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Sniffing bacterial volatile compounds for healthier plants

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Bacterial volatile compounds (BVCs) are not waste or by-products of primary metabolism but rather have critical roles in the biology and ecological competence of bacteria. BVCs are exploited as a source of nutrients and information in plant–bacteria interactions. They target key points in plant physiology, activating downstream metabolic pathways by a domino effect. BVCs are an ancient signal and are involved in plant–bacteria communication, which was shaped during evolutionary history and established before the development of higher plants. This type of communication is not exclusive to mutualistic interactions, because pathogens also use volatiles to alter plant physiology. Here, fragmented information is drawn together to provide a clearer view of how BVCs affect such interactions.

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Introduction

Volatiles are low molecular weight compounds with high vapour pressure that can evaporate and disperse easily. They act as intraspecies and interspecies signals that are mobile in air, water and soil [1–3]. The number of identified biogenic volatiles has increased rapidly in recent decades, as a result of the development of state of the art technologies for detection and characterisation of biogenic volatiles. Elementary information on their structure and biological functions can be found in specific database. For example, information on 2300 biogenic volatiles can be found in the SuperScent database [4]. In addition, the latest version of microbial volatile organic compounds (mVOC2.0) contains details of 1860 volatile compounds from 604 species of bacteria and 340 species of fungi [5•].

The roles of bacterial volatile compounds (BVCs) in promoting plant growth and inducing plant defence were discovered in 2003 and 2004 respectively [6,7]. Today, research on BVCs is leading to the discovery of missing pieces of the plant–bacteria interaction puzzle [8–11]. In this review, we draw together the various pieces of this puzzle to provide a clearer view of plant–bacteria communication, identify unanswered questions and make suggestions for future work, including studies into the modification of BVC production by other microbes or host plants, BVC-mediated plant responses, and evolutional aspects of BVCs in plant-microbe interactions (Table 1).

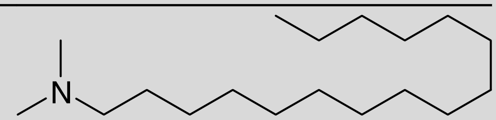
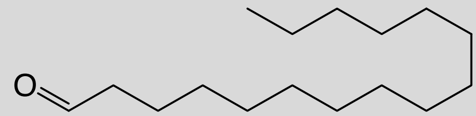
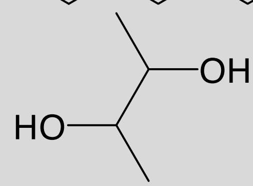
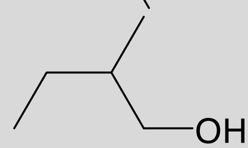
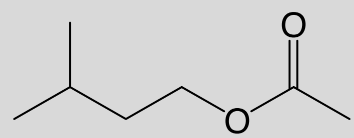
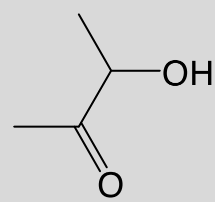
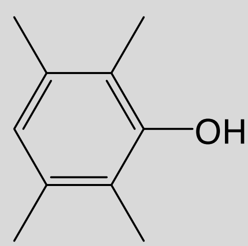
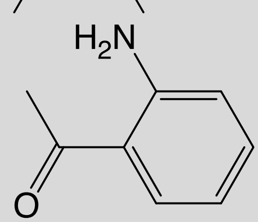
Regulation and role of BVCs in intra-kingdom and inter-kingdom interactions

BVC modulation by neighboring plants and microbes

Volatile synthesis in bacteria can be affected by different internal and external stimuli. Indeed, the volatiles themselves are potential candidates for intraspecies and interspecies and inter-kingdom signaling [12,13]. For example, volatiles from the plant *Medicago truncatula* can change the volatile profile of *Sinorhizobium meliloti* and *Arthrobacter agilis* [13,14]. In both bacteria, volatiles from *M. truncatula* increased the emission of the volatile dimethyl hexadecylamine noticeably (Figure 1). Fungal volatiles also alter volatile blends emitted from bacteria. For instance, volatile organic compounds from *Verticillium longisporum* increased emission of 2-methyl-1-butanol and hexadecanal and decreased isoamyl acetate and durenol in *Paenibacillus polymyxa* [15]. *Fusarium culmorum* increased the emission of sodorifen in *Serratia plymuthica* [16•]. Further study revealed that perception of inter-kingdom volatiles can alter the transcriptome of bacteria, leading to changes in bacterial volatile production. Two component regulatory systems were potential candidates among differentially expressed transcripts [16•]. The GacS/GacA two component regulatory system has a critical role in regulating volatile production in *Pseudomonas* spp. [17,18] (Figure 1). A GacS mutant of *Pseudomonas fluorescens* SBW25 caused differential emission of 24 volatile compounds and subsequently reduced the effect of bacterial volatiles on tobacco growth and defence [17]. A GacA mutant of *Pseudomonas donghuensis* also loosed it ability to emit HCN and sulphur containing volatiles, dimethyl sulfide, methyl thiocyanate, S-methyl thioacetate, dimethyl trisulfide [19]. Furthermore, the emission of the respiration-inhibiting volatile hydrogen cyanide

Table 1

List of bacterial volatile compounds mentioned in current review.

Names	PubChem ID	Molecular formula	Molecular weight	Chemical structure
Dimethyl hexadecyl amine	16221	$C_{18}H_{39}N$	269.517	
Hexadecanal	984	$C_{16}H_{32}O$	240.431	
2,3-Butanediol	262	$C_4H_{10}O_2$	90.12	
2-Methyl-1-butanol	8723	$C_5H_{12}O$	88.15	
Isoamyl acetate	31276	$C_7H_{14}O_2$	130.187	
Acetoin	179	$C_4H_8O_2$	88.106	
Durenol	10694	$C_{10}H_{14}O$	150.221	
2-Amino-acetophenone	11086	C_8H_9NO	135.166	
Sodorifen	46187193	$C_{16}H_{26}$	218.384