

# Bidirectional interaction between phyllospheric microbiotas and plant volatile emissions

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3 **Abstract**

4 **Due to their antimicrobial effects and their potential role as carbon sources, plant**  
5 **VOC emissions play significant roles in determining the characteristics of the**  
6 **microbial communities that can establish on plant surfaces. Furthermore,**  
7 **epiphytic microorganisms, including bacteria and fungi, can affect plant VOC**  
8 **emissions in different ways: by producing and emitting their own VOCs, which are**  
9 **added to and mixed with the plant VOC blend; by affecting plant physiology and**  
10 **modifying the production and emission of VOCs; and by metabolizing the VOCs**  
11 **emitted by the plant. The study of the interactions between plant VOC emissions**  
12 **and phyllospheric microbiotas is thus of great interest and deserves more**  
13 **attention.**

14

15 **The phyllosphere**

16 The phyllosphere includes all aboveground plant surfaces that provide habitats for  
17 microorganisms. The total surface area of the global phyllosphere has been estimated to  
18 represent approximately  $10^9$  km<sup>2</sup>, which could be colonized by bacterial populations of  
19 approximately  $10^{26}$  cells [1,2]. Aboveground plant surfaces harbor hundreds of species  
20 of bacteria and fungi with deleterious or beneficial effects on plants [2,3]. Among these,  
21 bacteria are by far the most abundant phyllospheric colonists and can reach densities of  
22  $10^7$  cells/cm<sup>2</sup> of leaf surface [4]. These microbial communities are very biodiverse and  
23 can vary their composition between and within plant species, depending on several  
24 environmental factors [5–8]. The phyllosphere consists of various aboveground surfaces  
25 of plants, including the surfaces of stems (caulosphere), flowers (anthosphere), fruits

26 (carposphere) and leaves (phylloplane), all of which can significantly differ in their  
27 microbial composition [9,10].

28

### 29 *Bidirectional effects between plant volatiles and phyllospheric microbiota*

30 Plant VOC (volatile organic compound) emissions play a relevant role in determining  
31 the characteristics of the microbial communities that inhabit plant surfaces, through  
32 their antimicrobial effects and their role as carbon sources for some microorganisms  
33 (Figure 1A). By contrast, plant phyllospheric microbiotas have the potential to affect  
34 plant physiology and modify plant biochemistry. Phyllospheric microorganisms reside  
35 at the interface between the plant surface and the atmosphere, where gases are  
36 exchanged, so the organisms can significantly modify the specific conditions of this  
37 microhabitat and interfere with plant VOC emissions [11] (1B). We review the current  
38 information on the bidirectional effects established between VOC emissions from  
39 aboveground plant surfaces and phyllospheric microbiotas. The interaction between  
40 plants and bacteria through VOCs is a research topic that warrants an increased research  
41 effort for providing useful information for understanding the emission of VOCs from  
42 vegetation.

43

### 44 **Effects of plant VOC emissions on phyllospheric microbiotas**

45 Plant VOCs can affect the phyllospheric microbiota by serving as carbon sources [12–  
46 18]. Microorganisms such as the yeast *Candida boidinii* and the bacteria  
47 *Methylobacterium extorquens* use plant VOCs such as methanol or methane as

48 substrates for their growth, although they are facultative methylotrophs, so they do not  
49 rely only or mostly on the consumption of methanol for their subsistence [12–14].  
50 Methylotrophic metabolism thus represents a selective advantage for bacterial  
51 colonization of the phyllosphere [12]. This advantage allows the microorganisms that  
52 use plant VOCs as substrates to grow preferentially on the surface of plants that are  
53 abundant emitters of these compounds.

54 Plant VOCs play a significant role in determining the characteristics of the  
55 microbial communities that can establish on each plant tissue, also through their  
56 antimicrobial effects [10]. Several studies have reported growth-inhibiting effects of  
57 VOCs on microbes [19,20]. Terpenoids, phenylpropanoids and benzenoids are major  
58 constituents of plant VOC emissions that have antimicrobial properties and strongly  
59 influence phyllospheric microbial colonization [21–23]. Main constituents of plant  
60 VOC extracts such as the common monoterpenes limonene and  $\beta$ -pinene have inhibiting  
61 effects on bacterial growth [21]. Aldehydes such as benzaldehyde, acetaldehyde, and  
62 cinnamaldehyde also strongly inhibit microbial growth [21,24].

63 Although the VOC concentrations tested in most studies revealing antimicrobial  
64 effects of VOCs are high compared to the amounts that are probably present on plant  
65 surfaces, because these works test doses from leaf extracts, strong evidence suggests  
66 that plant VOC emissions play a relevant role in structuring plant-microbe interactions  
67 on aboveground plant surfaces [10,25–27]. The antibacterial and antifungal properties  
68 of plant VOC emissions may play a significant role in selecting the microorganisms that  
69 can establish on plant surfaces by limiting their ability to colonize and grow.  
70 Furthermore, different plant parts have developed different degrees of chemical  
71 protection by emitting different amounts and profiles of VOCs that may depend on the

72 relevance and function of each organ. It has been observed that the composition of the  
73 epiphytic bacterial communities of *Saponaria officinalis* and *Lotus corniculatus* plants  
74 differed significantly between petals and leaves, with less bacterial diversity on petals  
75 that was attributable to the antibacterial VOCs released by the floral tissues [10].

76

## 77 **Effects of phyllospheric microbiotas on plant VOC emissions**

### 78 *Emission of microbial VOCs*

79 Phyllospheric microbiotas consisting of bacteria and fungi contribute to plant volatile  
80 blends with their own emissions of VOCs from de novo biosynthesis [28–30] and  
81 biotransformation [15,31–33]. In general, bacterial VOC emission profiles have been  
82 described to be rich in alkenes, alcohols, ketones and terpenes, while in contrast, fungal  
83 VOC profiles are dominated by alcohols, benzenoids, aldehydes, and ketones (Figure 2)  
84 [30]. However, these VOC emission profiles were obtained from bacteria and fungi  
85 grown on rich media, and microorganisms growing on the phyllosphere that is much  
86 more limited in nutrients can probably show different profiles [34,35]. The composition  
87 of VOCs emitted by microorganisms is species-specific and can show different levels of  
88 complexity. The relative composition of microbial VOC blends varies with growth  
89 conditions (temperature, oxygen availability, pH), the carbon source availability and the  
90 age of the culture. Ultimately, the microbial VOC profile is a consequence of specific  
91 metabolic activities of the particular microorganism. Floral microbiotas, for example,  
92 can significantly affect the composition and the amounts of volatile terpenes emitted by  
93 flowers, which play crucial ecological roles in pollinator attraction. A comparison of  
94 floral terpene emissions and contents in untreated *Sambucus nigra* plants and plants  
95 submitted to fumigation with antibiotics showed that the removal of the microbiota

96 significantly decreased the rates of floral terpene emission, even though the floral  
97 terpene contents did not change. This suggests that the microbiota of the anthosphere  
98 significantly contributes to floral VOC emissions [31]. Microorganisms that live on fruit  
99 surfaces also produce and emit VOCs that can significantly contribute to fruit aroma.  
100 This was demonstrated by the clearly distinguishable patterns of VOC emission  
101 produced by the bacteria and fungi from the carposphere of wine grapes [32].

102

### 103 *Effects of microbial VOCs on plants*

104 Phyllosphere microbes emit different types of VOCs [30] and therefore have a great  
105 potential to affect plant physiology. Some microbial VOCs enhance plant growth and  
106 stress resistance [36]. The VOCs emitted by some non pathogenic microbes also prevent  
107 the colonization of plant tissues by fungal and bacterial pathogens [36]. The endophytic  
108 bacterium *Enterobacter aerogenes* increased plant pathogen resistance and affected  
109 tritrophic interactions in maize (*Zea mays*) plants by the production and release of 2,3-  
110 butanediol, a VOC that acts as a phytohormone [37]. Microbial VOCs can mediate  
111 several interactions between bacteria and fungi that have negative or neutral effects on  
112 plants [38]. These studies indicate that phyllospheric microbiotas have significant  
113 effects on the host plant and its interactions with other organisms by emitting their own  
114 VOC profiles.

115

### 116 *Microbes induce plant VOC emission*

117 Microbes can also alter the plant VOC emissions by inducing plant defensive responses.  
118 Some pathogenic microbes such as the fungi *Melampsora epitea* and *Fusarium* sp., or  
119 the bacteria *Pseudomonas syringae* affect VOC production when they elicit an immune  
120 response on the plant [39–41], but other species can be tolerated by the immune system  
121 of the host plant [42]. Some studies have reported the induction of plant VOC emission  
122 by bacterial and fungal pathogens. Among these, terpenoids play a major role as  
123 defensive VOCs that are emitted in greater amounts after fungal infection [39,40,43,44].  
124 Also, VOCs from the lipoxygenase pathway are emitted from green leaves in  
125 considerable amounts after infection and play a relevant role in inducing defensive  
126 responses in neighboring plants [39,40,44,45]. This induction has a positive effect on  
127 total VOC emissions and may also change VOC composition when the production and  
128 emission of new compounds that are not among the constitutively emitted VOCs are  
129 elicited [46].

130

### 131 *Transformation of plant VOCs*

132 Microbes can change the VOC compositions of plants by degrading and consuming  
133 plant VOCs as carbon sources [42]. Ubiquitous VOCs that are abundant in the  
134 atmosphere also accumulate in significant amounts on plant surfaces by uptake and  
135 deposition [47] and can thereby become accessible to phyllospheric microorganisms.  
136 Some foliar microorganisms can degrade these VOCs that are released by the plant or  
137 are adsorbed to the leaf cuticle in considerable amounts, such as methanol, methane,  
138 phenol and toluene [14,48–51]. Methanol, for example, is a prominent carbon source for  
139 epiphytic components of microbiotas, such as the methylotrophic bacterium  
140 *Methylobacterium extorquens* [12] or the methylotrophic yeast *Candida boidinii* [13].

141 Bacteria in the genus *Methylobacterium*, facultative methylotrophs found on the surface  
142 of strawberry leaves, can consume the methanol that is constantly emitted by the plant  
143 [14]. Diverse common soil microorganisms that are also ubiquitous on plant surfaces  
144 can degrade other VOCs such as monoterpenes [15–17] and aromatic compounds [18].  
145 Phyllospheric microorganisms are thus able to degrade the plant-emitted VOCs that  
146 play significant roles in the plant biotic and abiotic environments [52–54].

147

#### 148 **Concluding remarks and future directions**

149 Phyllospheric microbiology is an emerging research field at an initial stage. The  
150 inclusion of phyllospheric microbiota into ecological studies will allow making a key  
151 step forward in terrestrial ecology. The consideration of phyllospheric communities on  
152 the understanding of plant and community ecology will open the doors to a vast field of  
153 work. The composition of phyllospheric communities and their effects on plant  
154 physiology and on many ecological processes remain to be elucidated or investigated in  
155 more detail by exploiting the current genomic and metabolomic techniques [3]. Plant  
156 VOC emissions that play multiple relevant roles in plant and community ecology and  
157 also in atmospheric chemistry can be significantly affected by the activities of  
158 microorganisms living on the phyllosphere. Future research efforts should thus be  
159 devoted to continuing the study of the modes in which microorganisms can affect plant  
160 VOC emissions in various aboveground plant tissues, while also characterizing the  
161 magnitude of the changes and the resulting impacts on ecological interactions that are  
162 mediated through VOCs. This information may be of relevant interest for assessing the  
163 adequacy of different treatments applied in crop management to control fungal and  
164 bacterial plant pathogens (see also outstanding questions). Assuming that pesticide



165 application changes or removes the natural phyllospheric microbiota from crop plants,  
166 then plant VOC emissions as well as other plant traits may be affected, and as a result,  
167 interactions with other organisms such as pollinators, herbivores or parasitoids will be  
168 affected. Pesticides have strong effects on community composition in the phyllosphere,  
169 suggesting that pesticide treatments could interfere with the natural interactions between  
170 phyllospheric microbiotas and plant defenses [55–57], or even with flower scent [46].  
171 Addressing this question in future experiments may reveal indirect impacts of antifungal  
172 and antibacterial pesticides on herbivory and pollination, which are very relevant for  
173 crop production.

174       New studies should also assess the role of plant VOC emissions on determining  
175 the types and numbers of microorganisms that can establish and grow on the  
176 phyllosphere, relative to many other environmental variables. For example, the use of  
177 modified plant lines in which the expression of specific VOCs is suppressed can be used  
178 to assess this question in a more realistic way than exposing cultured monospecific  
179 microbial colonies to the VOCs. Tests with microbial cultures, however, can also  
180 complement and support the experiments by providing direct evidence of the  
181 antimicrobial effects of individual VOCs or complex VOC mixtures [19,20].

182       A better knowledge of the effects of phyllospheric microbiotas on VOC  
183 emissions from vegetation may also help to better understand and estimate the impacts  
184 of these microorganisms on atmospheric chemistry and even climate. A few recent  
185 studies indicate that phyllospheric microbiotas contribute greatly to the composition and  
186 amount of VOCs emitted by plants [46,58]. After better characterizing the effects of  
187 phyllospheric microbiotas on VOC emissions from a variety of plant species and under

188 different conditions, future models of VOC emission should implement this information  
189 to better predict VOC emissions from terrestrial ecosystems and vegetation.

190

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345 **GLOSSARY**

346 **Aromatic compounds:** the second largest class of plant VOCs, comprising  
347 phenylpropanoid and benzenoid compounds. They are synthesized from the aromatic  
348 amino acid phenylalanine via the shikimate biosynthesis pathway.

349 **Benzenoids:** chemical group of VOCs that are characterized by containing a benzene  
350 ring. They are aromatic compounds.

351 **Biotransformation:** chemical modification (or modifications) made by an organism on  
352 a chemical compound.

353 **Epiphytic:** those organisms that live on the surface of a plant.

354 **Monoterpenes:** a group of volatile terpenes that consist of two isoprene units.

355 **Phenylpropanoids:** VOCs that are synthesized by plants from the amino  
356 acid phenylalanine through the shikimate/phenylpropanoid biosynthesis pathway. They  
357 are aromatic compounds.

358 **Terpenoids:** the largest and most diversified class of secondary metabolites with many  
359 volatile constituents. They are synthesized through the mevalonic acid (MVA) and the  
360 methylerythritol phosphate (MEP) pathways.

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370 **Figure Legends**

371 **Figure 1. (A) Effects of volatile organic compounds (VOCs) emitted by plants on**  
372 **phyllospheric microbiotas.** Plant VOCs that have antimicrobial properties, such as  
373 some terpenoids and aldehydes, can inhibit the growth of microorganisms on the  
374 phyllosphere. Some plant VOCs, such as methanol or methane, can serve as substrates  
375 for bacteria and fungi that use them as carbon sources. **(B) Effects of phyllospheric**  
376 **microbiotas on the emission of plant VOCs.** Phyllospheric microorganisms can  
377 consume plant VOCs or biotransform them into new VOCs. Microorganisms can affect  
378 the physiology of the host plant, with resulting changes to their VOC emissions, and can  
379 also produce and emit their own VOCs. Microbial VOCs can have antimicrobial effects  
380 on potential plant pathogens that can colonize the phyllosphere and can also enhance  
381 plant growth and resistance to stress.

382

383 **Figure 2. Distribution of microbial volatile organic compound (VOC) emissions.**  
384 Richness of VOCs emitted by bacteria (yellow columns) and by fungi (red columns) for  
385 different chemical classes. Chemical classes are ordered according to the number of  
386 different compounds within a class. Data from *mVOC: a database of microbial volatiles*  
387 [30].