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Highlights

- Plant-associated bacteria interact with their environment through exchange of chemicals, including volatile compounds. Innovative agricultural technologies may exploit the inherent advantages of bacterial airborne signals, including diffusibility, independence from water availability and physical connection, and absence of pesticide residuals.
- Volatile compounds resulting from plant-pathogens interactions allow non-destructive disease diagnosis on bulk samples of asymptomatic plant material.
- Volatile compounds, expressing a direct biocidal activity, interfering with signalling, or stimulating plant host defences, contribute to biological control of pests and pathogens.
- Bacterial volatile compounds modulate plant hormones enhancing plant growth, stress tolerance, crop quality, aroma and nutraceutical characteristics, and reduce post-harvest losses.

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1 **Applications based on bacterial volatile compounds for crop management and quality**

2

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8

9 **Keywords**

10 Plant growth promoting bacteria, Biological control, VOC-based diagnosis, Crop protection, Abiotic
11 stress tolerance

12

13 **Abstract**

14 Bacteria produce a huge diversity of metabolites, many of which mediate ecological relations.
15 Among these, volatile compounds allow broad-range effects at low doses and may therefore be
16 exploited for applications in plant defence and agricultural production. Such applications are still in
17 their early development. Here we review the latest technologies involving the use of bacterial
18 volatile compounds for phytosanitary inspection, biological control, plant growth promotion, and
19 crop quality. We highlight a variety of effects with a potential applicative interest, based on either
20 live biocontrol and/or biostimulant agents, or the isolated metabolites responsible for the
21 interaction with hosts or competitors. Future agricultural technologies may benefit from the
22 clarification of bacterial interactions with the environment, and the development of new analytical
23 tools.

24

25

26 **Bacterial volatile compounds in plant ecological interactions**

27 Bacterial metabolic products characterised by low vapour pressure, high lipophylicity and a
28 molecular weight below 300 Da are likely to be released as Volatile Organic Compounds (**VOCs**, see
29 glossary). Considering the enormous metabolic diversity of bacteria, such compounds may derive
30 from a large variety of chemical pathways, and are generally emitted as complex mixtures [1]. The
31 composition of the bacterial **volatilome** (see glossary) is highly influenced by the growth conditions
32 [2-5], including soil chemistry and structure, pH, availability of water and oxygen, presence of plant

33 exudates or other organic compounds, and light irradiation. Translating such considerations into
34 horticultural crop management, agricultural (tillage, cover cropping, fertilisation, watering, and
35 plant protection) or post-harvest (refrigeration, atmosphere control, and ethylene modulation)
36 practices that modify such parameters can influence BVC emissions as well [6].

37 Along with the characterisation of a growing number of bacterial volatile compounds (**BVCs**, see
38 glossary) [3,4,7], their roles in intra- or inter-specific signalling or competition are being discovered
39 (Figure 1). It should also be noted that the most commonly adopted analytical techniques in studies
40 concerning bacterial volatile compounds are unable to detect molecules with a low molecular
41 weight, such as CO₂, ethylene, nitrogen oxides, ethanol and H₂S (Box 1). Thus, part of the biological
42 effects mediated by bacterial airborne signals may still be eluding the researchers' efforts. In
43 comparison to water-soluble compounds, inherent advantages of VOCs in ecological interactions
44 reside in their high diffusibility, enabling both above- and belowground action, the ability to diffuse
45 through lipophilic barriers (such as cell membranes and plant cuticle), and the independence from
46 water and physical connection among the VOC-producing organism and the signal recipient.

47 Technological applications based on the release or the exchange of VOCs are most likely to succeed,
48 when they take advantage of these characteristics. Volatility is possibly one of the key points, as it
49 allows a relative uniformity of the gas phase even in cases of poor accessibility of the target (for
50 instance, in the soil, in stored bulk samples, or in internal plant tissues). In addition, biogenic VOCs
51 do not pose problems with residues and environmental accumulation. By contrast, one should
52 consider possible drawbacks deriving from the generally low concentration, impermanence, low
53 target specificity, and difficult handling of VOCs used for plant treatment.

54 The above reasons may be responsible for the so-far limited enactment of VOC-based technologies.
55 However, some work-arounds may be envisaged to reduce the weight of drawbacks. The use of
56 microbes that form stable populations on plant hosts, exploiting naturally occurring resources and
57 constantly delivering their bio-active function, or that survive harsh conditions (e.g. *Bacillus* spp.
58 spores), may grant a durable effect of the treatment. In this light, the screening of bacterial species
59 forming endophytic and/or specialised symbiosis offers a source of biological functions expressed
60 in an efficient and highly focused way. Recent technological advancement in genomics,
61 **metagenomics** and **gnotobiotics** (see glossary) has enabled breeding programs centered on the
62 plant **holobiont** (see glossary), in which, in addition to plant genetic resources, microbial diversity
63 (overlooked in traditional breeding, and even possibly lost during domestication or selection) is also
64 explored [8-10]. Alternatively, when live bacteria cannot be used, their active principles could still

65 be considered for field application with encapsulation methods allowing a controlled release [11].
66 Caution should be taken for such treatments in dosing the active principle's release rates (as plant
67 stress may derive from its excess) and avoiding wastes due to volatilisation.

68

69 **VOC profiling for plant disease diagnosis**

70 Along with visual inspection, immunochemical and molecular methods represent the standard
71 techniques for disease diagnosis, due to their reliability, sensitivity, specificity, and reasonable
72 practicality in terms of costs and work effort [12,13]. However, these methods still pose a number
73 of issues. Since all of them are destructive, the assessment of plant or fruit health status causes an
74 economic loss and cannot be applied to unique samples. The development and production of
75 specific antibodies, and the design and validation of PCR primers require a laborious set-up and are
76 conditioned by the availability of sequence or protein data. Moreover, both PCR and
77 immunochemical methods are targeted to single organisms, and the screening for multiple
78 pathogens results consequently in a multiplication of work. Finally, representativity at the sampling
79 stage is a major constraint, particularly when pathogen populations are relatively small, and the
80 chance of false negatives must be minimised by increasing the sample size.

81 As a consequence of the bacterial metabolism and the concurrent activation of plant defences, the
82 VOC emission by pathogen-infected plants is, in principle, discernible from that of healthy ones [14].
83 Thus, the possibility of a VOC-assisted plant diagnosis has been put forward, and the recognition of
84 bacterial diseases by volatile fingerprinting has been attempted in several species and/or crops
85 (Table 1). VOC screening is non-destructive and can be applied to crops or live plants without
86 compromising their economic value or viability. Unlike molecular and immunochemical methods,
87 VOC-assisted plant diagnosis, in principle, allows the screening for multiple pathogens in the same
88 run [15,17,25,30,31]. Finally, bulk samples can be analysed as a whole with minimal risks of sampling
89 errors.

90

91 *Analytical technologies and methods*

92 **GC-MS, PTR-MS, SIFT-MS, E-NOSE** and **FAIMS** (see glossary) are among the technologies available
93 for VOC-based diagnosis (Table 2). A major distinction can be made between techniques allowing
94 the analytical determination of the chemical components of the VOC blend (e.g. GC-MS), and
95 techniques that only allow overall VOC profiling (e.g. most E-NOSE models), with in-between cases
96 of techniques with analytical power restricted to certain conditions. Techniques of the first class

97 may be used to identify distinctive marker compounds for determinate pathogens [15,17,18,20-
98 22,29]. Alternatively, the recognition of infected samples may be done through multivariate
99 statistical analysis or artificial neural networks. These recognition procedures may be applied to any
100 technique, but they are an obligate choice for non-analytical methods.

101 Based on the technology and the recognition method, several sampling systems are available.
102 Portable instruments may allow the direct application to ambient air. In these cases, the
103 instrumental sensitivity can be adjusted by regulating the input flow rate (i.e. the air volume
104 screened). Ambient air analysis or headspace sampling in odourless gas bags or canisters are the
105 simplest options, with the smallest chance of artifactual results. However, when such options are
106 not practical (e.g. gas samples are too small, or marker compounds are in trace amounts), the use
107 of VOC-sorbent materials may be envisaged to concentrate the VOC sample [14].

108

109 *Sample recognition and applicative perspectives*

110 Besides pathogen infection, other irrelevant factors (such as plant genotype, secondary microbial
111 colonisation, tissue age and environmental conditions during sampling) are predicted to influence
112 VOC emissions with additional levels of complexity. Furthermore, diagnostic power is influenced by
113 disease severity [15,32,33], thus latent infection stages or sporadic pathogen presence are harder
114 to detect. Physico-chemical factors influencing volatilisation and relative composition of air samples
115 (temperature, relative humidity, sorbent saturation or chemical affinity) also require to be
116 accounted for.

117 Thus, the main challenge for VOC-based diagnosis seems to be the development of feature
118 extraction methods, to isolate disease-related information from background noise. For this reason,
119 E-NOSE methods have not progressed beyond the proof-of-principle status so far. In fact,
120 discrimination power is related to the independence among the components of data variability [35],
121 while E-NOSE models tested for plant diagnosis include no more than 32 sensors with partially
122 overlapping chemical sensitivity [14]. Recent developments in E-NOSE construction, such as
123 coupling with chromatographic separation [36] and colorimetry [37] may overcome current
124 discrimination power limits.

125 With regard to techniques with high analytical power, methods based on unsupervised machine
126 learning and bacteria-VOCs association database were studied for human diagnostic purposes [38].
127 The implementation of such methods in plant health monitoring could be integrated with existing

128 microbial VOC databases [3]. An effort is required to expand such databases, currently limited in the
129 number of bacterial species covered.

130 The current technology readiness of VOC-based diagnostic systems may support standard
131 phytosanitary inspection by pre-screening plant material, to focus more in-depth, time- and
132 resource-consuming analyses on dubious cases. Significant advances may come in the future with
133 the development of more versatile instruments [36,37]. Whatever technology may become
134 dominant, coordination among researchers, field operators and industry is a requisite for the setting
135 of standards, databases and accepted practices.

136

137 **Bacterial volatile compounds in biological control**

138 Biological control has raised an interest over time, as a tool to achieve a stable level of disease
139 control by environmentally sustainable means. Biocontrol agents (**BCAs**, see glossary) are organisms
140 that reduce a pathogen's population size, or its chance to cause disease, by directly killing the
141 pathogen (with antibiotics, lytic enzymes and other toxic compounds), by interfering with its
142 signalling or regulatory metabolism, or by direct competition (i.e. better exploitation of resources,
143 determining the pathogen's starvation). These interactions contribute to microbial antagonism
144 (Figure 1). In this scenario, several BVCs have drawn attention as possible mediators of long-range
145 effects. While it may be expected that their gas-phase concentrations never reach biologically active
146 levels as they diffuse in the atmosphere, the competition among microbes in the phyllosphere takes
147 place in matrices (such as biofilms, mucilages, plant waxes) or sites (sub-stomatal chambers, soil
148 pores) where local BVC may attain substantial concentrations [39]. In this light, the identification of
149 BVC-releasing symbiotic endophytes may be desirable, as their beneficial effects would be delivered
150 close to their target and in a concentrated form.

151 Alternatively, BVCs can induce systemic plant defences (Box 2). Notably, such induction occurs at
152 low BVC rates, acts systemically and persists after the removal of the emitter bacterium, whereas
153 BVC-mediated microbial antagonism would require a local and continuous emission at higher rates.
154 Low BVC rates prime, rather than activate plant defences, i.e. responses are more prompt and
155 intense upon pathogen attack, but no phenotypic changes (including in yield and crop quality) are
156 expressed otherwise. In addition, the same plant may release pre-alert signals to neighbouring ones
157 [40]. Thus, even signals in low concentrations may lead to significant large-scale consequences.

158 BVCs may also influence plant-pest interactions, insect behaviour and survival rate, and thus could
159 be possibly used for pest control strategies (Box 3).

160 In spite of the potential applications, the use of BCAs presents some inherent difficulties, such as an
161 inconstant effectiveness, depending on environmental, agricultural and ecological factors that may
162 vary in different areas, plant species or growing seasons. In addition, the efficacy of BCAs depends
163 on their population size, which usually decreases steeply after the release, and co-formulants are
164 often required to extend the BCA's field life. For these reasons, BVCs have not yet found specific
165 applications in biological control. As a promising perspective, the development of synthetic bacterial
166 communities may overcome some of these drawbacks, by achieving a better stability or resilience
167 of the microbial biocoenosis, along with the integration of multiple mechanisms of action [41,42].

168

169 *Direct toxicity against pathogens*

170 In exerting direct toxicity against plant pathogens, BVCs are influenced by several factors. Along with
171 the chemical nature of the compound, its release rate, the occurrence of the conditions for its
172 production, and the gas phase dynamics that regulate its volatility and stability all contribute to its
173 ecological role and the technological usefulness [39]. The best-studied bacteria, in relation to
174 characterisation of BVC toxicity, include several actinomycetes, *Pseudomonas*, *Bacillus*, *Serratia*,
175 *Burkholderia*, *Xanthomonas* and *Erwinia* species.

176 Among the volatile compounds hindering the growth of competitors, ammonia, cyanide and sulfur-
177 containing metabolites are believed to play a major role [43]. However, bacterial strains not
178 releasing such compounds can still display antimicrobial properties, indicating that other BVCs
179 substantially contribute to inhibition of microbial growth, and that synergistic effects exist between
180 different compounds. Antimicrobial effects were described for alkanes, alkenes, alcohols,
181 aldehydes, ketones, esters, terpenoids, pyrazines, phenolics, amines, quinolones, chlorine and
182 sulfur compounds (Table 3) [44-57]. The most common molecular targets of toxic BVCs include
183 metal cofactors, sulfhydryl groups, and protein folding.

184 Fungi and oomycetes often show a considerable sensitivity to BVCs, both for the elongation of
185 mycelia and for spore germination [43,46-49]. In contrast, fewer cases are reported regarding BVC-
186 mediated control of bacterial pathogens, namely, *Agrobacterium* species [48,58], *Clavibacter*
187 *michiganensis* [59,60], *Xanthomonas oryzae* pv. *oryzae* [61] and *Ralstonia solanacearum* [62].
188 Reasons for such difference in susceptibility may reside in differences between bacteria and
189 eukaryotic organisms, for instance in plasma membrane composition or gene expression.

190 The importance of BVC toxicity for interspecific competition in real conditions is debated [63],
191 because of its dependence on BVC production rates and chances of accumulation. Thus, BVC-

192 mediated suppression of pathogens was not considered as a trait for selection of new biocontrol
193 agents until recently [49,64]. Nonetheless, this mechanism has been documented for several
194 commercial biocontrol agents, and some of the BVCs involved, such as benzothiazole and dimethyl
195 sulfides [49,64] have been adopted as active principles in exogenous biocide treatments.
196 Biomimicry, i.e. the simulation of biological processes and interactions for applicative purposes, may
197 be advisable in field conditions for a number of reasons, including the caution in introducing
198 organisms into a new environment with potentially irreversible effects, and the higher control of
199 chemical nature, dosage and timing of the treatments [65]. Conditions for exogenous VOC
200 treatments, however, include the technological feasibility of gas application to the target (soil,
201 canopy, stored crops) and the low toxicity at the treatment dosages for the operator and for non-
202 target organisms.

203

204 *Disruption of quorum sensing*

205 The complex of regulatory functions connecting the perception of intra- or inter-specific bacterial
206 population density to the expression of 'social' phenotypes is termed Quorum Sensing (**QS**, see
207 glossary). The typical QS signalling circuit consists of the production of a signal compound, along
208 with the expression of specific receptors for the same signal(s). Among the traits governed by QS,
209 bacterial motility, formation of biofilms, biosynthesis of secondary metabolites and virulence factors
210 have been observed, implying their role in improving bacterial fitness in a crowded, diverse and
211 competitive environment [66]. As a consequence, several species may form stable symbiotic
212 consortia, based on the reciprocal exchange of nutrients and signals [67,68]. In the case of
213 pathogenic bacteria, the full expression of virulence can require a stimulation by other microbial
214 neighbours [69].

215 N-acyl-homoserine lactones (AHLs) are the best-studied example of QS signals, since they are
216 employed by a wide array of Gram-negative bacteria, including plant pathogens such as
217 *Pseudomonas*, *Erwinia/Pectobacterium* and *Agrobacterium* species. Other compounds mediating
218 QS include peptide, aminoacid or fatty acid derivatives. While QS activity was only studied in
219 aqueous solutions for most of these compounds, their semi-volatile nature presumably also allows
220 airborne signalling.

221 The disruption of QS systems (Quorum Quenching, QQ) may be pursued to reduce the population
222 of pathogens and/or to control the incidence and severity of plant diseases [70]. Interference in QS
223 has been demonstrated for some BVCs. Among these, DMDS reduces the production of AHLs in *P.*

224 *chlororaphis* [71]. Linear ketones (2-heptanone, 2-nonanone, 2-undecanone) and 2-amino-
225 acetophenone showed an activity on engineered AHL biosensors [72,73].

226 Indole and its derivatives may act as QS signals, being produced by some bacterial species in a
227 population-dependent manner and eliciting specific responses. Non-producing pathogenic bacteria
228 may also perceive it, possibly by means of AHL receptors [74]. Although auxin (indole-3-acetic acid)
229 and indole are structurally related, in *Agrobacterium tumefaciens* (specialised in auxin biosynthesis,
230 but not releasing indole) only indole can induce bacterial motility, biofilm formation, antibiotic
231 resistance and expression of virulence genes, while reducing bacterial growth in the 0.2-1 mM
232 concentration range [75].

233

234 **Biostimulation**

235 After the initial observation of plant growth promotion by 2,3-butanediol-emitting bacteria [76], it
236 has become evident that BVC-mediated biostimulation is a widespread phenomenon involving
237 numerous bacterial species and compounds [2,77], with potential applications still to be tested. The
238 adaptive rationale of some biological effects promoted by plant-associated bacteria is, in many
239 cases, evident. Symbiotic organisms, for instance, take benefit from increasing root growth and
240 plant nutritional status. Conversely, pathogens can release BVCs to modify plant metabolism to their
241 own advantage [78,79]. However, some methodological caveats should be pointed out in the study
242 of influences of VOCs on complex plant traits. Several molecules of great importance for plant
243 metabolism, but not easily detected in the most common experimental settings, for instance, may
244 be neglected (Box 1).

245 Plant growth is the result of several factors, such as hormonal signalling, nutrition, stress tolerance
246 (Figure 1). Thus, the observation of a plant growth-promoting effect by a bacterial strain in
247 laboratory conditions, in absence of nutritional or cultural constraints, is possibly not indicative of
248 the applicability of the same strain in field. Secondly, plant growth may not correlate (or even
249 inversely correlate) with crop yield, for which not only carbon fixation, but also reallocation of
250 photosynthates is relevant. Thirdly, the effects of BVCs are generally pleiotropic, i.e. they interact
251 with multiple signalling pathways, and are not specific to a definite target organism [43].

252

253 *Plant growth promotion and nutrition*

254 Growth promotion by BVCs was shown on several cultivated species, including alfalfa, barley, basil,
255 broccoli, lettuce, poplar, soybean, tobacco, tomato [43,77]. These effects have been related to

256 modulation of plant hormones, such as cytokinins [76], auxins, brassinosteroids [80], gibberellins,
257 ethylene [81] and strigolactones [82].

258 While hormonal effects may shape the allocation of resources within the plant and its phenological
259 progression [79], plant growth promotion and biomass increase should come with a corresponding
260 nutritional enhancement. The stimulation of auxin metabolism and/or signalling, for instance, leads
261 to changes in plant root architecture, which contributes to the uptake of water and nutrients [83].
262 Ethylene participates in the activation of mineral uptake systems [84]. BVCs were implied in
263 counteracting carbohydrate- and ABA-mediated inhibition of photosynthesis, thus enabling higher
264 CO₂ fixation rates [85], and stimulating iron uptake [86,87]. It should be noted that most research
265 was conducted in laboratory or controlled conditions, where nutrients and water are generally not
266 limiting.

267

268 *Abiotic stress tolerance*

269 Plant growth promotion by microbes can result from increased tolerance to environmental stresses.
270 Although mechanisms are often far from being elucidated [88], such effects are generally induced
271 by the release of volatile hormones by the microbes (notably ethylene, methyl-jasmonate and
272 methyl-salicylate), or involve the signalling cascade of plant hormones [89].

273 Current knowledge on BVC-induced tolerance refers mainly to osmotic, salt and/or water stress (Box
274 4). In addition, this research area may provide significant advancement to phytoremediation and to
275 the adaptation of crops to stresses related to climate change [90]. The recovery of marginal soils,
276 for instance, may be enhanced by the root branching stimulation, exerted by some symbiotic
277 bacteria to increase the release of organic carbon into the rhizosphere. Among the BVCs implicated
278 in this plant-microbe interaction, 1-butanol and the QS signal butyrolactone may play a role [91].

279

280 **Crop quality**

281 A list of examples of bacterial interactions with crops, influencing crop quality, is shown in Table 4.
282 In all the cases in which crop quality depends on secondary metabolites, such as essential oils and
283 aromas, a close link between the elicitation of plant defences and an increased crop value is easily
284 explained. In fact, essential oils form one of the first lines of plant defence and inter-plant
285 communication, and their contents are raised by BVCs from several defence-inducing bacteria. Thus,
286 an increased essential oil content was obtained by exposing aromatic plants, including peppermint

287 and basil [92,93], or medicinal plants such as *Atractylodes lancea* [94], to BVCs emitted by several
288 *Pseudomonas*, *Bacillus* and *Azospirillum* spp.

289 In the determination of the aromatic profiles of fruit, a remarkable role has been observed for the
290 associated microflora. *Methylobacterium* spp. include endophytic species expressing alcohol
291 dehydrogenase (ADH) activity, which converts plant-derived alcohols to the corresponding
292 aldehydes or ketones [95,96]. The substrate-specificity of bacterial ADH is low, but distinct from that
293 of plant ADH, thus explaining the diversity, along with the higher intensity, of VOC emissions from
294 microbe-colonised plants.

295 During post-harvest storage, crops may incur in spoilage by pathogens, with consequent loss of
296 produce and/or contamination by mycotoxins. Because of the use of controlled atmosphere on a
297 large variety of crops, VOC-based technologies may fit well in post-harvest disease control. In fact,
298 on one hand, relatively high concentrations of bioactive volatiles can be obtained in a closed storage
299 cell; on the other hand, in comparison to synthetic fungicides, the application of biogenic VOCs and
300 BVC-emitting bacteria to products for human consumption poses lower concerns. Several *Bacillus*
301 spp. strains releasing antifungal BVCs were identified and tested on citrus, mango, cherry, litchi and
302 peach [97-102], while *Streptomyces* spp. were tested on strawberry, citrus, tomato and chili [103-
303 107]. Some compounds mediating antifungal effects, such as cedrol, 2-pentylfuran [102] and
304 acetophenone [107], are commonly found among fruit aromas, and their efficacy was proved on a
305 large spectrum of pathogens. Therefore, their technical use may encounter few restrictions by
306 policy-makers, and possibly even higher appreciation by consumers.

307 The microbial population living on grapevine berries (including *Paenibacillus* spp.) produces volatile
308 compounds possibly improving the quality of wine [108]. Thus, while fruit technology has been so
309 far oriented to the limitation of microbial populations on the crop, future work should address and
310 exploit the contribution of the microflora to aromatic properties of fruit or derivate products.

311

312 **Concluding remarks**

313 Despite the great diversity of bacterial metabolites and of biological relations mediated by them,
314 which form a huge reservoir of resources with a potential applicative interest, BVC applications have
315 been explored so far only marginally, and their practical use is at its dawn especially for improving
316 crop tolerance and quality [95]. The present overview was limited to volatile compounds emitted
317 by bacteria, but other organisms (including fungi, moulds and, to some extent, plants) also release
318 bioactive compounds. In addition, biogenic inorganic volatile compounds were only marginally

319 considered. Thus, future agricultural and environmental engineering applications may benefit from
320 the study of a wider range of biological relations, or by the development of new analytical tools and
321 protocols.

322 In modern agricultural systems, there is a growing interest in finding environmentally sustainable,
323 effective and inexpensive solutions for the problems encountered at each step of the production
324 chain. The diffusion of biological control methods, and the programs for phytoremediation or
325 recovery of marginal soils are examples of such dynamics. However, the novelty of these solutions
326 also poses some legislation and registration issues [113,114]. In addition, live biostimulant or
327 biocontrol agents may not adapt to all cultural conditions [90], and promising biological functions
328 may come along with potential risks for human health or environmental equilibrium.

329 Therefore, the mechanisms of interaction among different bacterial species and with their
330 eukaryotic (plant, insect) hosts deserve in-depth investigation, to develop more efficient and flexible
331 solutions for emerging problems. Volatile compounds may show inherent advantages related to
332 their diffusibility, low dose of action and absence of toxic residues [89]. Extensive field testing is
333 required as a key step to the commercial and industrial application of technologies based on BVCs
334 (see also the outstanding questions).

335

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694 deoxy-D-xylulose-5-phosphate pathway in *Bacillus subtilis*. *Appl Environ Microbiol.* 77, 2399–
695 405

696

697 **Box 1. Low molecular weight volatile compounds**

698 Some volatile compounds, characterised by a small and simple chemical structure, interact directly
699 with plant metabolism or signalling cascades. However, these molecules have received, in
700 explorative studies, only marginal attention, because of technical limits, including the impossibility
701 of a correct identification by GC-MS (due to short retention times and/or scarcely indicative spectral
702 profiles), or the occurrence of artifacts (such as accumulation effects in sealed cuvetts, or
703 interference with growing media) linked with the experimental setting.

704 Carbon dioxide fuels photosynthesis and it is often the most important limiting factor of this process.
705 CO₂ regulates stomata opening and, consequently, photosynthesis and transpiration [115]. CO₂ may
706 contribute to the growth and resistance promoting effects observed in plants treated with bacterial
707 VOCs [116]. CO₂ produced by respiration of bacterial endophytic symbionts can reenter the
708 photosynthetic pathway, not being limited by stomata opening, and has been estimated to be able
709 to provide up to 57% of total CO₂ photo-assimilated by the plant [117]. In this view, plants colonised
710 by endosymbionts may have a better water use efficiency and a higher availability of
711 photoassimilates for growth and defences.

712 Ethylene is a gaseous plant hormone playing a central role in plant development and resistance
713 response to abiotic and biotic stresses [118], also interacting with salicylic acid- and jasmonic acid-
714 dependent signalling pathways. Ethylene and its precursor 1-aminocyclopropane-1-carboxylate
715 (ACC) are subjected to sophisticated co-regulation by plants and associated microbes, thus shaping
716 the plant microbiome [119,120]. In fact, bacteria can actively produce ethylene, or reduce its
717 biosynthesis in plants subtracting ACC by ACC-deaminase activity, thus lowering plant ethylene
718 levels and promoting plant growth.

719 Nitric oxide (NO) is a radical gas mediating a large variety of physiological responses in plants. Plant-
720 associated bacteria can produce NO, as a result of denitrification, by enzymatic conversion of L-
721 arginine or by release from siderophores [121,122]. One important effect of bacterial NO, observed
722 e.g. in *Azospirillum* spp. [123], is the enhancement of root branching, promoting both plant
723 nutritional status and bacterial colonisation.

724 While commonly regarded as a toxic and/or defence compound, hydrogen sulfide (H₂S) also has a
725 regulative role in plants by interacting with NO and thiols [124,125]. Plant-associated bacteria
726 synthesise H₂S through cysteine desulfhydrylation or sulfite reduction.

727 Ethanol and methanol are common products of fermentation, originated by both plants and
728 bacteria under anoxic conditions, and have been implied in the activation of plant stress responses
729 [126].

730

731 **Box 2. BVC-elicited induction of plant defences**

732 Since the discovery of induced systemic resistance (**ISR**, see glossary) by 2,3-butanediol [127], the
733 potential application of BVCs for the elicitation of plant defences has drawn attention. Notably,
734 induction of plant defences is one of the very few measures that can be adopted against viral
735 diseases [128]. ISR is often stimulated as the result of a specific symbiotic interaction between the
736 host plant and bacteria, which also promote plant nutrition and growth. Thus, the two aspects of
737 defence and growth promotion coexist in the same symbiotic relation and are somewhat difficult to
738 tell apart (e.g. activation of stress responses in Figure 1). However, relevant details for plant defence
739 engineering, including mechanisms of signal perception and decoding (i.e., how relatively simple
740 molecules drive specific responses), remain obscure [88].

741 2,3-butanediol biosynthesis, for instance, was observed both in defence-eliciting (*Bacillus* and
742 *Serratia* spp., *Pseudomonas chlororaphis*) and pathogenic (*Erwinia/Pectobacterium*, *Dickeya* spp.)
743 bacteria [127,129-131]. In different pathosystems, the action of 2,3-butanediol and related
744 compounds (acetoin, 2,3-butanedione) has been connected to different combinations of salicylic
745 acid, jasmonate and/or ethylene signal cascades [127,128,132]. According to the relative
746 stimulation of these pathways, specific subsets of plant defensive responses may be activated.

747 While 2,3-butanediol and related compounds are the best-studied example of defence-inducing
748 BVCs, other molecules [43,133] were identified which could stimulate plant defences. In some cases,
749 such as for DMDS and benzothiazole, direct antimicrobial and plant defence induction effects may
750 coexist [134]. One advantage of these compounds is that, although acting through plant hormone
751 signal cascades, they are less prone than hormones to cause drastic physiological reprogramming.
752 For instance, ISR is expressed only after pathogen challenge, and is not generally associated to
753 changes in plant phenotype or crop yield [40,135].

754 Synergism of BVCs in complex mixtures may also occur in natural conditions [88]. By modulating the
755 simultaneous activation of several signal cascades (ethylene, jasmonate, salicylate, and other
756 hormones), BVC mixtures could attain protection against a broader range of pathogens [135].

757

758

759 **Box 3. Pest management by BVCs**

760 Survival and replication rate of pests (including *Drosophila suzukii* and several nematodes) were
761 reduced by means of bacterial volatile emissions [48,136]. However, the use of toxic BVCs seems
762 impractical against most motile animal species, due to limitations in exposure time and
763 concentration. Instead, microbial biocontrol agents releasing toxic compounds may act as effective
764 biopesticides for soil-borne or sessile pests, with a significantly reduced environmental impact.

765 Insects and nematodes use a variety of semiochemicals to coordinate their life functions, including
766 feeding, mating, ovipositing and alarm behaviour. Pest- or plant-associated bacteria contribute to the
767 production of biologically active BVCs (Figure 1), and many cases of attraction to microbes
768 associated to the host have been observed [137]. Fruit flies (*Drosophila* spp.), for instance, are
769 attracted by BVCs from symbiotic *Lactobacillus* spp. acting as aggregation pheromones [138], and
770 are repelled by the common BVCs, 1-octen-3-ol and geosmin [139]. Locusts use guaiacol derivatives,
771 produced by *Pantoea agglomerans* residing in their intestines, as an aggregation pheromone [140].
772 Finally, the association with certain bacteria may determine the insect's preference for BVCs
773 emitted by those microbes, by effect of conditioning or learning [141]. Parasitoid recruitment can
774 be mediated by BVCs, either by direct attraction to microbes indicating a food source [142], or
775 indirectly by eliciting a more intense release of plant VOCs [143]. Concerning nematodes,
776 experiments on the model organism *Caenorhabditis elegans* showed that attractive BVCs produced
777 by *Bacillus nematocida*, such as benzyl benzoate, benzaldehyde, 2-heptanone, and acetophenone,
778 stimulate bacterial swallowing by the host. Thus, the bacterium colonises the worm's intestines,
779 leading to its death [144].

780 BVCs may, therefore, find an application in pest management. VOC-based technologies, employing
781 attractants, deterrents and pheromone-like compounds have been applied to lure-and-kill, push-
782 pull and sexual confusion control strategies. However, information concerning semiochemicals for
783 such technologies is currently restricted to a relatively small number of species (mostly Lepidoptera,
784 Diptera and Coleoptera). New impulse, in this sense, may derive from metagenomic analyses
785 performed either on the insect or on its hosts [145]. With the exception of specialised symbiotic
786 relations, insect guts have often been demonstrated to host relatively simple microbiota, dominated
787 by Enterobacteriaceae (notably *Enterobacter/Pantoea* and *Klebsiella* spp.), to be highly influenced
788 by the diet, and possibly transmitted by parents [141,146,147]. This body of knowledge may provide
789 useful information for the selection of effective and persistent biocontrol agents interacting with
790 insects.

791 **Box 4. Examples of abiotic stress tolerance induced by BVCs**

792 Abiotic stresses elicit NO and ethylene production in plants, which exert several and multifaceted
793 physiological effects. Plant-associated bacteria may indirectly influence plant NO and ethylene
794 emission or produce these bioactive compounds (Box 1).

795 Water deficiency, osmotic stress and salt toxicity are partially interconnected and overlapping both
796 in causes and in the induction of plant responses. 2,3-butanediol, or total BVCs from 2,3-butanediol-
797 emitting bacteria *Bacillus subtilis* GB03 and *Pseudomonas chlororaphis* O6, increased Arabidopsis
798 tolerance to water deficiency and osmotic stress. Abscisic acid, salicylic acid, ethylene, and jasmonic
799 acid signaling pathways were implicated in *P. chlororaphis* O6- and 2,3-butanediol-induced stomata
800 closure, increasing tolerance to drought [148]. *B. subtilis* GB03 stimulates the biosynthesis of
801 osmoprotectants (choline, glycine-betaine) in the plant, enhancing its growth under water
802 withholding and osmotic treatment [149].

803 Several cases of improved plant tolerance to salt stress have been observed after interaction with
804 BVC-releasing bacteria. *B. subtilis* GB03 and its main volatile, acetoin, enhance peppermint
805 tolerance to salt stress by stimulating SA biosynthesis and reducing ABA [150]. Another mechanism
806 of induction of Na⁺ stress tolerance in Arabidopsis consists of the tissue-specific modulation of HKT
807 ion transporters [151]. Such transporters are downregulated in roots to reduce Na⁺ uptake and
808 upregulated in shoots to promote internal recirculation. NO, produced by salt-stressed plants, was
809 also implicated in the enhanced colonisation of the rhizosphere by *Pseudomonas simiae* strain AU,
810 which in turn elicits antioxidant defences, osmoprotection and expression of ion transporters in
811 soybean [152]. Other salt tolerance-inducing BVCs (namely, 2-undecanone, 1-heptanol and 3-
812 methyl-butanol) were identified from *Parabulkoheria phytofirmans* [153].

813 Drought stress and high temperature promote isoprene emission by plants [154]. Isoprene is the
814 most abundantly produced biogenic VOC on Earth, with an estimated emission of more than 2% of
815 all photoassimilates. Isoprene has a likely a role in protection from reactive oxygen and nitrogen
816 species formed under diverse stress conditions [155]. Many Proteobacteria, Actinobacteria and
817 Firmicutes produce isoprene. *Bacillus* and related genera are among the terrestrial bacteria
818 accounting for the highest production of isoprene. Interestingly, isoprene emission by *Bacillus*
819 *subtilis* is enhanced by supra-optimal temperature and salinity [156], suggesting that also plant-
820 associated *B. subtilis* may mediate the plant reactions to these stresses. Soil and phyllosphere
821 bacteria may also directly influence the host isoprene metabolism by using plant-derived isoprene
822 as carbon source [155].

823

824

Table 1. Applications of VOC-based recognition of bacterial pathogens in different plant species and organs, indicating the diagnostic techniques and the VOCs marker/s

Crop species and conditions	Bacterial pathogen/contaminant	Methods	Distinctive features and remarks	Reference
Apple, dormant plants	<i>Erwinia amylovora</i> <i>Pseudomonas syringae</i> pv. <i>syringae</i>	GC-MS E-NOSE PTR-MS	Multiple pathogen discrimination Dilution effects Markers: acetoin, 2,3-butanediol, 2-hexenal, phenylethanol (<i>E. amylovora</i>)	[15]
Bell pepper-derived medium	<i>Leuconostoc gelidum</i> ssp. <i>gasicomitatum</i> and <i>Lactococcus piscium</i>	GC-MS SIFT-MS	Control of spoilage off-odours by controlled atmosphere	[16]
Carrot, roots	<i>Pectobacterium carotovorum</i>	GC-MS	Multiple pathogen discrimination Markers: 3-methyl-butan-1-ol, 1-propanol, 2,3-butanedione	[17]
<i>Citrus sinensis</i> , asymptomatic plant	<i>C. liberibacter</i>	GS-MS FAIMS	Correct identification of PCR-false negatives Severity-dependent markers: methyl-salicylate (severe), geranyl acetone, linalool (mild)	[18]
<i>Ficus benjamina</i> and <i>Spathiphyllum wallisii</i> , <i>in vitro</i> cultures	<i>Escherichia coli</i> contamination	SIFT-MS		[19]
Grapefruit, leaves	<i>Xanthomonas axonopodis</i> pv. <i>citri</i>	GC-MS	Marker: phenylacetaldehyde O-methylxime	[20]
Grapevine, rootstock cuts	<i>Agrobacterium vitis</i>	GC-MS E-NOSE	Marker: styrene	[21]
Kiwifruit, <i>in vitro</i> explants	<i>Pseudomonas syringae</i> pv. <i>actinidiae</i>	GC-MS E-NOSE PTR-MS	Marker: 1-undecene	[22]
Lettuce	Resident microflora (mainly <i>Pseudomonas</i> spp.)	GC-MS SIFT-MS	Control of spoilage off-odours by packaging	[23]
Onion, bulbs	<i>Burkholderia cepacia</i>	GC-MS E-NOSE	Markers: 2-nonanone, 2-octyl-5-methyl-3(2H)-furanone	[24]
Onion, bulbs	<i>Pectobacterium carotovorum</i>	GC-MS	Multiple pathogen interaction Marker: 3-bromo-furan	[25]
Onion, bulbs	<i>Burkholderia cepacia</i>	FAIMS		[26,27]
Poplar, wood	Bacterial wetwood (non-determined species)	E-NOSE		[28]
Potato, tubers	<i>Clavibacter michiganensis</i> ssp. <i>sepedonicus</i>	GC-MS PTR-MS	Marker: 2-propanol	[29]
Potato, tubers	<i>Pectobacterium carotovorum</i> <i>Bacillus polymyxa</i> <i>Arthrobacter</i> sp.	GC-MS	Markers: 2-propenal, DMDS, 1-alkenes, branched alkanes, octanal, naphtalene, butanoic acid (<i>P. carotovorum</i>); N,N-dimethylformamide, 1-pentadecene (<i>B. polymyxa</i>); 2,3-dihydrofuran (<i>Arthrobacter</i> sp.)	[30]
Potato, tubers	<i>Pectobacterium carotovorum</i>	GC	Multiple pathogen discrimination	[31]
Potato, tubers	<i>Ralstonia solanacearum</i> , <i>Clavibacter michiganensis</i> ssp. <i>sepedonicus</i>	E-NOSE	Lab- to real scale Threshold of disease severity for recognition	[32]
Potato, tubers	<i>Pectobacterium carotovorum</i>	E-NOSE	Pre-symptomatic recognition	[33]
Potato, tubers	<i>Pectobacterium carotovorum</i>	FAIMS	Early detection (1 d post inoculation)	[34]
Potato, tubers	<i>Pectobacterium carotovorum</i>	FAIMS		[26]

825

826

827 **Table 2. Overview of analytical techniques employed for VOC-based plant diagnosis, with working**
 828 **principles and potential advantages and drawbacks**

Analytical technique	Working principle	Operative features	Diagnostic principle
GC-MS	Differential retention time and fragmentation profile of VOCs	+ High analytical power (identification of single compounds) + May use sample concentration on sorbents (e.g. SPME)	Recognition of markers Multivariate statistical analysis
PTR-MS SIFT-MS	Fragmentation profile of VOCs	+ Partial analytical power + Quick response	Partial recognition of markers Multivariate statistical analysis
Electronic nose	Electric properties of the overall VOC mixture	+ Simple operation, portability + Quick response + May adjust sensitivity by regulating flow - Interference by water - No analytical power - Instrumental drift	Multivariate statistical analysis Neural network machine learning
FAIMS	Differential mobility of ion fragments in electric field	+ Partial analytical power + Portability	Partial recognition of markers Multivariate statistical analysis

829

830 **Table 3. Volatile organic compounds exerting direct toxicity against plant pathogens**

Compound(s)	Emitting species	Target organism(s)	Reference
Hydrogen cyanide Ammonia 1-Undecene	<i>Pseudomonas</i> spp. <i>Bacillus</i> spp. others	<i>Phytophthora infestans</i> <i>Rhizoctonia solani</i> <i>Helminthosporium solani</i> <i>Fusarium oxysporum</i> <i>Dickeya dianthicola</i>	[49]
2-(2'-heptyl)-3-methyl-4-quinolone	<i>Burkholderia cepacia</i>	<i>Aspergillus niger</i> and other fungi	[44]
Alkylated benzene derivatives Phenol derivatives Naphthalene derivatives Benzothiazole 2-Ethyl-1-hexanol 2-Undecanol 2-Nonanone 2-Decanone 2-Undecanone Nonanal Decanal	<i>Bacillus amyloliquefaciens</i> NJN-6	<i>Fusarium oxysporum</i> f. sp. <i>cubense</i>	[45]
N,N-dimethyl- hexadecanamine	<i>Arthrobacter agilis</i> UMCV2	<i>Botrytis cinerea</i> <i>Phytophthora cinnamomi</i>	[46]
2-methyl-isoborneol	<i>Streptomyces alboflavus</i> TD-1	<i>Fusarium moniliforme</i>	[47]
1-Undecene 2-Nonanone 2-Undecanone	<i>Pseudomonas chlororaphis</i>	<i>Agrobacterium tumefaciens</i> <i>Synechococcus</i> spp. <i>Rhizoctonia solani</i>	[48]
Dimethyl disulfide 2-Heptanone	<i>Serratia proteamaculans</i>	<i>Agrobacterium tumefaciens</i> <i>Synechococcus</i> spp. <i>Rhizoctonia solani</i>	[48]
3-hexanone 1-dodecene isovaleric acid S-methyl-butanethioate S-methyl-methanethiosulfonate furfuryl alcohol acetophenone phenylpropanedione 2- acetylthiazole nitropentane	<i>Pseudomonas</i> spp.	<i>Phytophthora infestans</i>	[49]

2-(2-Methylpropyl)-3-(1-methylethyl) pyrazine 2- Isopropylpyrazine 2- methyl-1-butanol Hexadecanal Isoamyl acetate	<i>Paenibacillus polymyxa</i> Sb3-1	<i>Verticillium longisporum</i>	[51]
Phenylethyl alcohol Methyl salicylate Ethyl phenylacetate Methyl anthranilate α -Copaene Caryophyllene 4-Ethylphenol Humulene	<i>Streptomyces fomicarius</i> BWL-H1	<i>Peronophythora litchii</i>	[52]
2,3,5-Trimethylpyrazine 2-Nonanone 2-Decanone 2-Dodecanone Dimethyl disulfide Dimethyl trisulfide	<i>Bacillus</i> spp. <i>Pseudomonas</i> spp.	<i>Fusarium</i> spp. <i>Colletotrichum gloeosporioides</i>	[53]
Hexanedioic acid, bis(2-ethylhexyl) ester Octadecane 1-Hexadecanol Docosane Chloroacetic acid, tetradecyl ester	<i>Bacillus atrophaeus</i> HAB-5	<i>Colletotrichum gloeosporioides</i>	[54]
2-methyl-1-butanol ethyl hexanoate 3-methyl-1-butanol ethyl octanoate phenylethyl acetate phenylethyl alcohol	<i>Pseudomonas chlororaphis</i> subsp. <i>aureofaciens</i> SPS-41	<i>Ceratocystis fimbriata</i>	[55]
2-methylbutyrate 2-phenylethanol	<i>Streptomyces yanglinensis</i> 3-10	<i>Aspergillus flavus</i> <i>A. parasiticus</i>	[56]
Isooctanol Linalool 3-Octanone 2-Naphthalene methanol 3-Undecanone 2-Tridecanone	<i>Corrallococcus</i> sp. EGB	<i>Fusarium oxysporum</i> f. sp. <i>cucumerinum</i> <i>Penicillium digitatum</i>	[57]
Dimethyl disulfide	<i>Pseudomonas fluorescens</i> B-4117 <i>P. fluorescens</i> Q8r1-96 <i>Serratia plymuthica</i> IC1270	<i>Agrobacterium tumefaciens</i> <i>A. vitis</i>	[58]
2,4-diacetylphloroglucinol Hydrogen cyanide	<i>Pseudomonas</i> sp. LBUM300	<i>Clavibacter michiganensis</i> ssp. <i>michiganensis</i>	[59]
Benzaldehyde Nonanal Benzothiazole Acetophenone	<i>Bacillus subtilis</i> FA26	<i>Clavibacter michiganensis</i> ssp. <i>sepedonicus</i>	[60]
3,5,5-trimethylhexanol Decyl alcohol	<i>Bacillus cereus</i> D13	<i>Xanthomonas oryzae</i> pv. <i>oryzae</i>	[61]
Toluene Ethyl benzene m-xylene Benzothiazole 2-decanol 2-tridecanol 1-undecanol Dimethyl disulfide Benzaldehyde 1-Methyl naphthalene	<i>Pseudomonas fluorescens</i> WR-1	<i>Ralstonia solanacearum</i>	[62]

831

832

833 **Table 4. Examples of bacterial interactions with crops influencing quality parameters**

Crop plant	Bacterial species	Quality parameter(s)	Mechanism of interaction	Reference
Sweet basil	<i>Bacillus subtilis</i> GB03	Increased production of essential oils		[92]
Peppermint	<i>Pseudomonas fluorescens</i> WCS417r, <i>Bacillus subtilis</i> GB03, <i>Azospirillum brasilense</i> SP7	Increased production of essential oils		[93]
<i>Atractylodes lancea</i>	<i>Pseudomonas fluorescens</i> ALEB7B	Increased production of essential oils	Benzaldehyde mediates the effect	[94]
Strawberry	<i>Methylobacter</i> spp.	Production of aromatic compounds (furanones)	Bacterial alcohol dehydrogenase	[95,96]
Raspberry	<i>Methylobacter</i> spp., <i>Bacillus</i> spp.	Production of aromatic compounds (frambinone)		[109,110]
Strawberry	<i>Bacillus megaterium</i>	Production of aromatic compounds (2,3-dialkylacroleins)	Conversion of linear aldehydes	[111]
Basmati rice	<i>Acinetobacter</i> spp.	Production of aromatic compounds (2-acetyl-1-pyrroline)		[112]
Citrus, mango, cherry, litchi, peach	<i>Bacillus</i> spp.	Protection from spoilage	Antifungal action of cedrol and 2-pentylfuran	[97-102]
Strawberry, citrus, tomato, chili	<i>Streptomyces</i> spp.	Protection from spoilage	Antifungal action of acetophenone	[103-107]
Grapevine	<i>Paenibacillus</i> spp.	Production of aromatic compounds in wine production		[108]

834

835 **Figure 1. Summary of VOC-mediated biological functions of plant-associated bacteria.**

836 Biological effects of plant-associated bacteria and their mechanisms of interaction with the host
837 plant and the environment can be exploited in the agricultural practice. The resident bacteria may
838 increase the availability of certain mineral nutrients, or stimulate plant growth and stress responses
839 by means of hormones or other signalling compounds. As a result, a better nutritional status and a
840 better ability to cope with stresses is achieved in the host plant. In their interaction with pests and
841 pathogens, plant-associated bacteria may act as direct competitors and/or predators with a biocidal
842 action, or exert a disturbance in long-range signalling, possibly influencing the pest's behaviour, its
843 recognition by natural enemies, and the expression of «social» phenotypes related to virulence in
844 pathogens.

845

846 **Glossary**

847 **BCA:** Biological Control Agent, an organism exerting directly (e.g. by killing or preying) or indirectly
848 (by competition for resources, or through the action of other organisms) a limiting effect on the
849 population of a pest or pathogen.

850 **BVCs:** Bacterial Volatile Compounds, including organic (i.e. carbon-containing) and inorganic (e.g.
851 H₂S, nitrogen oxides) compounds.

852 **E-NOSE:** Electronic nose, a device including an array of electric sensors with differential affinity for
853 different chemical classes, and varying their electric conductance upon interaction with the
854 components of a gas blend. Used to compare gas samples, has good portability and ease of
855 operation, allows real-time analysis, but not chemical identification.

856 **FAIMS:** Field Asymmetric Ion Mobility Spectrometry, analytical method based on the separation of
857 ions in an oscillating electric field. Allows real-time analysis of gas profiles with good portability, and
858 can be coupled to GC-MS for chemical identification.

859 **GC-MS:** Gas Chromatography-Mass Spectrometry, analytical technique based on separation of
860 molecules in a gas mixture according to affinity to a chromatographic column, followed by their
861 fragmentation to yield a typical spectrum. Most used technique for identification of volatile
862 compounds.

863 **Gnotobiotics:** study of test organisms, in which the resident microbial community is artificial,
864 controlled and/or completely characterised.

865 **Holobiont:** the complex formed by a host organism and its associated microflora.

866 **ISR:** Induced Systemic Resistance, condition of increased and generalised plant resistance to
867 potential pathogens and pests, activated after interactions with microbes (including beneficial
868 symbionts).

869 **Metagenomics:** study of the complex of genomes associated in one super-organism, such as a plant
870 with its associated microflora.

871 **PTR-MS:** Proton Transfer Reaction-Mass Spectrometry, analytical technique based on
872 fragmentation of gas compounds in an electric field. Allows highly sensitive real-time detection and
873 tentative identification of compounds.

874 **QS:** Quorum Sensing, bacterial communication system allowing the coordination of 'social'
875 phenotypes (motility, biofilm formation, etc.) according to population density.

876 **SIFT-MS:** Selected Ion Flow Tube-Mass Spectrometry, analytical technique based on fragmentation
877 of gas compounds in an air flow. Allows real-time detection and tentative identification of
878 compounds.

879 **VOCs:** Volatile organic compounds, organic molecules characterised by low vapour pressure, high
880 lipophilicity and low molecular weight, normally found in the gas phase in standard conditions.

881 **Volatilome:** the complete set of volatile compounds originating from an organism or biological
882 system.

