Methylpentadecanoic acid, 13-Methyltetradecanoic acid, 3-Hydroxy-15-Methylhexadecanoic acid, 15-Methylhexadecanoic acid, 3-Hydroxypentadecanoic acid, 3-Hydroxyhexadecanoic acid, 10-Methyldecanoic acid	Brondz and Olsen, 1991
<i>Prevotella distens</i>	28130	Hexadecanoic acid, Tetradecanoic acid, 12-Methyltridecanoic acid, 12-Methyltetradecanoic acid, 14-Methylhexadecanoic acid, 11-Methyldecanoic acid, 14-Methylpentadecanoic acid, 13-Methyltetradecanoic acid, 3-Hydroxy-15-Methylhexadecanoic acid, 15-Methylhexadecanoic acid, 3-Hydroxypentadecanoic acid, 3-Hydroxyhexadecanoic acid, 10-Methyldecanoic acid	
<i>Prevotella heparinolyticus</i>	28113	Hexadecanoic acid, Tetradecanoic acid, 12-Methyltridecanoic acid, 11-Methyldecanoic acid, 13-Methyltetradecanoic acid, 3-Hydroxy-15-Methylhexadecanoic acid, 15-Methylhexadecanoic acid, 3-Hydroxypentadecanoic acid, 3-Hydroxyhexadecanoic acid, 10-Methyldecanoic acid	
<i>Prevotella intermedia</i>	28131	Acetic acid, Butyric acid, Isobutyric acid, Isovaleric acid	Kurita-Ochiai et al., 1995
<i>Prevotella loeschii</i>	840	Acetic acid, Butyric acid, Propionic acid, Valeric acid, Isovaleric acid	
<i>Prevotella oralis</i>	28134	Hexadecanoic acid, Tetradecanoic acid, 12-Methyltridecanoic acid, 12-Methyltetradecanoic acid, 14-Methylhexadecanoic acid, 11-Methyldecanoic acid, 14-Methylpentadecanoic acid, 13-Methyltetradecanoic acid, 3-Hydroxy-15-Methylhexadecanoic acid, 15-Methylhexadecanoic acid, 3-Hydroxypentadecanoic acid, 3-Hydroxyhexadecanoic acid	Brondz and Olsen, 1991
<i>Prevotella oris</i>	28135	Hexadecanoic acid, Tetradecanoic acid, 12-Methyltridecanoic acid, 12-Methyltetradecanoic acid, 14-Methylhexadecanoic acid, 11-Methyldecanoic acid, 14-Methylpentadecanoic acid, 13-Methyltetradecanoic acid, 3-Hydroxy-15-Methylhexadecanoic acid, 15-Methylhexadecanoic acid, 3-Hydroxypentadecanoic acid, 3-Hydroxyhexadecanoic acid	
<i>Prevotella spp.</i>	838	11-Methyldecanoic acid, 13-Methyltetradecanoic acid	
<i>Prevotella veroralis</i>	28137	Hexadecanoic acid, Tetradecanoic acid, 12-Methyltridecanoic acid, 12-Methyltetradecanoic acid, 11-Methyldecanoic acid, 14-Methylpentadecanoic acid, 13-Methyltetradecanoic acid, 3-Hydroxy-15-Methylhexadecanoic acid, 15-Methylhexadecanoic acid, 3-Hydroxypentadecanoic acid, 3-Hydroxyhexadecanoic acid, 10-Methyldecanoic acid	
<i>Pseudoalteromonas</i> spp.	53246	Methylolide	Schulz and Dickschat, 2007
<i>Pseudomonas aeruginosa</i>	287	Ethylene glycol, Acetic acid, Acetone, Ethanol, Indole, 4-Methylphenol, Acetonitrile, 2-Pentanone, 2-Aminoacetophenone	Zhu et al., 2010
		Butanol, 2-Undecanone, Dimethyldisulfide, 2-Nonanone, Dimethyltrisulfide, Isopentanol, Undecene, 2-Aminoacetophenone	Labows et al., 1980
<i>Pseudomonas aurantiaca</i>	86192	Benzaldehyde, Benzothiazole, 2-Ethyl-1-hexanol, Phenylendiamine, Cyclohexanol, 2-Methylpyrazine, Nonane, 2-Undecanone, Decanol, Dodecane, Pyrazine, 2-Tridecanone, Tetradecane, Pentadecane, Nonadecane, 1-Undecene, Undecane, 1-Heptadecanol, Decane, 4-Octylbenzoic acid, Dimethyltrisulfide, Nonanal, Hexadecane	Fernando et al., 2005
<i>Pseudomonas cepacia</i>	292	Dimethyldisulfide, Dimethyltrisulfide	Labows et al., 1980
<i>Pseudomonas chlororaphis</i>	587753		Fernando et al., 2005

Table 2 (continued)

Species	Tax ID (NCBI)	Volatile Synonym	References
<i>Pseudomonas corrugata</i>	47879	Benzaldehyde, Benzothiazole, 2-Ethyl-1-hexanol, Phenylenediamine, Cyclohexanol, 2-Methylpyrazine, Nonane, 2-Undecanone, Decanol, Dodecane, Pyrazine, 2-Tridecanone, Tetradecane, Pentadecane, Nonadecane, 1-Undecene, Undecane, 1-Heptadecanol, Decane, 4-Octylbenzoic acid, Dimethyltrisulfide, Nonanal, Hexadecane Benzothiazole	Schulz and Dickschat, 2007 Fernando et al., 2005
<i>Pseudomonas douderoffii</i>	84158	Benzaldehyde, Benzothiazole, 2-Ethyl-1-hexanol, Phenylenediamine, Cyclohexanol, 2-Methylpyrazine, Nonane, 2-Undecanone, Decanol, Dodecane, Pyrazine, 2-Tridecanone, Tetradecane, Pentadecane, Nonadecane, 1-Undecene, Undecane, 1-Heptadecanol, Decane, 4-Octylbenzoic acid, Dimethyltrisulfide, Nonanal, Hexadecane	Schulz and Dickschat, 2007 Lee et al., 1979; Pittard et al., 1982
<i>Pseudomonas fluorescens</i>	294	Methanethiol, Dimethylsulfide Acetoin	Lee et al., 1979; Fernando et al., 2005 Frag et al., 2006
		Benzaldehyde	
		2,3-Butanediol, 1-Butanol, 2,3-Butanedione, Glyoxylic acid, 1-Pentanol, Acetylene, Isoprene, 2-Methyl-1-propanol, Diethylacetic acid, 2-Methylbutanal, Cyclohexane, 2-Methyl-1-butanol, 2-Methylfuran, Hexadecane, Tetrahydro-2,5-dimethylfuran, 3-Methyl-1-butanol, Butanol-3-methyl acetate, 2-Hydroxy-3-pentanone, 2,4-Hexadienal, Benzaldehyde, Acetoin, Ethanol, Methanethiol, 2-Butanone, Dodecane, Undecane, Methylbutanal, Dimethyldisulfide, 1-Undecene, Dimethyltrisulfide	Labows et al., 1980 Freeman et al., 1976 Pittard et al., 1982
		Butanol, Isopentanol, Dimethyltrisulfide	
		Ethanol, Methanol, Methyl propionate, Dimethylsulfide, Dimethyldisulfide, Methylthiol acetate	
		Methanethiol, 2-Butanone, Dimethylsulfide, Toluene, 2-Nonanone, 4-Methyl-2,6-di-tert-butylphenol, Dimethyldisulfide, 1-Undecene, Dimethyltrisulfide, Nonanal, Methylthiol acetate, 2-Butanol, 3-Octanone, Dimethylbenzenes, Ethylmethylsulfide, 2-Octanol, 1-Nonene, Cycloheptene, 4-Octanone, 2-Pentanone, 2-Heptanone, Trimethylbenzene, 3-Pentanone	
		Toluene, 2-Nonanone, 4-Methyl-2,6-di-tert-butylphenol, Methyl propionate, Methyl isothiocyanate, Methyl-2-methyl butyrate, Methyl-2-enoate, Methylbutanal, Dimethyldisulfide, 1-Undecene, Dimethyltrisulfide, Methylthiol acetate Benzothiazole, 2-Ethyl-1-hexanol, Phenylenediamine, Cyclohexanol, 2-Methylpyrazine, Nonane, 2-Undecanone, Decanol, Tetradecane, Pentadecane, Nonadecane, 1-Heptadecanol, Decane, 4-Octylbenzoic acid, Hexadecane, 2-Tridecanone, Pyrazine, Dodecane, Undecane, 1-Undecene, Dimethyltrisulfide, Nonanal	Lee et al., 1979 Fernando et al., 2005
		Dimethyltelluride	
		Undecene	Schulz and Dickschat, 2007 Kai et al., 2007
<i>Pseudomonas fragi</i>	296	Acetaldehyde, Ethylalcohol, Methylmercaptan, Butanone, Ethyl butyrate, Ethyl hexanoate, Dimethylsulfide, Ethyl acetate, Dimethyldisulfide Ethanol, Methanol, Methyl acetate, Dimethylsulfide, Ethyl acetate, Dimethyldisulfide	Miller et al., 1973 Freeman et al., 1976 Ercolini et al., 2009
		Toluene, Menthol, Dibutylphthalate, Hexanal, Carbondisulfide, Linalool, alpha-Pinene, 2-Ethylphenol, 4-Methylguaiacol, 2-Ethyl-1,3-hexandiol, ortho-Dimethylbenzene, para-Dimethylbenzene, 1-Butene, 2,4,4-Trimethyl-1-pentene, Decanal, Dodecene, 10-Undecenal, 1-Dodecanol, 4(1,1,3,3-Tetramethylbutyl)phenol, 1-Nonanol, Citronellyl acetate, 1-Hexadecene, 2-Undecanol, alpha-Terpinol, 1-Octen-3-ol, 2-Butyl-1-octanol, 1,9-Nonanediol, 2-Pentylthiophene, Limonene, 2-Ethylhexyl-2-ethyl hexanoate, 2-Dodecanol, Tridecanal, Nonanal, Butylhydroxytoluene, Decenyl acetate, 2-Methyl-1-dodecanol, Hexadecanediol, 2-Methyl-1-decanol, 1-Nonen-3-ol, 1,2-Dodecanediol, 3-Hydroxydodecanoic acid, 2-Methyl-3-buten-1-ol, 2-Hexyl-1-decanol, 4-Methoxybenzylalcohol, 2-Pentadecanol, Tetradecen-1-ol, Dodecyl hexanoate, 5-Butyl-4-nonene, 2-Methyl-2-decene, 5-Methylundecene, 2,3-Epoxygeranyl acetate, 2-Ethylundecanol, 2-Ethyl-1-decanol, 2-Methyl-2-dodecene, Dodecanal, 3-Tetradecene, 3-Decen-2-one, Undecene, 6-Dodecenol, 2,5-Octanedione, 2-Methylundecanethiol, 2-Butylloctenol	
<i>Pseudomonas maltophilia</i>	40324	Butanol, 2-Undecanone, Dimethyldisulfide, Dimethyltrisulfide, Isopentanol	Labows et al., 1980
<i>Pseudomonas putida</i>	303		Lee et al., 1979

Table 2 (continued)

Species	Tax ID (NCBI)	Volatile Synonym	References
<i>Pseudomonas putrefaciens</i>	24	Acetone, 4-Methyl-2,6-di-tert-butylphenol, Methylthiol acetate, 2-Nonanone, 2-Butanone, Toluene, Benzaldehyde, Methyl benzoate, Methyl isothiocyanate, Methyl butanal, Methylpent-2-enoate, 1-Undecene, Dimethyldisulfide, Dimethyltrisulfide	Labows et al., 1980
		Butanol, Isopentanol, 2-Undecanone, Dimethyldisulfide, Dimethyltrisulfide	Freeman et al., 1976
		Ethanol, Heptadiene, Methanol, Dimethyldisulfide	Pittard et al., 1982
		Methanethiol, 3-Pentanone, 2-Pentanone, 2-Heptanone, Trimethylbenzene, 4-Octanone, n-Nonanal, Ethylmethylsulfide, 3-Octanone, Dimethylbenzenes, Acetone, 4-Methyl-2,6-di-tert-butylphenol, Methylthiol acetate, 2-Nonanone, 2-Butanone, Toluene, Carbondisulfide, Dimethyldisulfide, Dimethyltrisulfide	Schulz and Dickschat, 2007
		Phenylacetate, Carbondisulfide	Labows et al., 1980
		Butanol, Dimethyltrisulfide, Isopentanol, Dimethyldisulfide	Freeman et al., 1976
		Ethanol, Methylmercaptan, Methanol, Dimethyldisulfide	Stotzky and Schenk, 1976
		Ethylene	Freeman et al., 1976
		Methylmercaptan, Methyl acetate, Ethylbenzene, Ethyl acetate, Dimethyldisulfide, Xylene, Dimethylsulfide	Schulz and Dickschat, 2007
		Methyl iodide, 1-Undecene, Dimethylselenenylsulfide	Pittard et al., 1982
		Methylthiol n-butyrate	Ercolini et al., 2009
		6-Methyl-1-octanol, Tetradecen-1-ol acetate, 4-Methylundecene	Schulz and Dickschat, 2007
		2-Methoxy-3-(1-methylethyl)pyrazine	Kai et al., 2007
		Undecadiene, Benzoyloxybenzonitrile, Undecene	Schulz and Dickschat, 2007
		Isoprene	
		Methyl iodide	
		Dimethylselenide	
		Methyl iodide	
		Dimethylselenide, Dimethyltelluride	
		2-Heptanone, 6-Methyl-5-hepten-2-one, beta-Cyclocitral, 2-Tridecanone, 2-Decanone, Limonene, 2,6,6-Trimethylcyclohex-2-en-1-one, 8-Methylheptadecane, beta-Ionone-5,6-epoxide, Geosmin	Höckelmann et al., 2004
		Sulcatone, Geosmin	Schulz and Dickschat, 2007
		2-Ethyl-5-methylpyrazine, 3-Ethyl-2,5-dimethylpyrazine, 5-Methyl-2-(1-methylethyl)pyrazine	Dickschat et al., 2005a
		Methanethiol, Dimethylsulfide, 2-Phenylethanol	Schulz and Dickschat, 2007
		Methyl iodide, Diiodomethane, Triiodomethane, Chloriodomethane	
		Isoprene	
		Acetic acid, Acetaldehyde, 1-Butanol, Ethanol, Methanethiol, Methanol, 2-Butanone, 2-Methyl-1-butanol	Bunge et al., 2008
		Ethylene glycol, Acetic acid, Acetone, Butanol, Ethanol, Indole, 4-Methylphenol, Acetonitrile, 2-Pentanone, Pyrimidine, 2-Nonanone, Isopentanol	Zhu et al., 2010
		Propanone, Benzaldehyde, Phenol, Benzenacetaldehyde, Propionic acid, 1-Hexadecanol, Benzenethanol, Phenylethane, Cyclohexene, Nonane, 2-Undecanone, Decanal, Dodecane, Hexadecane, Dimethyldisulfide, Tetradecane, 2-Nonanone, Terpineol, 2-Octanol, Trimethylpyrazine	Gu et al., 2007
		Beta-Phenylethanol, Dimethyldisulfide, Dimethyltrisulfide, Methanethiol, Sodorifen	
		Beta-Phenylethanol, Benzyl nitrile, trans-9-Hexadecene-1-ol	Kai et al., 2007 and 2010
			Kai et al., 2007
		Toluene, Menthol, Hexanal, Carbondisulfide, Linalool, alpha-Pinene, 2-Ethylphenol, 4-Methylguaiacol, ortho-Dimethylbenzene, Ethyl octanoate, para-Dimethylbenzene, 1-Propanethiol, Ethyl decanoate, Citronellyl acetate, 1-	Ercolini et al., 2009
<i>Roseobacter gallaeciensis</i>	60890		
<i>Roseobacter</i> spp.	2433		
<i>Roseovarius</i> spp.	74030		
<i>Saccharomonospora</i> spp.	1851		
<i>Salmonella enterica</i>	28901		
<i>Salmonella enterica</i> serovar typhimurium	90371		
<i>Serratia marcescens</i>	615		
<i>Serratia odorifera</i> 4Rx13	618		
<i>Serratia plymuthica</i>	82996		
<i>Serratia proteamaculans</i>	28151		

Table 2 (continued)

Species	Tax ID (NCBI)	Volatile Synonym	References
<i>Serratia</i> spp.	613	Methyl-2,1-methylethylbenzene, Methylthiolsulfide, 1-Hexadecene, 2-Hexen-1-ol, alpha-Terpineol, 1-Octen-3-ol, 2-Pentylthiophene, Limonene, 2-Ethylhexyl-2-ethyl hexanoate, 2-Dodecanol, Ethyl nonanoate, 3-Methyl-1-butanol, Ethyl hexanoate, Isoamyl acetate, Butylhydroxytoluene, Decenyl acetate, 2-Hexen-1-ol propanoate, Linalyl propanoate, Borneol, 1-Nonen-3-ol, 3-Hydroxydodecanoic acid, 4-Methoxybenzylalcohol, Tetradecen-1-ol, Dodecyl hexanoate, 3-Octanone, 5-Butyl-4-nonene, 6-Methyl-1-octanol, Tetradecen-1-ol acetate, 4-Methylundecene, 2,3-Epoxygeranyl acetate, 4-Hydroxy-3-methylbutanol, Dodecanol, trans-2-Hexen-1-ol, 2-Octen-1-ol, 2-Nonen-1-ol	Bruce et al., 2004
<i>Shewanella</i> spp.	22	Acetic acid, 3-Hydroxy-2-butanone, 2-Propanone, Ethanol, 1,2-Benzenedicarboxylic acid, 2-Propanol, 2-Methyl-1-propanol, 2-Butanone, 2-Methylpropanoic acid, 1,2-Dimethylbenzene, 2-Ethyl-1-hexanol, 2-Pentanone, Acetic acid ethenyl ester, 2-Heptanone, 2-Undecanone, 2-Methylbutanoic acid, Ethyl acetate, 3-Methylbutanoic acid, 2-Nonanone, Undecane, 2-Dodecanone, 2,5-Dimethylpyrazine, Limonene, Dimethyldisulfide, Dimethyltrisulfide	Schulz and Dickschat, 2007
<i>Shigella</i> spp.	623	Acetoin, Undecan-2-one, Nonan-2-one, Dodecan-2-one, Dimethyldisulfide, Dimethyltrisulfide	Bunge et al., 2008
<i>Shigella flexneri</i>	13687	Acetic acid, Acetaldehyde, Acetone, 1-Butanol, Ethanol, Indole, Methanethiol, Methanol, 2-Methyl-1-butanol	Schulz and Dickschat, 2007
<i>Shingomonas</i> spp.	118562	Methyl iodide	Zou et al., 2007
<i>Spirulina platensis</i>	363855	beta-Ionone-5,6-epoxide	Zhu et al., 2010
<i>Sporosarcina ginsengisoli</i>	1280	Acetamide, Benzaldehyde, Phenylacetaldehyde, Methanamine, Benzothiazole, Methylpyrazine, 1-Butanamine, Dodecane, Dimethyldisulfide, Nonadecane, 1-Decene, 2,5-Dimethylpyrazine	Kai et al., 2007
<i>Staphylococcus aureus</i>	1282	Ethylene glycol, Acetic acid, Acetone, Butanol, 4-Methylphenol, 2-Aminoacetophenone, 2-Pentanone, Pyrimidine, 2-Nonanone, Isopentanol	Schulz and Dickschat, 2007
<i>Staphylococcus epidermidis</i>	1279	Beta-Phenylethanol, Dodecanal	Beck et al., 2002
<i>Staphylococcus xylosum</i>	1288	Acetic acid, Acetoin, Butanoic acid, Butanedione, Propanoic acid, 2-Methylpropanal, 2-Methylbutanal, 3-Methylbutanal, Pentane-2,3-dione	Schulz and Dickschat, 2007
<i>Stappia marina</i>	281252	Acetic acid, Acetaldehyde, 2-Hydroxy-3-butanone, Acetone, Benzaldehyde, Butanoic acid, 3-(Methylthio)propanoic acid, Lactic acid, 2,3-Butanedione, Ethanol, Benzeneacetaldehyde, Benzeneacetic acid, Propanoic acid, 2-Propanol, 2-Phenylethanol, 2-Methylpropanol, 2-Methylpropanal, 2-Butanone, 2-Methylpropanoic acid, 2-Methylbutanal, Acetophenone, 2-Phenylethyl acetate, 2-Methylbutanol, 3-Methylbutanol, 2,3-Pentanedione, Dimethyldisulfide, 3-(Methylthio)propanal, 2,5-Dimethylpyrazine, 3-Methylbutanol, 3-Methyl-1-butyl acetate, 2-Methylbutanoic acid, 3-Methylbutanoic acid, 3-Methylbut-2-en-1-ol, 3-Methylbut-3-en-1-ol, 2-Methyltetrahydrothiophen-3-one	Dickschat et al., 2005e
<i>Stenotrophomonas maltophilia</i>	40324	3-Methylmercapto propionate, Phenylacetaldehyde, Phenyl acetate, 2-Phenylethanol, Methylpropanoic acid, 2-Methylbutanoic acid, 3-Methylbutanoic acid, 3-Methylbut-2-en-1-ol, 3-Methylbut-3-en-1-ol, 2-Methyltetrahydrothiophen-3-one	Zou et al., 2007
<i>Stenotrophomonas rhizophila</i>	216778	Methyltetrahydrothiophen-3-one	Gu et al., 2007
<i>Stigmatella aurantiaca</i>	41	Tetramethylpyrazine, 2-Ethyl-5-methylpyrazine, 5-Methyl-2-(1-methylethyl)pyrazine	Zou et al., 2007; Gu et al., 2007
		Acetamide, Benzaldehyde, Phenylacetaldehyde, Methanamine, Benzothiazole, Methylpyrazine, 1-Butanamine, Nonadecane, 1-Decene, 2,5-Dimethylpyrazine	Kai et al., 2007
		Propanone, Benzaldehyde, Phenol, Benzeneacetaldehyde, Propionic acid, 1-Hexadecanol, Benzeneethanol, Phenylethanol, Cyclohexene, Nonane, 2-Undecanone, Decanal, Hexadecane, Tetradecane, 2-Nonanone, Terpineol, 2-Octanol, Trimethylpyrazine	Dickschat et al., 2005b
		Dodecane, Dimethyldisulfide	
		beta-Phenylethanol	
		Dodecanal	
		Benzaldehyde, Benzylalcohol, Butyl acetate, Dimethyltrisulfide, Menthol, Hexadecan-1-ol, 2-Phenylethanol, 2-Methoxy-1,1'-biphenyl, Methyl benzoate, 4-Butanol, Acetophenone, 4-Pentanone, Undecan-2-one, Tetradecan-1-ol, 2-Methylbutyric acid, 6-Methylhept-5-en-2-one, 3-Methylbutyric acid, para-Menth-1-en-3-ol, Butyl propionate, Pent-2-en-4-olide, Pentadecan-1-ol, Methyl 3-methyl crotonate, 2-Acetylfuran, Undecan-2-ol, beta-Copaene, Guaioide, 13-Methyltetradecan-1-ol, Tetradecan-4-olide, N-Isopentylacetamide, N-Isopentylideneisopentylamine, 6,10-Dimethylbicyclo[4.4.0]dec-1-ene, N-Isopentylformamide, (E,E)-Farnesol, N-(2-Phenylethylidene)isopentylamine, Geranylacetone, Methyl-2-methyl crotonate, 2-Methyltetradecan-4-one, beta-Ylangene, Methyl salicylate, 4-	

Table 2 (continued)

Species	Tax ID (NCBI)	Volatile Synonym	References
		Methylquinoline, Hexahydrofamesylacetone, Nonadecan-10-one, 5-Methylhexan-3-one, Dodecan-3-one, alpha-Terpeneol, S-Methylmethanethiosulfonate, Dihydroactinidiolide, 1-Phenylundecan-1-one, 1-Phenylnonan-1-one, 1-Phenyldecan-1-one, beta-Eudesmol, 6,10-Dimethylundeca-5,9-dien-2-ol, Dodecan-3-ol, Methyl-5-methyl hexanoate, Nerolidol, Germacrene D, Valerianol, Geosmin, (1(10)E,5E)-Germacradien-11-ol	Schulz and Dickschat, 2007
		Methyl salicylate, 4-Methylquinoline, Hexahydrofamesylacetone, Nonadecan-10-one, 5-Methylhexan-3-one, Dodecan-3-one, alpha-Terpeneol, S-Methylmethanethiosulfonate, Dihydroactinidiolide, 1-Phenylundecan-1-one, 1-Phenylnonan-1-one, 1-Phenyldecan-1-one, beta-Eudesmol, 6,10-Dimethylundeca-5,9-dien-2-ol, Dodecan-3-ol, Methyl-5-methyl hexanoate, Nerolidol, Germacrene D, Valerianol, Menthol, 2-Methylisoborneol, S-Methylmethanethiosulfinate, N-(3-Methylbutyl)acetamide, N-3-Methylbutylidene-3-methylbutylamine, N-(3-Methylbutyl)formamide, Farnesol, N-(2-Phenylethylidene)-3-methylbutylamine, p-Meth-1-en-4-ol, Rosifolol, Isopropylidene, Octalinhydrocarbon, Geosmin, Stigmolone, (1(10)E,5E)-Germacradien-11-ol	Dickschat et al., 2005c Schulz et al., 2004; Dickschat et al., 2007 Dickschat et al., 2005d Schulz and Dickschat, 2007
		Stigmolone	
		(1(10)E,5E)-Germacradien-11-ol, Geosmin	
<i>Stigmatella</i> spp.	40	Methyl benzoate, 4-Butanolide, Octan-4-olide, Nonan-4-olide, Undecan-4-olide, Heptan-4-olide, 4-Pentanolide, Hexan-4-olide, Decan-4-olide, Methyl 3-methylbut-2-enoate, Dodecan-4-olide, Methyl 2-methylbut-2-enoate, Tetradecan-4-olide	Schöllner et al., 2002 Schulz and Dickschat, 2007
<i>Streptomyces albidoflavus</i>	1886	Acetone, 1-Butanol, 2-Phenylethanol, Isoprene, 2-Methyl-1-propanol, Cyclopentanone, 2-Methyl-1-butanol, Dimethyl-disulfide, 3-Methyl-3-buten-1-ol, Dimethyltrisulfide, 3-Methyl-1-butanol, Ethanethioic acid S-methyl ester, Geosmin, S-Methyl thiobutyrate, S-Methyl thioacetate, S-Methyl thio-3-methylbutyrate, S-Methyl thiopropionate, Albalavenone	Schöllner et al., 2002 Schulz and Dickschat, 2007
<i>Streptomyces albus</i>	1888	Acetone, 1-Butanol, Cyclopentanone, 2-Methyl-1-butanol, 2-Methylpropanoic acid methyl ester, Dimethyldisulfide, 3-Methyl-3-buten-1-ol, 2-Methylbutanoic acid methyl ester, Dimethyltrisulfide, 3-Methyl-1-butanol, Ethanethioic acid S-methyl ester, Geosmin	Schöllner et al., 2002
<i>Streptomyces antibioticus</i>	1890	Camphor, 3-Methylbut-3-en-1-ol, Geosmin Acetone, 1-Butanol, 2-Phenylethanol, Isoprene, 2-Methyl-1-propanol, Cyclopentanone, 2-Methyl-1-butanol, 2-Methylpropanoic acid methyl ester, 3-Methylbutanoic acid methyl ester, Methyl butyrate, Dimethyldisulfide, 3-Methyl-3-buten-1-ol, 2-Methylbutanoic acid methyl ester, Dimethyltrisulfide, 3-Methyl-1-butanol, Geosmin	Schulz and Dickschat, 2007 Schöllner et al., 2002
<i>Streptomyces aureofaciens</i>	1894	Acetone, 1-Butanol, Isoprene, 2-Methyl-1-propanol, Cyclopentanone, 2-Methyl-1-butanol, 2-Methylpropanoic acid methyl ester, 3-Methylbutanoic acid methyl ester, Methyl butyrate, Dimethyldisulfide, 2-Methylbutanoic acid methyl ester, 2-Methylisoborneol, Dimethyltrisulfide, Geosmin, 3-Methyl-1-butanol	Schulz and Dickschat, 2007 Schöllner et al., 2002
<i>Streptomyces caviscabies</i>	90079	Linalool, 4-Methylquinoline, 2-Aminoacetophenone, 3-Methylbut-2-en-1-ol, 3-Methylbut-3-en-1-ol, 6-Methylheptan-2-one, gamma-Murolene, 5-Methylheptan-2-one, Dimethyltetrasulfide, S-Methyl thiobenzate, Dimethylpentasulfide, alpha-Murolene, (E)-4,8-Dimethylnona-1,3,7-triene, 2-Methyl-2-borneone, Isothujone, delta-Cadinene, Geraniol, Cadina-1,4-diene, cis-Calamene, Kelsoene, alpha-Gurjunene, (1(10)E,5E)-Germacradien-11-ol, 10-Methylundecan-5-olide, 10-Methylundecan-4-olide, 10-Methylundecan-4-olide, 10-Methylundecan-5-olide, 10-Methylundec-2-en-4-olide, 10-Methylundec-3-en-4-olide, 10-Methylundec-3-en-4-olide, 10-Methylundec-3-en-4-olide, beta-Murolene	Schulz and Dickschat, 2007
<i>Streptomyces citreus</i>	67288	4-Methylpent-3-en-2-one, 3-Methylpentan-2-ol, 3-Methylbutan-2-ol, 2-Acetylfuran, Limonene, Geosmin, beta-Myrcene, delta-Elemene, delta-Cadinene, Geraniol, Bicyclogermacrene, Germacrene D, beta-Gurjunene, beta-Elemene, Dihydroarogofuran, (1(10)E,5E)-Germacradien-11-ol	Schöllner et al., 2002
<i>Streptomyces coelicolor</i>	1902	Acetone, 1-Butanol, Isoprene, 2-Methyl-1-propanol, Cyclopentanone, 2-Methyl-1-butanol, 2-Methylpropanoic acid methyl ester, Methyl butyrate, Dimethyldisulfide, 3-Methyl-3-buten-1-ol, 2-Methylbutanoic acid methyl ester, Dimethyltrisulfide, 3-Methyl-1-butanol, Ethanethioic acid S-methyl ester, Dimethyltetrasulfide, Geosmin	Dickschat et al., 2005a Schulz and Dickschat, 2007
		(1(10)E,5E)-Germacradien-11-ol	

Table 2 (continued)

Species	Tax ID (NCBI)	Volatile Synonym	References
<i>Streptomyces diastatochromogenes</i>	42236	Acetone, 1-Butanol, 2-Phenylethanol, Isoprene, 2-Methyl-1-propanol, Cyclopentanone, 2-Methyl-1-butanol, Dimethyl-disulfide, 3-Methyl-3-buten-1-ol, 2-Methylisoborneol, Dimethyltrisulfide, Geosmin, 3-Methyl-1-butanol	Schöller et al., 2002
<i>Streptomyces griseus</i>	1911	Acetone, 1-Butanol, 2-Phenylethanol, Isoprene, 2-Methyl-1-propanol, Cyclopentanone, 2-Methyl-1-butanol, Dimethyl-disulfide, 3-Methyl-3-buten-1-ol, 2-Methylbutanoic acid methyl ester, 2-Methylisoborneol, Dimethyltrisulfide, 3-Methyl-1-butanol, Ethanethioic acid S-methyl ester, Geosmin, Dimethyltetrasulfide	Schulz and Dickschat, 2007
		Alpha-Pinene, Beta-Pinene, S-Methyl thiobutylate, Dimethyltetrasulfide	Dickschat et al., 2005a;
		Geosmin	Nawrath et al., 2008
		beta-Gurjunene	Dickschat et al., 2005d
<i>Streptomyces hirsutus</i>	35620	Acetone, 1-Butanol, 2-Phenylethanol, Isoprene, 2-Methyl-1-propanol, Cyclopentanone, 2-Methyl-1-butanol, 3-Methylbutanoic acid methyl ester, Methyl butyrate, Dimethyl-disulfide, 3-Methyl-3-buten-1-ol, Dimethyltrisulfide, Geosmin, 3-Methyl-1-butanol, Ethanethioic acid S-methyl ester, Dimethyltetrasulfide	Schöller et al., 2002
<i>Streptomyces hygroscopicus</i>	1912	Acetone, 1-Butanol, 2-Phenylethanol, Isoprene, Cyclopentanone, 2-Methyl-1-butanol, 2-Methylpropanoic acid methyl ester, 3-Methylbutanoic acid methyl ester, Methyl butyrate, Dimethyl-disulfide, 2-Methylbutanoic acid methyl ester, 2-Methylisoborneol, Dimethyltrisulfide, Geosmin, 3-Methyl-1-butanol, Dimethyltetrasulfide	
<i>Streptomyces lateritis</i>	67313	Propanone, Benzaldehyde, Phenol, Benzenacetaldehyde, Propionic acid, 1-Hexadecanol, Benzenethanol, Phenylethanone, Cyclohexene, Nonane, 2-Undecanone, Decanal, Dodecane, Hexadecane, Dimethyl-disulfide, Tetradecane, 2-Nonanone, Terpineol, 2-Octanol, Trimethylpyrazine	Gu et al., 2007
<i>Streptomyces lavendulae</i>	1914	(-)-2-Methylisoborneol	Dickschat et al., 2007
<i>Streptomyces murinus</i>	33900	Acetone, 1-Butanol, 2-Phenylethanol, Isoprene, 2-Methyl-1-propanol, Cyclopentanone, 2-Methyl-1-butanol, 2-Methylpropanoic acid methyl ester, Methyl butyrate, Dimethyl-disulfide, 3-Methyl-3-buten-1-ol, 2-Methylisoborneol, 2-Methyl-1-butanol	Schöller et al., 2002
<i>Streptomyces olivaceus</i>	47716	Acetone, 1-Butanol, 2-Phenylethanol, 2-Methyl-1-propanol, 2-Methyl-1-butanol, 2-Methylpropanoic acid methyl ester, Dimethyl-disulfide, 3-Methyl-3-buten-1-ol, 2-Methylisoborneol, Dimethyltrisulfide, Geosmin, 3-Methyl-1-butanol	
<i>Streptomyces platensis</i>	58346	Butanoic acid 2-methyl ester, 1a,2,3,3a,4,5,6,7b-Octahydro-1,1,3a,7-tetramethyl-1H-cyclopropa[a]naphthalene, trans-1,10-Dimethyl-trans-9-decalol, 5-Methoxy-1,3-dimethyl-1H-pyrazole, 1,1,4,4-Tetramethyl-2,5-dimethylene- cyclohexane, 3,3,7,11-Tetramethyltricyclo [5.4.0.0 (4,11)] undecan-1-ol, 2-(2,4-Dimethoxybenzylidenehydrazino)-N-ethyl-2-oxoacetamide,	Wan et al., 2008
<i>Streptomyces risiriensis</i>	68264	Acetone, 1-Butanol, Isoprene, 2-Methyl-1-propanol, Cyclopentanone, 2-Methyl-1-butanol, Dimethyl-disulfide, 3-Methyl-3-buten-1-ol, Dimethyltrisulfide, Geosmin, 3-Methyl-1-butanol	Schöller et al., 2002
<i>Streptomyces</i> spp.	1883	Acetoin, Butane-2,3-diol, Isoprene, Methyl benzoate, 2-(Hydroxymethyl)furan, Hexanoic acid, 3-Methylfuran, S-Methyl thioacetate, Pentalene, Germacrene A, Protoilludene, Benzylalcohol, Benzothiazole, 2-Phenylethyl acetate, 1-Phenylpropan-2-one, Benzyl acetate, 4-Methylquinoline, 3-Methylbut-2-en-1-ol, 2-Phenylpropan-2-ol, Dimethyl-disulfide, 3-Methylbut-3-en-1-ol, Dodecan-4-olide, Butylphenyl acetate, Dimethyltetrasulfide, 4-Methylhexan-1-ol, 4-Methylquinazoline, 2-Phenylethanol, 2-Methylisoborneol, Dimethyltrisulfide, Geosmin	Schulz and Dickschat, 2007
		Acetone, 1-Butanol, Isoprene, Cyclopentanone, 2-Methyl-1-butanol, 3-Methyl-1-butanol, 2-Phenylethanol, 2-Methylisoborneol, Dimethyltrisulfide, Geosmin	Schöller et al., 2002
		Vinylguaiacol, Hexadecanoic acid, Octadecanoic acid, Methyl-4-hydroxy benzoate, Heptadecanoic acid, Tetradecanoic acid, Pentadecanoic acid, 12-Methyltetradecanoic acid, 14-Methylhexadecanoic acid, 14-Methylpentadecanoic acid, 13-Methyltetradecanoic acid, 15-Methylhexadecanoic acid, 12-Methyltridecanoic acid, Pentadecenoic acid, 9-Octadecenoic acid, Squalene, 9-Hexadecenoic acid, (R)-10-methyl-6-undecanolid, (6R,10S)-10-methyl-6-dodecanolide, 2-Phenylethanol, Geosmin	Stritzke et al., 2004
		Benzophenone, Isobornyl acetate, Linalool, Ethyl-2-methyl propionate, Methylpyrazine, Heptan-2-one, Hexan-1-ol, Benzylcyanide, 6-Methylhept-5-en-2-one, 2-Aminoacetophenone, 6-Methylheptan-2-one, 2-Acetyl-furan, gamma-Murolene, Heptane-2,5-dione, Geranylacetone, 5-Methylheptan-2-one, Butyl acetate, Cyclooctasulfur, S-Methyl thiobenzoate, Dimethylpentasulfide, Guaixoxide, Methyl methylthiomethyl disulfide, alpha-Murolene, Isolongifolene, Citronellylacetone, (E)-4,8-Dimethylnona-1,3,7-triene, 2-Methyl-2-bornene, Isothujone, delta-Cadinene, 1-epi-	Dickschat et al., 2005d

Table 2 (continued)

Species	Tax ID (NCBI)	Volatile Synonym	References
<i>Streptomyces sulphureus</i>	47758	Cubenol, 2-Methoxy-3-(1-methylpropyl)pyrazine, Geraniol, Cadina-1,4-diene, cis-Calamenene, beta-Gurjunene, Kelsoene, alpha-Gurjunene, 10-Methylundecan-5-olide, 10-Methylundecan-4-olide, 10-Methyldodecan-4-olide, 10-Methyldodecan-5-olide, 10-Methylundec-2-en-4-olide, 10-Methyldodec-2-en-4-olide, 10-Methylundec-3-en-4-olide, 10-Methyldodec-3-en-4-olide, beta-Murolene, Benzylalcohol, Benzothiazole, 2-Phenylethyl acetate, 1-Phenylpropan-2-one, Benzyl acetate, 4-Methylquinoline, 3-Methylbut-2-en-1-ol, 2-Phenylpropan-2-ol, Dimethyldisulfide, 3-Methylbut-3-en-1-ol, Dodecan-4-olide, Butylphenyl acetate, Dimethyltetrasulfide, 4-Methylhexan-1-ol, 4-Methylquinazoline, 2-Phenylethanol, 2-Methylisoborneol, Dimethyltrisulfide, (1(10) <i>E</i> ,5 <i>E</i>)-Germacradien-11-ol, Geosmin	Stotzky and Schenk, 1976 Ryan and Dow JM, 2008 Dickschat et al., 2007 Nawrath et al., 2008 Schulz and Dickschat, 2007 Schöller et al., 2002
<i>Streptomyces thermoviolaceus</i>	1952	Ethylene Butyrolactone Geosmin (1(10) <i>E</i> ,5 <i>E</i>)-Germacradien-11-ol, 8,10-Dimethyl-1-octalin Geosmin	Stotzky and Schenk, 1976 Ryan and Dow JM, 2008 Dickschat et al., 2007 Nawrath et al., 2008 Schulz and Dickschat, 2007 Schöller et al., 2002
<i>Sulfitobacter dubius</i>	218673	Acetone, 1-Butanol, 2-Phenylethanol, Isoprene, 2-Methyl-1-propanol, Cyclopentanone, 2-Methyl-1-butanol, 2-Methylpropanoic acid methyl ester, Methylbutyrate, Dimethyldisulfide, 3-Methyl-3-buten-1-ol, 2-Methylbutanoic acid methyl ester, Dimethyltrisulfide, Geosmin, 3-Methyl-1-butanol, Ethaneithioic acid S-methyl ester	Dickschat et al., 2005e
<i>Sulfitobacter pontiacus</i>	60137	Tetramethylpyrazine, 3-Ethyl-2,5-dimethylpyrazine, 2,5-Dimethyl-3-(3-methylbutyl)pyrazine, 3-Butyl-2,5-dimethylpyrazine, 2-Ethyl-5-methylpyrazine, 3-Ethyl-2,5-dimethylpyrazine, Ethyltrimethylpyrazine, 5-Methyl-2-(1-methylethyl)pyrazine, 2,5-Dimethyl-3-(3-methylbutyl)pyrazine, 2,5-Dimethyl-3-(2-methylpropyl)pyrazine, 3-Butyl-2,5-dimethylpyrazine, 2,5-Dimethyl-3-methylsulfanylpiazine	Dickschat et al., 2005e
<i>Sulfitobacter</i> spp.	60136	2,5-Dimethyl-3-methylsulfanylpiazine 2-Ethyl-5-methylpyrazine, 3-Ethyl-2,5-dimethylpyrazine, 5-Methyl-2-(1-methylethyl)pyrazine 2-(3-Methylbutyl)-3,6-dimethylpyrazine, 2-Isobutyl-3,6-dimethylpyrazine, 2-Butyl-3,6-dimethylpyrazine, 2-(2-Methylbutyl)-3,6-dimethylpyrazine, 2,5-Dimethyl-3-methylsulfanylpiazine	Schulz and Dickschat, 2007 Dickschat et al., 2005e Schulz and Dickschat, 2007
<i>Thermoactinomyces</i> spp.	2023	Isoprene, 2-Methylfuran	
<i>Thermomonospora fusca</i>	2021	5-Methylhexan-3-one, S-Methyl thiobutyrate	
<i>Thermomonospora</i> spp.	2019	Isoprene	
<i>Tolypothrix distorta</i>	119534	Octanal, alpha-Pinene, 2-Heptanone, Decanal, 6-Methyl-5-hepten-2-one, beta-Cyclocitral, 2-Tridecanone, Heptadecane, 2-Decanone, 6-Methylheptan-2-one, Limonene, Heptadecene, Geosmin, 7-Methylheptadecane, Nonanal, 1-Octen-3-one, 8-Methylheptadecane, beta-Ionone, 2-Decenal, beta-Ionone-5,6-epoxide	Höckelmann et al., 2004
<i>Tolypothrix</i> spp.	111782	Sulcatone	Schulz and Dickschat, 2007
<i>Treponema denticola</i>	158	Methanethiol, L-Methionine	
<i>Variovorax</i> spp.	34072	Methyl iodide	Hinton and Hume, 1995
<i>Veillonella</i> spp.	29465	Acetate, Succinate, Isobutyrate, Isovalerate	Schulz and Dickschat, 2007
<i>Vibrio</i> spp.	662	Methyl iodide	Brondz and Olsen, 1991
<i>Wolinella curva</i>	200	Hexadecanoic acid, Dodecanoic acid, Octadecanoic acid, Tetradecanoic acid, 3-Hydroxytetradecanoic acid, 3-Hydroxyhexadecanoic acid, Hexadecenoic acid	
<i>Wolinella recta</i>	203	Hexadecanoic acid, Dodecanoic acid, Octadecanoic acid, Tetradecanoic acid, 3-Hydroxytetradecanoic acid, 3-Hydroxyhexadecanoic acid, Hexadecenoic acid	
<i>Wolinella succinogenes</i>	844	Hexadecanoic acid, Dodecanoic acid, Octadecanoic acid, Tetradecanoic acid, 3-Hydroxytetradecanoic acid, 3-Hydroxyhexadecanoic acid, Hexadecenoic acid	
<i>Xanthomonas campestris</i> pv. <i>campestris</i>	340	Butyrolactone, cis-11-Methyl-2-dodecenoic acid	Ryan and Dow JM, 2008
	316273		Weise et al., 2012

Table 2 (continued)

Species	Tax ID (NCBI)	Volatile Synonym	References
<i>Xanthomonas campestris</i> pv. <i>vesicatoria</i> 85-10		Hexan-2-one, 2-Methylpropyl acetate, n-Octane, 5-Methylhexan-2-one, 2-Methylbutyl acetate, 3-Methylbutyl acetate, Heptan-2-one, 2,5-Dimethylpyrazine, 2-Methylpropyl propionate, n-Nonane, 6-Methylheptan-2-one, 5-Methylheptan-2-one, 2-Methylbutyl propionate, 3-Methylbutyl propionate, Octan-2-one, 2,3,5-Trimethylpyrazine, Hexyl acetate, Benzylalcohol, 3-Methylbutyl 3-methylbutyrate, Acetophenone, 7-Methyloctan-2-one, Nonan-2-one, 2-Phenylethanol, 8-Methylnonan-2-one, 7-Methylnonan-2-one, 8-Methylnonan-2-ol, 7-Methylnonan-2-ol, Decan-2-one, 2-Phenylethyl acetate, 9-Methyldodecan-2-one, Undecan-2-one, Undecan-2-ol, 3,6-Dimethyl-2-(3-methylbutyl)pyrazine, 10-Methylundecan-2-one, 9-Methylundecan-2-one, 10-Methylundecan-2-ol, 9-Methylundecan-2-ol, Dodecan-2-one, Geranylacetone, 11-Methyldodecan-2-one, Tridecan-2-one, Tridecan-2-ol, 12-Methyltridecan-2-one, 11-Methyltridecan-2-one, 12-Methyltridecan-2-ol, 11-Methyltridecan-2-ol, Tetradecon-2-ol, 13-Methyltetradecon-2-one, Pentadecan-2-one, 14-Methylpentadecan-2-one, 13-Methylpentadecan-2-ol, Methyl iodide	Schulz and Dickschat, 2007
<i>Zoogloea</i> spp.	349		

The name of the volatile producing species corresponds to a taxonomy ID (<http://www.ncbi.nlm.nih.gov/taxonomy>)

2005a; von Reuss et al., 2010). It is, for example, not known whether these volatiles act as communication signals or are used as carbon sources. Important future tasks are, therefore, elucidation of the plethora of bacterial and fungal VOCs and determination of their chemical structures and biological and ecological roles.

Volatile Mediated Bacterial-Fungal Interactions

Bacterial and fungal volatiles may play multiple roles in microbial communities belowground. Although volatiles can serve as nutrient sources, under highly competitive but symbiotic conditions they are particularly important for antibiosis and signaling, and may serve as regulative principles in any ecosystem. Subsequently, interactions between bacteria and fungi can be beneficial or detrimental. In the latter situation, the term microbiostasis is used to describe the inability of bacteria and/or fungi to multiply in natural soils (Ho and Ko, 1982). Although nutrient depletion or suboptimal environmental conditions also may account for this effect, the involvement of microbial biogenic inhibitors, including volatiles, in microbiostasis is widely accepted (Hora and Baker, 1972; Griffin et al., 1975; Stotzky and Schenck, 1976 and citations therein; Chuankun et al., 2004; Zou et al., 2007; Garbeva et al., 2011). The role of volatiles in signaling events within microbial communities has not yet been well-studied. Wheatley (2002) described volatiles as infochemicals that could mediate bacterial and fungal interactions. This was also proposed by Bending et al. (2006) for the mycorrhizal community. Fungi and plants produce volatile signal molecules that bacteria in the mycorrhizosphere may also synthesize, thereby affecting mycorrhiza formation. A similar situation has been described for the rhizobacterial community (Chernin et al., 2011). Volatiles of *Pseudomonas fluorescens* and *Serratia plymuthica* inhibited quorum-sensing in various other bacteria such as *Agrobacterium*, *Chromobacterium*, *Pectobacterium*, and *Pseudomonas* due to suppression of the transcription of N-acyl-homoserine lactone synthase genes.

Effects of Bacterial Volatiles on Fungi

Influence of Bacterial Volatiles on Germination and Mycelial Growth

The phenomenon of fungistasis was first described by Dobbs and Hinson (1953), which can be due to the negative influence of bacterial volatiles on germination and growth of soil-borne fungi. McCain (1966) showed that volatiles produced by *Streptomyces griseus* induced early sclerotia formation in *Sclerotium cepivorum* and *Rhizoctonia solani*, and

Table 3 Compilation of VOC producing fungi

Species	Tax ID (NCBI)	VOC Synonym	References
<i>Acronium obclavatum</i>	132114	Acetone, Benzene, Ethanol, 2-Butanone, 2-Ethylhexanol, Pentane, Cyclohexane, Limonene, Arsenous acid, Cyclotrisiloxane	Ezeonu et al., 1994
<i>Agaricus bisporus</i>	5341	Isovaleric acid	Stotzky and Schenk, 1976
<i>Agaricus campestris</i>	56157	2,3-Dimethyl-1-pentene	van Lancker et al., 2008
<i>Alternaria alternata</i>	5599	2-Methylpropanol, 2-Ethylhexanol, 2-Methylbutanol, 1-Octen-3-ol, 3-Methylbutanol, Methyl-2-ethyl hexanoate, 3-Octanone	Kaminski et al., 1974
<i>Alternaria</i> spp.	5598	1-Octen-3-ol, 3-Methylbutanol, 3-Octanone, 2-Octen-1-ol	Börjesson et al., 1992
		Ethylbenzene, 1-Penten-3-ol, 2-Methyl-1-propanol, 2-Methyl-1-butanol, 3-Methylfuran, Thujopsene, Dimethylbenzene	Fischer et al., 1999
<i>Aspergillus clavatus</i>	5057	Methoxybenzene, 1-Ethyl-2-methylbenzene, 1-Octen-3-ol, 3-Methyl-1-heptene, 2-Methyl-1-propanol, 2-Methyl-1-butanol, 3-Methyl-1-butanol, Hexanoic acid ethyl ester, 3-Cyclohepten-1-one, 3-Octanone, 2,3,5-Trimethylfuran, 1,3,6-Octatriene	Stotzky and Schenk, 1976
<i>Aspergillus flavus</i>	5059	Ethylene	
		1-Octanol, 3-Octanol, 1-Octen-3-ol, 3-Methylbutanol, 3-Octanone	Börjesson et al., 1992
<i>Aspergillus fumigatus</i>	746128	Nitromethane, 2-Methyl-1-propanol, Ethylbenzene, 1-Penten-3-ol, 3-Methylfuran, Limonene, Thujopsene, 1,3-Octadiene, Dimethylbenzene	Fischer et al., 1999
		2-Methyl-1-propanol, Camphene, Alpha-Pinene, 2-Methyl-1-butanol, 3-Methyl-1-butanol, Citronellol, Limonene, alpha-Farnesene, trans-beta-Farnesene	Matysika et al., 2008
<i>Aspergillus glaucus</i>	40379	Methylbenzoate, 2-Ethyl-1-hexanol, 2-Pentanone, 2-Heptanone, Butoxyethoxyethanol, 3-Octanol, 2-Nonanone, 1-Octen-3-ol, 2-Pentanol, 3-Octanone, 2-Nonen-1-ol, 3-Methyl-1-butanol	Menetrez and Foad, 2002
<i>Aspergillus niger</i>	5061	1-Octen-3-ol, 2,4-Pentadiene, 3-Octanone	Nieminen et al., 2008
		2-Methyl-1-propanol, Styrene, 2-Pentanone, Ethylacetate, 1,3-Pentadiene, 2-Pentanol, 3-Methyl-1-butanol	Matysika et al., 2008
		2-Methyl-1-propanol, 2-Pentanone, 2-Heptanone, 3-Octanol, 3-Octanone, 3-Methylfuran, 1-Octen-3-ol, Pentadecene, Ethyltiglate, 1,3-Nonadiene, iso-Amylglutrate, 2-Pentanol, 3-Methyl-1-butanol	Kaminski et al., 1974
<i>Aspergillus ochraceus</i>	40380	3-Octanol, 1-Octen-3-ol, 3-Methylbutanol, 2-Octen-1-ol, 3-Octanone	Kaminski et al., 1974
<i>Aspergillus oryzae</i>	5062	1-Octanol, 3-Octanol, 1-Octen-3-ol, 3-Methylbutanol, 3-Octanone, 2-Octen-1-ol	
<i>Aspergillus parasiticus</i>	5067		
<i>Aspergillus</i> spp.	5052	Dimethylselenide	Stotzky and Schenk, 1976
<i>Aspergillus versicolor</i>	46472	Benzene, Ethanol, Methylbenzene, Cyclotetrasiloxane, Xylene, Cyclotrisiloxane, 2-Ethylhexanol, 1,3-Dimethoxybenzene, Limonene	Ezeonu et al., 1994
		Ethylbenzene, 1-Penten-3-ol, Thujopsene, Dimethylbenzene, 3-Methylfuran, Limonene, 2-Methyl-1-propanol, 3-Methyl-1-butanol, 1,3-Octadiene	Börjesson et al., 1992
		Anisole, 1-Octene, 3-Methoxyanisole, 3-Methyl-2-butanone, 3-Methyl-2-pentanone, Dimethyldisulfide, 3-Methyl-3-buten-1-ol, 1,3-Pentadiene, 4-Methyl-3-hexanone, 3-Octanone, 3-Methylfuran, 2-Ethylhexanol, 3-Octanol, 1-Octen-3-ol, 2-Methyl-1-propanol, 5-Ethyl-4-methyl-3-heptanone	Sunesson et al., 1995
		2-Ethyl-1-hexanol, 2-Pentanone, 2-Heptanone, 2,6-di-tert-Butyl-p-benzoquinone, 2-Nonanone, 2-Pentanol, 3-Octanone, 1,3-Dimethoxybenzene, 3-Octanol, 1-Octen-3-ol, 1,3-Octadiene, 5-Ethyl-4-methyl-3-heptanone	Matysika et al., 2008
		2-Methyl-1-butanol, 6-Methyl-2-heptanone, alpha-Murolene, gamma-Curcumene, 1-Octen-3-ol Limonene, 3-Methyl-1-butanol	Fischer et al., 1999

Table 3 (continued)

Species	Tax ID (NCBI)	VOC Synonym	References
<i>Aureobasidium pullulans</i>	5580	2-Methylbutanol, 3-Methylbutanol, Methyl-2-ethyl hexanoate, 2-Ethylhexanol, 1-Octen-3-ol, 1,3-Octadiene	van Lancker et al., 2008
<i>Bjerkandera adusta</i>	5331	1,3-Dimethoxybenzene, 3-Octanol, 1-Octen-3-ol	Menetrez and Foadre, 2002
<i>Blastomyces dermatitidis</i>	5039	2-Methyl-1-propanol	Wilkins et al., 2000
<i>Boletus variegatus</i>	48592	Ethanol	Stotzky and Schenk, 1976
<i>Candida humicola</i>	109387	Phenyl pyruvate, 2-Hydroxy-3-phenylpropionic acid, Cinnamic acid,	Schulz and Dickschat, 2007
<i>Candida tropicalis</i>	5482	Ethylene	Stotzky and Schenk, 1976
<i>Cephalosporium</i> spp.	81097	Acetoin, Ethanol, Isobutanol, Isobutyric acid, 3-Methylbutanol	Bunge et al., 2008
<i>Ceratocystis fagacearum</i>	72029	Dimethylselenide, Trimethylarsine, Dimethylarsine	Kaminski et al., 1974
<i>Ceratocystis fimbriata</i>	5158	Acetic acid, Acetaldehyde, Acetone, 1-Butanol, Ethanol, Methanethiol, Methanol, 2-Butanone, 2-Methyl-1-butanol	Lin and Phelan, 1992
<i>Ceratocystis</i> spp.	5157	3-Octanol, 1-Octen-3-ol, 3-Methylbutanol, 3-Octanone, 2-Octen-1-ol	Stotzky and Schenk, 1976
<i>Cladosporium cladosporioides</i>	29917	Acetaldehyde, Ethyl propionate, Propyl acetate, Isobutyl acetate, Methyl isovalerate, Methyl butyrate, Butyl acetate	
<i>Cladosporium sphaerospermum</i>	92950	Ethylene	
<i>Cladosporium</i> spp.	5498	Acetone, Ethanol, Formaldehyde, 2-Methylpropanal, 2-Methylbutanal, Furfural, 2-Heptanone, Ethyl acetate, 2-Hexenal	
<i>Daedalea juniperina</i>	239201	Phenylethylalcohol, 1-Pentanol, 2-Pentanone, 2-Heptanone, 1-Octene, 3-Octanol, 3-Methyl-3-buten-1-ol, 1-Octen-3-ol, 2-Pentanol, Pentadecene, 3-Methyl-1-butanol, 3-Octanone, 1,3-Nonadiene, Tetradecene	Matyska et al., 2008
<i>Dipodascus aggregatus</i>	44075	3-Pentanone, 1-Octene, 3-Methylfuran	Sunesson et al., 1995
<i>Emicella nidulans</i>	162425	Alpha-Humulene, Tetramethyltetrahydrofuran	Menetrez and Foadre, 2002
<i>Emicella</i> spp.	5071	2-Pentanone	Niemenen et al., 2008
<i>Fistulina hepatica</i> (Schaeffer: Fr.)	40457	Anisaldehyde	Stotzky and Schenk, 1976
		Ethyl propionate, Ethyl acetate	
		2-Methyl-1-propanol, 2-Methyl-1-butanol, alpha-Terpinolene, 1-Octen-3-ol, Limonene, 3-Methyl-1-butanol, 2,3-Dimethylbutanoic acid methyl ester, Cyclooctene	Fischer et al., 1999
		Styrene, 2-Pentanone, 2-Heptanone, 2-Pentanol, 3-Methyl-1-butanol, 1,3-Pentadiene	Niemenen et al., 2008
		Benzaldehyde, 1-Butanol, Butanoic acid, Octanal, 1-Octanol, Hexadecanoic acid, Phenylacetaldehyde, Phenylacetic acid, 1,8-Cineole, Decanoic acid, Hexanal, Linalool, 2-Methyl-1-propanol, 2-Methylpropanoic acid, Benzoic acid methyl ester, 2-Methyl-pentanoic acid, 2-Ethyl-1-hexanol, Citronellal, Pentanoic acid, Nonanoic acid, 1-Dodecanol, Methyl stearate, Hexanoic acid, 6-Methyl-5-hepten-2-one, Sabinene, 1-Octen-3-ol, Limonene, Isopropyl dodecanoate, 4-Hydroxy-4-methyl-2-pentanone, Isoamylalcohol, 1-Octen-3-one, (+)-Cuparene, Bisabololoxide B, (E)-2-Methyl-2-butenic acid, 3-Octanone, Cinnamic aldehyde, (Z)-2-Methyl-2-butenic acid, (E)-2-Heptenal, (E)-2-Octenal, (E)-Nerolidol	Wu et al., 2005
<i>Fomes annosus</i>	13563	Hexa-1,3,5-triene	Stotzky and Schenk, 1976
<i>Fomes pomaceus</i>	123902	Methylbromides	
<i>Fomes</i> spp.	40441	Ethanol, Methylbromides, Methylchloride, Isobutanol	
<i>Fusarium sambucinum</i>	5128	Beta-Santalene, beta-Himachalene, beta-Chamigrene, alpha-Bergamotene, Acoradiene, Ar-Curcumene, Elixene, Trichodiene, Longifolene, beta-Bisabolene, beta-Selinene, Di-epi-alpha-Cedrene, alpha-Farnesene, beta-Farnesene	Jelen et al., 1995

Table 3 (continued)

Species	Tax ID (NCBI)	VOC Synonym	References
<i>Fusarium</i> spp.	5506	1-Octen-3-ol, 3-Methylbutanol, 3-Octanone	Kaminski et al., 1974
<i>Mucor hiemalis</i>	64493	Ethylene	Stotzky and Schenk, 1976
<i>Mucor plumbeus</i>	97098	2-Methyl-1-propanol, 2-Pentanone, Ethyl acetate, Ethyl-2-methyl butyrate, 3-Methyl-1-butanol	Nieminen et al., 2008
<i>Muscoder albus</i>	152623	Acetone, Phenylethylalcohol, 2-Methyl-1-propanol, 2-Butanone, Acetic acid, methyl ester, 2-Methylpropanoic acid, Tetrahydrofuran, Acetic acid ethyl ester, 2-Methylfuran, 2-Methylpropanoic acid methyl ester, 3-Methyl-1-butanol acetate, 4-Nonanone, Aciphyllene, Caryophyllene	Atmosukarto et al., 2005
<i>Muscoder fengyangensis</i>	910323	Phenylethylalcohol, 2-Methylpropanoic acid, 3-Methyl-6-(1-methylethyl)-2-cyclohexen-1-one, alpha-Phellandrene, Acetic acid 2-phenylethyl ester, Acetic acid 2-methylpropyl ester, 1-Ethenyl-1-methyl-2,4-bis(1-methylethenyl)-[1S-(1-alpha,2-beta,4-beta)]-cyclohexane, 2-Methylpropanoic acid methyl ester, beta-Phellandrene, Caryophylleneoxide, 3-Methyl-1-butanol, 3-Methyl-1-butanol acetate, 3,5-Dimethoxytoluene, 2-Cyclohexen-1-ol, cis-3-Methyl-6-(1-methylethyl)-2-Cyclohexen-1-ol, trans-3-methyl-6-(1-methylethyl)-2-Cyclohexen-1-ol, 2,6-Dimethyl-6-(4-methyl-3-pentenyl)-bicyclo[3.1.1]hept-2-ene, 2,6-Dimethyl-6-(4-methyl-3-pentenyl)-bicyclo[3.1.1]hept-2-ene, 1-Methyl-4-[5-methyl-1-methylene-4-hexenyl]-[S]-cyclohexene, cis-1-Methyl-4-(1-methylethyl)-2-cyclohexen-1-ol, Isoaromadendrene epoxide, Dipecedrene-1-oxide, 2-Methylene-4,8-trimethyl-4-vinyl-bicyclo[5.2.0]nonane, 3,3,7,11-Tetramethyl-tricyclo[6.3.0.0(2,4)]undec-8-ene, Caryophyllene, cis-alpha-Bisabolene, Caryophyllene-[11]	Zhang et al., 2010
<i>Paecilomyces variotii</i>	45996	Acetone, 2-Pentanone, Propylacetate, 2-Heptanone, 1-Hexanol, 3-Methyl-2-pentanone, 2-Hexanone, 1-(1,1-Dimethylethyl)-4-ethylbenzene, 2-Methyl-1-propanol, 3-Methyl-1-butanol, 2,5-Dimethylfuran, 3-Methylfuran, 2,3,5-Trimethylfuran	Sunesson et al., 1996
		Octane, 2-Propanol, 2-Butanone, Methylacetate, Furan, Trimethylbenzene, 2-Methylpropyl formate, 2,4-Dimethylfuran, 1-Methylpropylformate, alpha-Curcumene, 2-Methyl-1,3-pentadiene, 2-Methyl-1-prop-1-anol, 3-Methyl-1-butanol, 2-Methyl-1-butanol, 2,5-Dimethylfuran, 3-Methylfuran, Xylene	Sunesson et al., 1995
		alpha-Phellandrene, alpha-Terpinene, beta-Phellandrene, gamma-Cadinene, Myrcene, Germacrene B, neo-allo-Ocimene, Megastigma-4,6(e),8(Z)-triene, +alpha-Longipinene, 2-Methyl-1-propanol, 3-Methyl-1-butanol, 3-Methyl-1-butanol, 2,3,5-Trimethylfuran	Fischer et al., 1999
<i>Penicillium aurantiogriseum</i>	36655	Acetic acid, Ethanol, 1-Propanol, 2-Methyl-1-propanol, 3-Methylfuran, 1-Octen-3-ol, 3-Methyl-1-butanol, 3-Octen-2-ol	Börjesson et al., 1990
<i>Penicillium brevicompactum</i>	5074	Acetone, 2-Propanol, 2-Butanone, 3-Pentanone, 3-Methylfuran, 2-Methyl-1-propanol, 2-Methyl-1-butanol	Börjesson et al., 1992
<i>Penicillium chrysogenum</i>	5076	Styrene, 1-Octen-3-ol, Limonene, 3-Methyl-1-butanol, 2-Methyl-1-propanol, 2-Methyl-1-butanol	Fischer et al., 1999
		Acetic acid, Ethanol, 2-Propanol, Isoprene, 2-Methyl-1-propanol, 2-Butanol, 2-Butanone, alpha-Pinene, 3-Pentanone, 1-Pentene, 2-Octanone, 1-Dodecene, 2-Methyl-1-butanol, 2-Heptanol, 3-Pentanol, 2-Hexanone, 1-Hexene, Dimethyldisulfide, 2-Hexanol, 2-Nonanol, 1-Undecene, Methyl-2-methylbutyrate, beta-Pinene, 1-Tridecene, 2-Octanol, Nonadiene, 2-Pentanone, 3-Methyl-1-butanol 2-Heptanone, 1-Octene, 1-Heptene, 2-Nonanone, 1-Pentadecene, 1-Nonene, 1-Octen-3-ol, 1,3-Octadiene	Wilkins et al., 2000
		1-Octanol, 2-Octen-1-ol, 3-Octanol, 1-Octen-3-ol, 3-Methyl-1-butanol, 3-Octanone	
		3-Methylanisole, 1,3-Dimethoxybenzene, Hexadecane, 2-Pentanol, Geosmin, 1,4-Dimethoxy-2-methylbenzene, Ethyltiglate, 1,3-Nonadiene, iso-Amyltiglate, 2-Pentanone, 2-Heptanone, 1-Octene, 1-Heptene, 2-Nonanone, 1-Pentadecene, 1-Nonene, 2-Methylbutanol, 3-Octanol, 1-Octen-3-ol, 3-Methyl-1-butanol, 3-Octanone, 1,3-Octadiene, Tetradecene	Kaminski et al., 1974
		2-Ethylhexanol, 2-Methylbutanol, 3-Octanol, 1-Octen-3-ol, 3-Methyl-1-butanol, 1,3-Octadiene	Matysika et al., 2008
<i>Penicillium citrinum</i>	5077	1-Octen-3-ol, 3-Octanone, Tetradecene	van Lancker et al., 2008
		1-Octanol, 3-Octanol, 1-Octen-3-ol, 3-Methylbutanol, 3-Octanone, 2-Octen-1-ol	Menetrez and Foadre, 2002
			Kaminski et al., 1974

Table 3 (continued)

Species	Tax ID (NCBI)	VOC Synonym	References
<i>Penicillium clavigerum</i>	29841	2-Methyl-1-propanol, alpha-Terpinene, Styrene, 2-Methyl-1-butanol, Dimethyldisulfide, Limonene, Myrcene, 3-Methyl-1-butanol, Bicyclo-(3.2.1)-octan-2-one, beta-Caryophyllene, beta-Elementene	Fischer et al., 1999
<i>Penicillium commune</i>	36653	Acetone, Dimethylsulfide, Cresol, Camphene, alpha-Pinene, Ethyl propanoate, Ethyl butanoate, Propyl acetate, 2-Methylpropyl acetate, Cyclopentanone, 2-Methyl-1-butanol, Ethyl acetate, Heptane, 3-Methylfuran, beta-Pinene, Limonene, Ethyl-2-methyl butanoate, 3-Methylbutylacetate, Methyl-(1-methylethenyl)benzene, alpha-Curcumene, Ethanethioic acid-S-(2-methyl)butyl ester	Sunesson et al., 1995
		2-Ethyl-1-hexanol, 2-Pentanone, 2-Heptanone, 1-Hexanol, 2-Methyl-1-butanol, 1-Octen-3-ol, Dimethyltrisulfide, Geosmin, 1-Methoxy-4-(1-methylethyl)benzene, 1-Methoxy-3-methylbutane, 3-Octanone	Sunesson et al., 1996
		2-Methyl-1-propanol, 2-Butanone, Methyl acetate, 3-Methylanisole, Dimethyldisulfide, 2,5-Dimethylfuran, 3-Methyl-1-butanol	Sunesson et al., 1995, 1996
<i>Penicillium crustosum</i>	36656	2-Methyl-1-propanol, Styrene, Dodecane, 2,5-Dimethylfuran, 2-Ethylfuran, Limonene, 3-Methyl-1-butanol, 2,3,5-Trimethylfuran	Fischer et al., 1999
<i>Penicillium cyclopium</i>	60167	2-Methyl-1-propanol, 2,5-Dimethylfuran, γ -Cadinene, 2-Methylenebornane, 2-Methyl-2-bornene, 2,3,5-Trimethylfuran, Cyclooctene, Germacrene A	
<i>Penicillium digitatum</i>	36651	Ethane, Ethylene, Acetylene, Propane, Propylene	Stotzky and Schenk, 1976
<i>Penicillium expansum</i>	27334	1-Pentanol, 2-Methyl-1-propanol, 3-Methylanisole, 2-Ethyl-1-hexanol, 2-Pentanone, 2-Heptanone, 2-Methyl-1-butanol, 3-Octanol, Dimethyldisulfide, alpha-Terpineneol, 1-Octen-3-ol, 2-Pentanol, 3-Octanone, 1,3-Octadiene	Matysika et al., 2008
		Styrene, 1-Methoxy-3-methylbenzene, Aromadendrene, Elemol, Germacrene B, γ Curcumene, Bicyclopentene	Fischer et al., 1999
<i>Penicillium funiculosum</i>	28572	Geosmin	Mattheis and Roberts, 1992
<i>Penicillium glabrum</i>	69773	1-Octen-3-ol, 3-Methylbutanol, 3-Octanone, 2-Octen-1-ol	Kaminski et al., 1974
		2-Methyl-1-propanol, 2-Butanone, 3-Pentanone, 2-Methyl-1-butanol, 3-Methylfuran, 1-Octen-3-ol, 3-Octanone, 1,3-Octadiene, Dimethylbenzene, Limonene	Börjesson et al., 1992
<i>Penicillium italicum</i>	40296	Styrene, 2-Methyl-1-butanol, 3-Methyl-1-butanol, Limonene	Fischer et al., 1999
<i>Penicillium raistrickii</i>	69783	Methylbutenone, Cedrol, Cedrene	Menetrez and Foarde, 2002
<i>Penicillium roqueforti</i>	5082	1-Octen-3-ol, 3-Methylbutanol, 3-Octanone, 2-Octen-1-ol	Kaminski et al., 1974
		Toluene, 2-Methylpropanoic acid, Acetic acid 2-methylpropyl ester, Heptane, 3-Methyl-1-butanol, Isoamylacetate, 1,3-Octadiene, Xylene	Jelen et al., 1995
		2-Methyl-1-propanol, 2-Methyl-1-butanol, 3-Methylfuran, Dimethylbenzene, Limonene, 3-Octanone, 1,3-Octadiene	Börjesson et al., 1992
		Alpha-Phellandrene, Styrene, 3-Octanol, Undecane, beta-Himachalene, 1-Octene-3-ol, 3-Carene, beta-Myrcene, (+)-2-carene, beta-Patchoulene, Aristolochene, Di-epi-alpha-cedrene, beta-Elementene, beta-Bisabolene, Limonene, 3-Octanone	Jelen 2003
<i>Penicillium</i> spp.	5073	2-Methyl-1-propanol, Styrene, 2-Pentanone, Ethylacetate, 2-Pentanol, Ethyl-2-methylbutyrate, 3-Methyl-1-butanol, 1,3-Pentadiene, 2-Heptanone	Nieminen et al., 2008
		4-Allylanisole, 2-Heptanone	Björman et al., 1997
		Dimethylselenide	Stotzky and Schenk, 1976
<i>Penicillium variable</i>	28576	2-Ethylhexanol, 2-Heptanone, 2-Ethylhexanoic acid, 2-Methylbutanol, Terpinolene, 3-Octanol, 1-Octen-3-ol, 3-Methylbutanol, Methyl-2-ethyl hexanoate, 3-Octanone, 1,3-Octadiene	van Lancker et al., 2008
<i>Penicillium viridicatum</i>	60134	1-Octanol, 3-Octanol, 3-Octanone, 2-Octen-1-ol, 1-Octen-3-ol, 3-Methylbutanol	Kaminski et al., 1974

Table 3 (continued)

Species	Tax ID (NCBI)	VOC Synonym	References
<i>Phellinus</i> spp.	40470	2-Ethylhexanol, 2-Methylbutanol, 2-Ethylfuran, 2-Pentylfuran, 1,3-Octadiene, 1-Octen-3-ol, 3-Methylbutanol	van Lancker et al., 2008
<i>Phialophora fastigiata</i>	91935	Benzylalcohol, Methyl salicylate, Phenylethylalcohol, Methyl benzoate, Ethyl benzoate	Stotzky and Schenk, 1976
<i>Puccinia graminis</i> var. <i>tritici</i>	5297	Acetone, 2-Butanone, Methyl benzoate, Cyclopentanone, Methyl-3-methyl butanoate, Dimethyldisulfide, 1-Octen-3-ol, 3-Methyl-1-butanol, 3-Octanone, Caryophyllene	Sunesson et al., 1995
<i>Rhodotorula glutinis</i>	5535	Acetaldehyde, Furfural, Trimethylethylene, n-Nonanal, Methyl ferulate	Stotzky and Schenk, 1976
<i>Saccharomyces cerevisiae</i>	4932	Phenylethylalcohol, 2-Methyl-1-propanol, 3-Methyl-2-butanol	Menetrez and Foadre, 2002
		Acetic acid, 2-Propanone, 1,2-Benzenedicarboxylic acid, 2-Propanol, Phenylethylalcohol, 2-Methyl-1-propanol, 2-Butanone, 2-Methyl-propanoic acid, 1,2-Dimethylbenzene, 2-Ethyl-1-hexanol, 2-Pentanone, Acetic acid ethenyl ester, 2-Methyl-butanioic acid, Pyrazine, 3-Methyl-butanioic acid, Dimethyldisulfide, Undecane, Limonene, 2,5-Dimethylpyrazine, Ethanol, Ethylacetate	Bruce et al., 2004
<i>Schizophyllum commune</i>	5334	Acetaldehyde, n-Propanol, Isobutanol, Ethanol, Ethylacetate	Stotzky and Schenk, 1976
<i>Scopulariopsis brevicaulis</i>	40375	Methylmercaptan, Dimethylselenide	Stotzky and Schenk, 1976
<i>Stachybotrys chartarum</i>	74722	Dimethylselenide, Trimethylarsine, Dimethylarsine	Wilkins et al., 2000
		1-Butanol, 2-Propanol, Isoprene, 2-Methyl-1-propanol, 2-Butanol, Methyl benzoate, Anisole, m-Methylanisole, Methyl-2-methyl propionate, Dimethyldisulfide, 3-Methylfuran, o-Methylanisole, Dimethylhexadiene	
<i>Staphylococcus xylosus</i>	1288	Pyridine	Matysika et al., 2008
<i>Thielaviopsis basicola</i>	124036	Acetone, Ethanol, Formaldehyde, 2-Methylpropanal, 2-Methylbutanal, Furfural, 2-Heptanone, Ethyl acetate, 2-Hexenal	Stotzky and Schenk, 1976
<i>Tilletia caries</i>	13290	Trimethylamine	Stotzky and Schenk, 1976
<i>Tilletia controversa</i>	13291	Trimethylamine	
<i>Tilletia foetida</i>	157183	Trimethylamine	
<i>Trichoderma atroviride</i>	63577	Phenylethylalcohol, α -Phellandrene, γ -Terpinene, α -Terpinene, 2-Heptanone, 2-Undecanone, β -Phellandrene, α -Terpinolene, 3-Octanol, 2-Nonanone, 1-Octen-3-ol, 2-Pentylfuran, 2-n-Heptylfuran, 6-Pentyl- α -pyrone, α -Bergamotene, α -Zingiberene, 3-Octanone, β -Bisabolene, α -Curcumene, p-Menth-2-en-7-ol, α -Farnesene, β -Farnesene, Nerolidol, γ -Curcumene, β -Sesquiphellandrene	Stoppacher et al., 2010
<i>Trichoderma aureoviride</i>	64502	Acetaldehyde, Acetone, Benzylalcohol, Chloroform, Isobutane, 2-Methyl-1-propanol, 2-Ethyl-4-methyl-1-pentanol, Heptanone, Nonane, Heptane, Decane, 2,4-Dimethylheptane, 3-Methyl-2-hexanol, 7-Octen-4-ol, 5-Methyl-5-hexen-3-ol, 1,3-Hexadien-5-yne	Bruce et al., 2000
<i>Trichoderma pseudokoningii</i>	317029	2-Propanone, Butanal, 1-Butanol, Octane, 1-Propanol, Hexanal, 1-Pentanol, Acetonitrile, 2-Methyl-1-propanol, 2-Butanone, p-Xylene, 2-Methylpentane, Methylcyclohexane, Hexane, n-hexane, 2-Octanone, 1-Hexanol, Heptanal, Formic acid heptyl ester, Decanal, 2-Methyl-butanol, Acetic acid ethyl ester, Heptane, Limonene, 3-Methyl-1-butanol, 2-Propyl-1-pentanol, 2-Octen-1-ol, 2,2,4,6,6-Pentamethyl-3-heptene, 2-Propenylidene-cyclobutene	Wheatley et al., 1997
<i>Trichoderma</i> spp.	5543	Acetaldehyde, Acetone, Ethanol	Stotzky and Schenk, 1976
		Styrene, 2-Pentanone, 3-Methyl-1-butanol, 1,3-Pentadiene	Nieminen et al., 2008
<i>Trichoderma viride</i>	5547	2-Propanone, Benzaldehyde, Butanal, 1-Butanol, Octane, Propanal, 1-Propanol, Isopropylalcohol, Hexanal, Acetonitrile, 2-Butanone, Benzothiazole, p-Xylene, Methylcyclohexane, 2-Heptanone, Hexane, 2-Octanone, Heptanal, Decanal, 2-Methyl-1-butanol, Acetic acid 2-ethyl ester, Heptane, 6-Methyl-5-hepten-2-one, 3-Methylhexane, 4-Penten-2-ol, Pentadecane, 3-Methyl-1-butanol, Nonanal, 2-Propyl-1-pentanol, 2,4,6-Trimethyl-1-nonene, Caryophyllene, 2-Methyl-1-propanol	Wheatley et al., 1997

Table 3 (continued)

Species	Tax ID (NCBI)	VOC Synonym	References
<i>Tuber aestivum</i>	59557	2-Propanol, 1-Pentanol, 2-Hexanone, 3-Methylfuran, 2-Methyl-1-propanol Acetaldehyde, Acetone (2-Propanone), 1-Butanol, Ethanol, 1-Propanol, Dimethylsulfide, 2-Methyl-1-propanol, 2-Butanol, 2-Butanone, Acetic acid methyl ester, Propanoic acid ethyl ester, Propanoic acid propyl ester, 2-Methyl-1-butanol, Acetic acid ethyl ester, Butanoic acid methyl ester, Acetic acid 2-methylbutyl ester, 4-Hydroxy-3-methyl-2-butanone, 2-Methyl-ethyl-1-butanone	Wilkins et al., 2000 March et al., 2006
<i>Tuber brumale</i>	60458	Acetaldehyde, Acetone (2-Propanone), 1-Butanol, Ethanol, Isopropylalcohol, 2-Methyl-1-propanol, 2-Butanol, 2-Butanone, Acetic acid methyl ester, 1-Methoxy-3-methylbenzene, Propanoic acid ethyl ester, Butanoic acid ethyl ester, Butanoic acid propyl ester, Propanoic acid methyl ester, 2-Methyl-1-butanol, Acetic acid ethyl ester, Butanoic acid methyl ester, Butanoic acid-1-methylpropyl ester, 4-Hydroxy-3-methyl-2-butanone, Butanoic acid 2-methyl-ethyl ester	March et al., 2006
<i>Tuber melanosporum</i>	39416	Acetaldehyde, Acetone (2-Propanone), 1-Butanol, 1-Propanol, Isopropylalcohol, 2-Methyl-1-propanol, Acetic acid methyl ester, Propanoic acid ethyl ester, Butanoic acid propyl ester, Propanoic acid methyl ester, Acetic acid-1-methylethyl ester, 2-Methyl-1-butanol, Acetic acid ethyl ester, Butanoic acid methyl ester, Butanoic acid 2-methyl-ethyl ester, 4-Hydroxy-3-methyl-2-butanone, Butanoic acid 2-methyl-ethyl ester, Pentanoic acid 4-methyl-ethyl ester, 2-Methyl-3-ethyl-2-pentene, Ethanol, Dimethylsulfide, 2-Butanol	March et al., 2006
<i>Tuber mesentericum</i>	92904	2-Butanone, 3-Octanol, bis(Methylthio)methane, 1-Octen-3-ol, 1-Octen-3-one, 3-Octanone, Ethanol, Dimethylsulfide, 2-Butanol Acetaldehyde, Acetone (2-Propanone), 1-Butanol, Ethanol, 1-Propanol, Dimethylsulfide, 2-Methyl-1-propanol, 2-Butanol, 2-Butanone, Acetic acid methyl ester, 1-methoxy-3-methylbenzene, Propanoic acid ethyl ester, Butanoic acid propyl ester, Propanoic acid methyl ester, 2-Methylbutan-1-ol, Acetic acid ethyl ester, 3-Methylbutanal, Butanoic acid methyl ester, 2-Methylbutyric acid methyl ester, 2-Methylbutyric acid ethyl ester, 2-Methyl-3-ethyl-2-pentene	Peluso et al., 1995 March et al., 2006
<i>Tuber rufum</i>	119233	Acetaldehyde, Acetone (2-Propanone), 1-Butanol, Ethanol, Dimethylsulfide, Isopropylalcohol, 2-Butanol, 2-Butanone, Acetic acid methyl ester, Propanoic acid ethyl ester, Butanoic acid ethyl ester, Butanoic acid propyl ester, Propanoic acid propyl ester, 2-Propyl acetate, Acetic acid propyl ester, 2-Methyl-1-butanol, Acetic acid ethyl ester, Propanoic acid methyl ester, Butanoic acid methyl ester, 2-Methylbutyric acid methyl ester, 4-Hydroxy-3-methylbutan-2-one, 2-Methylbutyric acid ethyl ester, Acetic acid butyl ester, N-methylene-ethenamine	March et al., 2006
<i>Ulocladium chartarum</i>	119957	2-Methylpropanol, 2-Pentanone, 2-Heptanone, 2-Ethylhexanoic acid, 2-Methylbutanol, 2-Hexanone, Dimethyldisulfide, 2-Nonanone, 6-Methyl-2-heptanone, 5-Methyl-2-heptanone, 3-Methylbutanol, Methyl 2-ethyl hexanoate	van Lancker et al., 2008

The name of the volatile producing species corresponds to a taxonomy ID (<http://www.ncbi.nlm.nih.gov/taxonomy>)

reduced sporulation in *Gloeosporium aridum*. A strong inhibition of spore germination of *Cladosporium cladosporioides* was caused by but-3-en-2-one produced by *Streptomyces griseoruber* (Herrington et al., 1987). Zou et al. (2007) screened 1080 bacterial isolates for fungistatic activity. A total of 328 isolates belonging to the family of Rhizobiaceae, Xanthomonadaceae, Micrococcaceae, Alcaligenaceae, and to the order of Bacillales were identified as decreasing germination and mycelial growth of *Paecilomyces lilacinus* and *Pochonia chlamydosporia*. The spore germination of both fungi also was strongly inhibited by soil direct fungistasis and soil volatile fungistasis. Both effects correlated closely with impaired spore germination and disappeared after autoclaving. Several volatiles were identified, and trimethylamine, benzaldehyde, and N,N-dimethyloctylamine showed strong antifungal activity (Chuankun et al., 2004).

In order to identify bacterial isolates specifically antagonistic to plant pathogens, many *in vitro* experiments have been done. The experimental setup had to ensure that only volatile metabolites would influence fungal growth. Split Petri dishes (Fernando et al., 2005; Kai et al., 2007; Vespermann et al., 2007), separated agar patches (Alharbi et al., 2011), or the inversion of one bottom plate over a second one (Bruce et al., 2000) assured the exchange of volatiles solely in the headspace. Vespermann et al. (2007) and Kai et al. (2007 and 2008) conducted a comprehensive investigation using *Bacillus subtilis*, *Pseudomonas fluorescens*, *Pseudomonas trivialis*, *Burkholderia cepacia*, *Staphylococcus epidermidis*, *Stenotrophomonas maltophilia*, *Stenotrophomonas rhizophila*, *Serratia odorifera*, and *Serratia plymuthica* against pathogenic fungi, including *Aspergillus niger*, *Fusarium culmorum*, *Fusarium solani*, *Microdochium bolleyi*, *Paecilomyces carneus*, *Penicillium waksmanii*, *Phoma betae*, *Phoma eupyrena*, *Rhizoctonia solani*, *Sclerotinia sclerotiorum*, *Trichoderma strictipile*, and *Verticillium dahliae*. All rhizobacteria inhibited the mycelial growth of most fungi. The extent of inhibition depended on the individual bacteria-fungus combination. Noticeably, *Fusarium solani* turned out to be resistant against the bacterial volatiles. The spectra of bacterial volatiles produced included many unknown components; however, 2-phenylethanol, 1-undecene, dodecanal, dimethyl disulfide (DMDS), and dimethyl trisulfide (DMTS) could be identified (Kai et al., 2007). DMDS and 1-undecene indeed inhibited the growth of *F. culmorum* when applied as individual compounds in dual-culture tests (Kai et al., 2009). Several other reports also confirmed the antifungal action of volatiles produced by antagonistic rhizobacteria. *Pseudomonas fluorescens* and *Pseudomonas pumila* inhibited most effectively the growth of *Gaeumannomyces graminis* var *tritici*, the cause of take-all disease in wheat (Babaeipoor et al., 2011). *Gluconacetobacter diazotrophicus* decreased the growth of *Fusarium oxysporum*

(Logeshwari et al., 2011), *Bacillus pumilus*, *Bacillus subtilis*, and *Bacillus cereus* hindered growth of *Botrytis mali* (Jamalizadeh et al., 2010), and volatiles produced by *Bacillus subtilis* showed antifungal activity towards *Rhizoctonia solani* and *Pythium ultimum* (Fiddaman and Rossall, 1993) and *Aspergillus alternatus*, *Cladosporium oxysporum*, *Fusarium oxysporum*, *Paecilomyces lilacinus*, *Paecilomyces variotii*, and *Pythium afertile* (Chaurasia et al., 2005). *Bacillus* spp. impaired the growth of *Phytophthora sojae*, which causes the soybean damping-off disease (Tehrani et al., 2002). Interestingly, the dual application of *Bacillus pumilus* and the mycorrhizal fungus *Glomus mosseae* improved the growth of mandarin plants, directly attributed in part to growth inhibition of fungal pathogens by rhizobacterial volatiles (Chakraborty et al., 2011). The volatiles 1-octen-3-ol, benzothiazol, and citronellol produced by *Paenibacillus polymyxa* strongly inhibited mycelial growth and impaired germination of eight fungal pathogens, including *Botrytis cinerea* (Zhao et al., 2011). Wan et al. (2008) investigated the effect of headspace volatiles of *Streptomyces plantensis* on phytopathogenic fungi. Two antifungal components were identified: 2-phenylethanol and a phellandrene derivative were responsible for the suppression of mycelial growth of *Rhizoctonia solani*, *Sclerotinia sclerotiorum*, and *Botrytis cinerea*. Ascospore germination was suppressed up to 90 % by volatiles released by *Pseudomonas* sp., which were isolated from canola and soybean plants (Fernando et al., 2005). *Staphylococcus pasteurii* showed a significant antifungal activity *in vitro* against *Tuber borchii* and inhibited ectomycorrhizal formation (Barbieri et al., 2005).

Many *Pseudomonas* species are known to produce HCN as an effective antifungal component (Voisard et al., 1989; Haas and Défago, 2005). Although HCN production could be correlated to fungistasis, its antifungal effect often could only be verified *in vitro*. Rhizobacterial isolates were screened for HCN production and diffusible antifungal metabolites, and tested against *Verticillium dahliae* and *Rhizoctonia solani* in dual-culture tests (Tehrani et al., 2001; Afsharmanesh et al., 2006), and subsequently used in greenhouse experiments. Interestingly, HCN producers showed the highest efficiency when applied to the soil, whereas non-producers were more efficient when applied to seeds. Antifungal properties also have been attributed to gaseous ammonia. Schippers et al. (1982) showed that ammonia release from soil as well as from an ammonium sulfate solution inhibited conidia germination of *Botrytis cinerea* and *Penicillium nigricans*. However, some fungi such as *Fusarium culmorum* and *Verticillium nigrescens* were not affected by ammonia. Furthermore, other volatiles released from the soil decreased conidia germination and tube growth of these two fungi. Similarly, Howell et al. (1988) identified ammonia to be the antifungal component

in dual-culture tests using *Enterobacter cloacae*, *Rhizoctonia solani*, and *Pythium ultimum*.

Fungal growth promotion by bacterial volatiles has hardly ever been reported. Mackie and Wheatley (1999) and Wheatley (2002) selected four fungi as representative of a range of several habitats and challenged them *in vitro* with headspace volatiles of a variety of randomly selected soil bacteria. The response was unique for each fungal-bacterial combination, and revealed positive, negative, as well as neutral effects on radial growth of *Trichoderma viride*, *Phanaerochaete magnoliae*, *Phytophthora cryptogea*, and *Gaeumannomyces graminis* var *tritici*. Only *P. cryptogea* exhibited a significant increase in growth upon exposure to volatiles of certain bacterial isolates.

Impact of Bacterial Volatiles on Fungal Morphology

Several reports also have focused on morphological changes in fungi following bacterial volatile treatment. Fiddaman and Rosall (1993) observed abnormal hyphae with deformation and enhanced vacuolation in *Rhizoctonia solani* and *Pythium ultimum* exposed to volatiles produced by *Bacillus subtilis*. The same bacterial species caused hyphal and conidial deformations in *Aspergillus alternaria*, *Cladosporium oxysporum*, *Fusarium oxysporum*, *Paecilomyces lilacinus*, *Paecilomyces variotii*, and *Pythium afertile*. Transverse and longitudinal septae completely disappeared in *Aspergillus alternaria*, and conidia became thick-walled and irregular in shape. Conidia formation was sometimes arrested, and in *Cladosporium oxysporum*, conidiophores became vegetative and stunted. Swelling of hyphae, vacuolization, and granulation lead finally to lysis of fungal mycelium in *Fusarium oxysporum*, *Paecilomyces lilacinus*, and *Paecilomyces variotii* (Chaurasia et al., 2005). Swollen terminal cells and bulging intercalary cells also were described for *Tuber borchii* upon exposure to volatiles emitted by *Staphylococcus pasteurii* and, finally, fungal mycelium showed swollen and contorted patterns when treated with 1-octen-3-ol (Barbieri et al., 2005). Benzothiazol caused a more frequent branching of the mycelium and increased conidia production, whereas citronellol only induced a slight hyphal contortion. All three compounds were components of the volatile mix produced by *Paenibacillus polymyxa* (Zhao et al., 2011).

Influence of Bacterial Volatiles on Mycorrhizal Fungi

Mycorrhiza is a complex symbiotic community including plant roots, mycorrhizal fungi, and associated bacteria (see Jung et al., 2012, this issue). Not only their physical contact but also the release of bioactive molecules, including volatiles, apparently play a regulatory role in a mycorrhizal network establishment (Bonfante and Anca, 2009). Associated bacteria comprise primarily the mycorrhiza

helper bacteria (MHB) as well as rhizobacteria with beneficial or deleterious functions (Bonfante and Anca, 2009; Miransari, 2011). In 1991, Tylka et al. demonstrated that the MHB *Streptomyces orientalis* stimulated spore germination in *Gigaspora margarita* and *Glomus mossae*. Garbaye and Duponnois (1992) proposed that MHB directly stimulate the growth of *Laccaria laccata* by releasing volatile substances. Volatiles emitted by a bacterial isolate originally associated with *Gigaspora margarita* also promoted *in vitro* host fungus growth (Horii and Ishii, 2006), and volatile and diffusible compounds produced by MHB strains obtained from *Glomus clarum* spores stimulated or arrested spore germination, dependent on the bacterial species. Complete inhibition of spore germination, however, was only related to the volatiles (Xavier and Germida, 2003). Aspray et al. (2006) revealed that stimulation of mycorrhiza formation of *Lactarius rufus* required close proximity or contact. Volatiles of the MHB *Paenibacillus* sp. alone had significant negative effects on mycorrhiza formation. Furthermore, volatiles of the MHB *Streptomyces* spp., which actually promoted growth of the ectomycorrhizal fungus *Amanita muscaria*, did not affect mycelial extension rates (Schrey et al., 2005). The antagonist *Bacillus subtilis* JA inhibited significantly the spore germination and hyphal growth of a monoxenic strain of *Glomus etunicatum* in dual-culture experiments (Xiao et al., 2008), whereas volatiles produced by *Klebsiella pneumonia* promoted hyphae extension distantly located from the germinated spores of *Glomus deserticola*. Both organisms were indigenous to the roots of sea oats (Will and Sylvia, 1990).

Impact of Bacterial Volatiles on Fungal Enzyme Activities and Gene Expression

Mackie and Wheatley (1999) and Wheatley (2002) investigated the effect of bacterial volatiles on physiological properties of fungi by monitoring laccase and tyrosinase activity of *Phanaerochaete magnoliae* and *Trichoderma viride* upon exposure to volatiles of three selected soil bacteria isolates (A, B, C). Laccase activity completely ceased in *P. magnolia* in the presence of isolates A, B, C, whereas tyrosinase activity was inhibited only by the presence of isolate B. Isolate B was the only one to affect laccase activity in *T. viride*. The observed decrease in fungal growth correlated with decreased enzyme synthesis rather than inhibition of enzyme activity (Wheatley, 2002). Laccase activity in *Rhizoctonia solani* was induced after co-cultivation with *Pseudomonas fluorescens*. Due to the experimental setup, it was not possible to distinguish between effects of diffusible and volatile metabolites (Crowe and Olsson, 2001). Inhibition of enzyme activities may also be involved in the complete loss of pigmentation after treatment of *Fusarium oxysporum* with citronellol, a compound emitted by *Paenibacillus polymyxa*

(Zhao et al., 2011). In contrast, Kai et al. (2009) observed a dark discoloration of the agar when fungi were exposed to rhizobacterial volatiles.

At present there are few reports that bacterial volatile components may affect gene expression. Minerdi et al. (2008, 2009) demonstrated an indirect volatile mediated effect of bacteria on fungal gene expression. The antagonistic wild type (WT) strain *Fusarium oxysporum* MSA35 lives in symbiosis with associated bacteria of the genera *Serratia*, *Achromobacter*, *Bacillus*, and *Stenotrophomonas*. Volatiles produced by the WT repressed the expression of two putative virulence genes of a pathogenic *Fusarium oxysporum* *lactucae* strain. When cured of the bacterial symbionts, the WT turned pathogenic and the sesquiterpene caryophyllene was no longer in the headspace of the cured WT. It also was not found in the headspace of the ectosymbionts, so this volatile seems to mediate a mechanism for the antagonistic properties of the *Fusarium oxysporum* WT. However, caryophyllene is only produced by the WT in the presence of the bacterial symbionts.

Possible Mechanisms of Actions of Volatiles

Presently, little is known about mechanisms of action and detoxification of bacterial volatiles in fungi. It is known that the cyanide ions from HCN are potent inhibitors of many metal-containing enzymes, in particular of copper-containing cytochrome c oxidases (Haas and Défago, 2005). However, it remains unclear how most volatiles develop their activity. One scenario relates to the production of melanin (Kai et al., 2009; Zhao et al., 2011). Melanins are known to reinforce the cell wall or accumulate on the cell surface where they develop antioxidative properties and scavenge free radicals. In fungi, melanins are synthesized via the polyketide synthase pathway (Jacobson, 2000), but phenol oxidizing enzymes such as laccases and tyrosinases may also be involved (Williamson, 1997). Intracellular laccases account for detoxification of chemicals (Champagne and Ramsay, 2010). In this regard, the increase of laccase activities reported by Crowe and Olsson (2001) might result from the presence of eligible volatile substrates, whereas the decrease in laccase and tyrosinase activity reported by Mackie and Wheatley (1999) might be a sign of impaired cell homeostasis. This again demonstrates that a deleterious bacterial volatile can be considered a toxin. Fungal cells respond to it as to any other biotic or abiotic stress factors. Whole-genome expression studies conducted in fungal model organisms including *Saccharomyces cerevisiae*, *Candida albicans*, and *Schizosaccharomyces pombe* have revealed that each species responded to environmental stress with an individual change in gene expression. Some species also expressed a common set of genes, referred to as environmental stress response (ESR) (Gasch, 2007). This can

include the response to cell wall stress and/or oxidative and osmotic stress. Compounds like gaseous ammonia could be considered a stress factor, impairing cell homeostasis and triggering ESR. On the other hand, sub-inhibitory concentrations of ammonia might play a part in signaling. Ammonia released from bacterial strains has been shown to stimulate *Bacillus licheniformis* to form biofilms and pigmentation (Nijland and Burgess, 2010) and to increase the antibiotic resistance of various gram-positive and gram-negative bacteria (Bernier et al., 2011). Therefore, the ecological role of microbial volatiles may be intrinsically to serve as a signal molecule within and between species. They may also function as chemical ‘manipulators’ to alter central metabolic pathways, contribute to nutrient scavenging, and participate in developmental processes (Hibbing et al., 2010). Interestingly, ammonia also has been identified as a long-distance signal in *Candida albicans*, warning the colony of approaching starvation (Palková and Váhová, 2003). In this sense, the mode of actions of microbial volatiles should be assessed in more detail.

Effects of Fungal Volatiles on Bacteria

Bacteriostasis, similar to fungistasis, is the inability of bacteria to multiply in soil (Ho and Ko, 1982). Bacteriostasis is influenced by environmental factors such as nutrient supply and habitat conditions, but active volatile inhibitors also may be involved (Davis, 1976). It is known to date that bacteria produce volatiles that inhibit bacterial growth (Brown, 1973; Ko and Chow, 1977; Acea et al., 1988), and that volatiles produced by fungi also affect fungi (Stotzky and Schenck, 1976; Calvet et al., 1992; McAllister et al., 1996; Bruce et al., 2000; Martinez et al., 2004), but fungal volatiles acting on bacteria has not been reported (to the best of our knowledge).

Ecological Significance of Volatile Mediated Bacterial-Fungal Interactions

Suitable microenvironments in soils attract macro- and microbiota that colonize and form microhabitats, thereby creating dynamic microecosystems. Consequently, at least in densely and diversely populated habitats, bacteria and fungi are involved in a ‘networking’ community characterized by mutualism, commensalism, cooperation, antagonism, competition, and coexistence (Pal and McSpadden Gardener, 2006). Interactions between organisms can be specific or non-specific, but they are mostly multitrophic, thus keeping the microecosystem in balance. This is especially true for the mycorrhizosphere, where rhizobacteria, including plant growth promoting rhizobacteria, mingle

with mycorrhizal fungi and their associated bacteria, free living bacteria and fungi, protozoa (amoeba) or metazoa (nematodes), including many phytopathogenic organisms. In this arena, interactions between bacteria and fungi could have a positive or a negative impact on third parties, which is useful if the weakened party is a pathogen and the strengthened party is a valuable member of the community. It is likely that volatile compounds are involved in these phenomena, since many bacterial volatiles affect phytopathogenic fungi directly or indirectly, i.e., as a result of bacterial-fungal interactions, pathogens are affected. In any case, the plant would benefit. An elucidation of this plant-fungus-bacterium network of interactions opens the way for biological control of plant diseases. An impressive example was given by Cao et al. (2011). They showed *in vitro* and *in vivo* that a GFP-tagged *Bacillus subtilis* strain, originally isolated from the rhizosphere of a non-infested cucumber plant, was able to successfully suppress the growth of *Fusarium oxysporum* f. sp. *cucumerinum* by colonizing the root and persisting on the rhizoplane, which is critical for an effective biocontrol in this case of cucumber wilt. Although not explicitly investigated, the authors proposed antibiosis caused by diffusible agents to be at least one mode of action. This, however, does not exclude volatile agents. Other experiments with a *B. subtilis* strain isolated from the rhizosphere of wheat and soybean showed that bacterial volatiles were involved in the biocontrol of *Botrytis mali* and *Phytophthora sojae*, respectively (Tehrani et al., 2002; Jamalizadeh et al., 2010). However, when using rhizobacteria as biocontrol agents, it is apparently important that the biocontrol strain is indigenous to the treated plant species in order to prevent damage of indigenous beneficial fungi (Will and Sylvia, 1990; Xiao et al., 2008).

Volatiles also might be involved in tritrophic interactions comprising bacteria, fungi, and nematodes. *Paenibacillus polymyxa* and *P. lentimorbus* exhibited strong antifungal activities, thereby interfering with the nematode-fungus interaction *Meloidogyne incognita* - *Fusarium oxysporum*, which significantly reduced nematode infestation of tomato plants (Son et al., 2009). In addition, soil bacteria, including one rhizobacterial strain, enhanced the nematophagous activity of the nematode-trapping fungus *Arthrobotrys oligospora* by increasing trap formation and predaceous activity (Duponnois et al., 1998). Volatile signaling cannot be excluded for either experiment.

In their entirety, the emission patterns of volatile metabolites of a belowground microecosystem reflect the dynamics of the community (McNeal and Herbert, 2009). Variations could be related to changes in the microenvironment such as pH, humidity, temperature, nutrient supply, and resulting changes in metabolic activities of micro- and macrobiota. In this respect, *in vitro* studies of volatile-mediated interactions between bacteria and fungi provide only limited

access to the overall picture. Artificial test conditions might produce results that cannot be postulated uncritically for natural conditions. This especially applies to artificial growth media and nutrient supplies that influence metabolic activities as well as to “out of range” concentrations of the volatile mediators emitted (Nannipieri et al., 2003; Blom et al., 2011a). The crucial question is: are these concentrations found in the habitat? Since measurements of volatile concentrations in microhabitats are presently not available, *in vitro* testing is a useful tool to reveal substantial relationships between certain partners that might come into contact in a microecosystem. The consideration of environmental conditions and the verification of *in vitro* derived results in *in situ/in natura* experiments will give an overall picture regarding the role of volatiles in bacterial-fungal interactions and the implications of these interactions in community networks.

Conclusion and Perspectives

Volatiles are only a small proportion of the total number of metabolites produced by living organisms. However, because of their unique properties they are predestined to act as infochemicals in intra- and interspecies communications in the atmosphere as well as in the soil. This paper describes the wealth of microbial volatile emissions. The number of microbial volatiles (presently comprising around 800 compounds) and presumably of those with novel structures will increase significantly as this new research field expands. Just consider i) the large number of bacteria and fungi whose volatile profiles have yet not been obtained, ii) the various growth conditions that determine and alter the VOC profiles, and iii) the huge number of not yet identified or isolated microbes (10^6 !!). This foreshadows the potential this research area has and where it may develop in the future. It seems very likely that only the “tip of the iceberg” of possible ‘volatile-wired’ interactions between underground bacteria and fungi (and elsewhere) has been seen. It will be a central task in the future to elucidate the plethora of bacterial and fungal VOCs and determine their biological and ecological roles in the soil. It also is quite likely that the naturally produced VOCs can be used as potent non-invasive indicators to study soil microbial ecosystems, including far-reaching spatiotemporal dynamics and environmental perturbations. Ultimately, these microbial volatiles – individually or in mixtures, chemically synthesized or biologically emitted – with their positive and/or negative effects on other organisms may develop into useful agricultural tools.

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