Growth media affect the volatilome and antimicrobial activity against *Phytophthora infestans* in four *Lysobacter* type strains

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ABSTRACT

Bacterial volatile organic compounds (VOCs) play important ecological roles in soil microbial interactions. *Lysobacter* spp. are key determinants of soil suppressiveness against phytopathogens and the production of non-volatile antimicrobial metabolites has been extensively characterised. However, the chemical composition and antagonistic properties of the *Lysobacter* volatilome have been poorly investigated. In this work, VOC emission profiles of four *Lysobacter* type strains grown on a sugar-rich and a protein-rich medium were analysed using solid-phase microextraction gas chromatography-mass spectrometry and proton transfer reaction-time of flight-mass spectrometry. *Lysobacter antibioticus*, *L. capsici*, *L. enzymogenes* and *L. gummosus* type strains were recognised according to their volatilome assessed using both headspace mass spectrometry methods. Moreover, the chemical profiles and functional properties of the *Lysobacter* volatilome differed according to the growth medium, and a protein-rich substrate maximised the toxic effect of the four *Lysobacter* type strains against *Phytophthora infestans*. Antagonistic (pyrazines, pyrrole and decanal) and non-antagonistic (delta-hexalactone and ethanol) VOCs against *Ph. infestans* or putative plant growth stimulator compounds (acetoin and indole) were mainly emitted by *Lysobacter* type strains grown on protein- and sugar-rich media respectively. Thus nutrient availability under soil conditions could affect the aggressiveness of *Lysobacter* spp. and possibly optimise interactions of these bacterial species with the other soil inhabitants.

Keywords: volatile organic compounds, *Lysobacter* spp., biological control, *Phytophthora infestans*, SPME/GC-MS analysis, PTR-ToF-MS analysis

Highlights

- Four *Lysobacter* type strains can be recognised according to their volatilome
- Composition and properties of the *Lysobacter* volatilome differ according to the growth media
- Protein-rich media increase the mission of antagonistic compounds by *Lysobacter* spp.

1. Introduction

Microorganisms produce a wide variety of secondary metabolites, including antibiotics, toxins, pigments and volatile organic compounds (VOCs). Volatile organic compounds are molecules of high vapour pressure and low molecular weight that readily diffuse through water- and gas-filled pores in soil environments (Schmidt et al., 2015). VOCs emitted by bacteria belong to different chemical classes (alcohols, aldehydes, alkenes, benzenoids, ethers, lactones, ketones, terpenoids and sulphur compounds) and are generated by complex metabolic pathways (Audrain et al., 2015; Schmidt et al., 2015; Schulz, 2007). Bacterial VOCs play essential ecological roles in communications with soil microorganisms, nematodes, insects and plants (Effmert et al., 2012; Kai et al., 2009). Notably, bacterial VOCs can inhibit spore germination and mycelial growth of several phytopathogens (De Vrieze et al., 2015; Kai et al., 2007; Weisskopf, 2013), promote plant growth (Blom et al., 2011; Ryu et al., 2003) and induce plant resistance (Lee et al., 2012; Ryu et al., 2004). The chemical composition of the bacterial volatilome is defined by genetic determinants and can be used as a chemotaxonomic marker in standardised conditions (Peñuelas et al., 2014). However, composition and functional properties of the bacterial bouquet are influenced by the nutrient source where bacteria are grown (Asari et al., 2016; Blom et al., 2011; Bruce et al., 2003; Fiddaman and Rossall, 1994; Garbeva et al., 2014; Weise et al., 2012), indicating metabolic changes in VOC production according to nutrient availability and growth conditions in the soil (Insam and Seewald, 2010).

Bacteria belonging to the *Lysobacter* genus are frequently found in soil and increased disease suppression of soil phytopathogens correlated significantly with increased populations of *L. antibioticus*, *L. capsici* and *L. gummosus* (Postma and Schilder, 2015; Postma et al., 2008). The *Lysobacter* genus (Christensen and Cook, 1978) includes species that are efficient antagonists of phytopathogens and potential candidates for biological control of crop diseases (Hayward et al., 2010; Kobayashi and Yuen, 2007). In particular, *L. antibioticus* DSM 2044^T (ATCC 29479), *L. enzymogenes* DSM 2043^T (ATCC 29487) and *L. gummosus* DSM 6980^T (ATCC 29489) were described as *Lysobacter* type strains by Christensen and Cook (1978), and the antagonistic mechanisms of these

75 species have been extensively characterised (Folman et al., 2004; Folman et al., 2003; Ko et al., 2009;
76 Qian et al., 2009; Yu et al., 2007). For example, *L. antibioticus* HS124 produced lytic enzymes and a
77 toxic compound against *Phytophthora capsici* (Ko et al., 2009). Likewise, the production of lytic
78 enzymes and antibiotics was shown for *L. enzymogenes* 3.1T8 (Folman et al., 2004; Folman et al.,
79 2003), *L. enzymogenes* C3 (Yu et al., 2007) and *L. enzymogenes* OH11 (Qian et al., 2009) against
80 *Fusarium graminearum*, *Pythium aphanidermatum*, *Py. ultimum*, *Ph. capsici, Rhizoctonia solani* and
81 *Sclerotinia sclerotiorum*. The antagonistic properties of *L. gummosus* were associated with proteolytic
82 degradation of biofilm (Gokcen et al., 2014) and biosynthesis of antifungal metabolites (Meyers et
83 al., 1985). Furthermore, the type strains *L. capsici* DSM 19286^T (YC5194) (Park et al., 2008) and *L.*
84 *capsici* AZ78 (Puopolo et al., 2014a; Puopolo et al., 2014b; Puopolo et al., 2016) produced secondary
85 metabolites that inhibit the growth of phytopathogenic fungi (*Botrytis cinerea*, *Colletotrichum*
86 *gloeosporioides*, *F. oxysporum* and *R. solani*) and oomycetes (*Ph. infestans*, *Plasmopara viticola* and
87 *Py. ultimum*) respectively.
88 Although the production of extracellular lytic enzymes (proteases, glucanases, chitinases and
89 cellulases) and antimicrobial compounds (pyrazines, tetramic acid-containing macrolactams and
90 other antifungal factors) has been widely characterised in *Lysobacter* spp. (Puopolo et al., 2014a; Xie
91 et al., 2012), the possible contribution of VOCs in antagonistic processes has been poorly
92 investigated. The limited studies available (Sang et al., 2011; Zou et al., 2007) suggest a significant
93 potential for VOC-mediated antagonistic processes. In particular, the VOCs emitted by *L. gummosus*
94 KCTC 12132 and *L. enzymogenes* ISE13 inhibited mycelial growth of nematicidal fungi
95 (*Paecilomyces lilacinus* and *Pochonia chlamydosporia*) (Zou et al., 2007) and phytopathogenic
96 microorganisms (*C. acutatum* and *Ph. capsici*) (Sang et al., 2011) respectively.
97 The aim of this study was to elucidate the antagonistic potential of *Lysobacter* spp., based on a
98 better understanding of the emission profiles and functional properties of VOCs. Therefore, we used
99 four *Lysobacter* type strains (*L. antibioticus* DSM 2044^T, *L. capsici* DSM 19286^T, *L. enzymogenes*
100 DSM 2043^T and *L. gummosus* DSM 6980^T) as representative of the biocontrol *Lysobacter* spp.

(Hayward et al., 2010; Kobayashi and Yuen, 2007; Postma and Schilder, 2015; Postma et al., 2008) and we assessed both volatilome composition and antagonistic effects against *Ph. infestans*, the causal agent of late blight of potato and tomato plants (Fry, 2008). The VOCs produced by the type strains on two growth media were analysed by solid-phase microextraction gas chromatography-mass spectrometry (SPME/GC-MS) and proton transfer reaction-time of flight-mass spectrometry (PTR-ToF-MS) to precisely analyse the chemical composition and rapidly monitor the emission profiles, respectively (Jordan et al., 2009b).

2. Materials and methods

2.1. Propagation of the Lysobacter *type strains and the plant pathogenic oomycete*

The *Lysobacter* type strains *L. antibioticus* DSM 2044^T, *L. capsici* DSM 19286^T, *L. enzymogenes* DSM 2043^T and *L. gummosus* DSM 6980^T were grown on Luria-Bertani Agar (LBA, Sigma-Aldrich, St. Louis, MO, USA) for 72 h at 27 °C and cell suspensions of each strain were prepared by flooding LBA dishes with 5 ml of sterile isotonic solution (0.85% NaCl). Bacterial cells were scraped from the medium surface with a sterile spatula and collected in a sterile 15 ml-tube. The resulting cell suspensions were centrifuged (4,300 × *g* for 15 min); pelleted cells were suspended in sterile isotonic solution to a final optical density of 0.1 at 600 nm (OD_{600}), corresponding to 1×10^8 cells/ml (Puopolo et al., 2016).

The *Ph. infestans* isolate (kindly provided by M. Finckh and A. Butz, University of Kassel, Germany) was grown on pea agar medium (PAM, 12.5% frozen peas and 1.2% agar in distilled water) at 17 °C, as described by Puopolo et al. (2015).

2.2. Bacterial growth conditions for headspace analysis of volatile organic compounds

For headspace VOC analysis, 5 ml of sterilised nutrient agar (NA, Oxoid, Basingstoke, United Kingdom) or potato dextrose agar (PDA, Oxoid) were poured into sterile 20 ml headspace vials (HS vials, Supelco, Sigma-Aldrich) and they were left open under a laminar flow for 2 h at room temperature to avoid condensation. Each HS vial was then inoculated with 20 µl of the cell suspension of a *Lysobacter* type strain (1×10^8 cells/ml) and left to dry under a laminar flow for 1 h at room temperature. Each HS vial was tightly sealed with a sterilised 18 mm screw metal cap assembled with silicone/PTFE septa of 1.3 mm (Supelco, Sigma-Aldrich). Additional HS vials containing non-inoculated NA or PDA (Uninoculated) were used as controls to exclude VOCs released from the culture medium in the absence of bacteria (Kluger et al., 2013). HS vials were incubated at 25 °C for ten days to accumulate VOCs before the headspace VOC assessment by SPME/GC-MS and PTR-ToF-MS analysis. This time point was selected because it showed the greatest antagonism of the *Lysobacter* type strains against *P. infestans*.

The number of *Lysobacter* cells developed in each inoculated HS vial was assessed one day after headspace VOC analysis (11 days after inoculation). Each HS vial was flooded with 4 ml of sterilised isotonic solution (0.85% NaCl) and bacterial cells were scraped from the medium surface by vigorous vortexing for 30 sec. The cell concentration of the resulting suspension was assessed by converting the OD_{600} values, with $OD_{600} = 0.1$ corresponding to 1×10^8 cells/ml (Puopolo et al., 2016), and the quantity of *Lysobacter* cells was then calculated for each HS vial.

2.3. Headspace analysis of volatile organic compounds using solid-phase micro extraction gas chromatography-mass spectrometry (SPME/GC-MS) analysis

Headspace VOC analysis was carried out with SPME/GC-MS using an Auto System XL gas chromatograph coupled with a Turbo Mass Gold Mass spectrometer (Perkin Elmer, Norwalk, CT, USA). For measurement automatisation and standardisation, the instrument was coupled with a thermostated autosampler (CTC CombiPAL, CTC Analytics, Zwingen, Switzerland) and HS vials were kept at 25 °C. After equilibration for 30 min, VOCs were extracted and pre-concentrated with

153 solid phase microextraction (SPME) using 2 cm PDMS/DVB/CAR fibre (Supelco, Bellafonte, PA,
154 USA), according to Endrizzi et al. (2012). The fibre collected VOCs from the headspace for 30 min
155 and desorbed them into the GC injector for 5 min at 250 °C. The chromatographic separation was
156 performed via an HP-Innowax fused-silica capillary column (length 30 m, inner diameter 0.32 mm,
157 film thickness 0.5 μm; Agilent Technologies, Palo Alto, CA, USA). The GC oven temperature
158 program was the following: 40 °C for 3 min, raised from 40 °C to 220 °C at 4 °C/min, 220 °C for 1
159 min, increased from 220 °C to 250 °C at 10 °C/min and 250 °C for 1 min. The carrier gas was helium
160 with a constant column flow rate of 1.5 ml/min. The transfer line temperature was maintained constant
161 at 220°C. Upon exiting the column, compounds were ionised via electron impact at 70 eV and
162 detected with a quadrupole mass spectrometer with a mass/charge ratio (*m/z*) ranging from 30 to 300
163 Thomson. Spectra analysis was carried out using TurboMass 5.4.0 software (Perkin Elmer, Norwalk,
164 CT; USA). Mass measure parameters were: background subtraction with a polynomial order of 1 and
165 a below curve of 33%, smooth mode with a peak width of 0.75 Da, minimum peak width at half
166 height of 4. Compound annotation was achieved by comparing the spectra with the NIST-98/Wiley
167 library (National Institute of Standards and Technology, www.nist.gov) using a mass spectrum
168 similarity greater than 85%, and by matching retention indices (RI) of authentic reference standards
169 computed under the same chromatographic conditions with the C7-C30 n-alkane series (Supelco,
170 Sigma-Aldrich) using a maximum tolerance of 4% RI deviation. The VOC content of each sample
171 was reported as the absolute peak area obtained with the TurboMass 5.4.0 software. Five replicates
172 (HS vials) of *L. enzymogenes* and four replicates of *L. antibioticus*, *L. capsici* and *L. gummosus* were
173 used for each media.
174
175 *2.4. Headspace analysis of volatile organic compounds using proton transfer reaction-time of flight-*
176 *mass spectrometry (PTR-ToF-MS)*
177 Rapid headspace VOC analysis was carried out using a commercial PTR-TOF 8000 instrument
178 (Ionicon Analytik GmbH, Innsbruck, Austria) (Jordan et al., 2009a). The instrument was coupled

with an adapted thermostated autosampler (MPS Multipurpose Sampler, Gerstel) and HS vials were kept at 25 °C. During VOC headspace measurement, 40 sccm of zero air were injected into the HS vial through a needle heated to 40 °C, and the outflow going through a second heated needle (40 °C) was delivered via Teflon fittings to the PTR-ToF-MS. Zero air was produced via a catalytic VOC scrubber (GCU unit, Ionicon Analytik, Innsbruck, Austria). HS vials were measured in random order and each measurement lasted for 3 min, with a waiting time of 5 min between samples to avoid memory effects. The PTR-ToF-MS was operated in H_3O^+ primary ion mode. The following conditions were set in the instrument drift tube: 2.3 mbar drift pressure, 480 V drift voltage, 110 °C drift tube temperature, leading to an *E/N* value (*E* corresponding to electric field strength and *N* to gas number density) of about 120 Townsend (Td; 1 Td=10^{-17} Vcm^2). The primary and product ions exiting the drift tube region were detected using a time-of-flight (ToF) mass spectrometer operated with its standard configuration (V mode). Each acquisition consisted of 350,000 channels with a sampling time of 0.1 ns per channel of ToF acquisition, resulting in a mass spectrum ranging up to *m/z* = 400. Each individual spectrum was the sum of about 28,600 acquisitions lasting for 35 μs, resulting in a time resolution of 1 s. Because the analysis time for each sample was set to 3 min, 180 spectra were acquired for each vial during each measurement.

PTR-ToF-MS spectra were processed according to the methodology reported by Cappellin et al. (2011a), with slight modifications. As the first data processing step, signal distortions related to detector dead time were calculated using a correction approach based on Poisson statistics, according to Cappellin et al. (2011b). Because the external calibration provided by the acquisition software did not achieve sufficient mass accuracy, internal mass calibration was carried out according to Cappellin et al. (2011b) and a mass accuracy of greater than 0.001 Th was obtained. Subsequent data processing of noise reduction, baseline removal and peak intensity extraction were carried out according to Cappellin et al. (2011b) using modified Gaussians to fit spectral peaks. Headspace VOC concentrations, expressed as parts per billion by volume (ppbv), were estimated from the integrated signal over the 3 min of spectra acquisition using the formula described by Lindinger et al. (1998),

205 considering hydronium H_3O^+ as primary ion and a constant reaction rate coefficient of 2×10^{-9} cm^3/s
206 in the calculations. This approach introduces a systematic deviation of up to 30% that can be
207 accounted for if the actual rate coefficient is known (Cappellin et al., 2012b). Four replicates (HS
208 vials) of *L. enzymogenes* and five of *L. antibioticus*, *L. capsici* and *L. gummosus* were grown on PDA.
209 Five replicates of *L. capsici* and four of *L. antibioticus*, *L. enzymogenes* and *L. gummosus* were grown
210 on NA.
211
212 *2.5. Functional analysis of bacterial volatile organic compounds against* Phytophthora infestans
213 Split Petri dishes (92 mm of diameter) with two compartments and ventilation cams (Sarstedt,
214 Nümbrecht, Germany) were used to analyse the effect of VOCs emitted by *Lysobacter* type strains
215 on *Ph. infestans* growth. Sterilised NA or PDA (5 mL) were poured into one half of the split dish
216 (*Lysobacter*-growth side) and 5 ml of sterilised PAM were poured into the other half (*Phytophthora*-
217 growth side). Once dried, 50 µl of the cell suspension of the *Lysobacter* type strain (1×10^8 cells/ml)
218 were spread onto the *Lysobacter*-growth side of the split dish containing NA or PDA using sterile
219 spatulas. As a control, split dishes containing non-inoculated NA or PDA (Uninoculated) on the
220 *Lysobacter*-growth side were used. Dishes were sealed with Parafilm tape (Beims, Neenah, WI, USA)
221 and incubated at 25 °C in the dark for 72 h. Subsequently, *Ph. infestans* plugs (5 mm) were cut from
222 the edge of ten-day-old colonies grown on PAM, as described by Puopolo et al. (2016), and a plug
223 was placed at the centre of the *Phytophthora*-growth side of each split dish. Inoculated dishes were
224 sealed with Parafilm tape and mycelial growth was evaluated by measuring the diameter (parallel to
225 the edge of the dish) of the *Ph. infestans* colony after seven days of incubation in the dark at 20 °C,
226 corresponding to ten days after *Lysobacter* spp. inoculation. Each *Ph. infestans* plug exposed to VOCs
227 of *Lysobacter* type strains grown on NA or PDA was then transferred to fresh PAM dishes and the
228 colony diameter was measured after seven days of incubation in the dark at 20 °C. Seven replicates
229 (split dishes) were analysed for each *Lysobacter* type strain and each growth medium and the
230 functional assay against *Ph. infestans* was carried out twice.

VOCs were selected according to their emission profiles; pure 2,5-dimethyl pyrazine, 2-methoxy-3-methyl pyrazine, decanal, delta-hexalactone, ethanol and pyrrole were purchased (Sigma-Aldrich) and tested against *Ph. infestans*. Sterilised PAM was poured into one half of a split dish (P*hytophthora*-growth side) and a pure VOC was applied to a filter paper disk placed into the other half (VOC side) at a concentration of and 190 mg/L (VOC-treated) of air volume, which is a dosage compatible for VOC-mediated functional assays (De Vrieze et al., 2015; Fernando et al., 2005). As control, distilled water was applied to a filter paper disk into the VOC side of control dishes. Each dish was sealed with Parafilm tape, incubated at 25 °C in the dark for 72 h and inoculated with a *Ph. infestans* plug (5 mm) into the *Phytophthora*-growth side. The diameter (parallel to the edge of the dish) of each *Ph. infestans* colony was measured after seven days of incubation in the dark at 20 °C and the inhibition of *Ph. infestans* growth (percentage) was calculated according to the following formula: (growth in control dishes — growth in VOC-treated dishes) / (growth in control dishes) × 100. Seven replicates (split dishes) were analysed for each treatment and the experiment was carried out twice.

2.6. Statistical analysis

To obtain background-corrected headspace VOC concentration, the background signal (the signal corresponding to the mean signal for empty HS vials) was subtracted from VOC emission values of both SPME/GC-MS and PTR-ToF-MS analysis. Emitted VOCs were identified as peaks with a background-corrected headspace concentration significantly greater than the corresponding signal for uninoculated HS vials for at least one strain and growth medium, according to the Kruskal-Wallis test with Bonferroni correction ($p \leq 0.05$).

Volatile emission data of SPME/GC-MS and PTR-ToF-MS analysis were analysed using in-house routines written in R (www.r-project.org), including the Agricolae package (https://cran.r-project.org/web/packages/agricolae/index.html) and Glmnet package (https://cran.r-project.org/web/packages/glmnet/index.html). Data exploration with principal component analysis

(PCA) was carried out using in-house routines written in R, on normalised variables that were obtained by subtracting the mean and dividing by the standard deviation, to obtain more homogeneous variables and prevent variance from being concentrated in few variables, affecting the results of PCA (Afifi et al., 2011).

Bacterial class prediction models based on VOC data were developed with both SPME/GC-MS and PTR-ToF-MS datasets, using the least absolute shrinkage and selection operator (LASSO) method described by Tibshirani (1996). Briefly, a linear model can be represented by the following equation: $Y = X \times B + E$, where Y is the matrix of the properties to be predicted (dependent variable), X is the matrix of the measurements to be employed in the prediction (independent variable), B is the matrix of regression coefficients to be estimated in the model optimisation procedure and E is the matrix of residuals. In the LASSO method, the model can be represented by the following equation: $Y = X \times B + E + \lambda \times |B|$, which includes a penalisation term ($\lambda \times |B|$) of the absolute values of coefficient B, multiplied by a factor λ, corresponding to the penalty coefficient to be optimised. During model optimisation, the size of the penalty coefficient λ needs to be optimised and cross-validation is used for this purpose (Tibshirani, 1996). Models for all possible λ values were calculated simultaneously as an ordinary linear regression, as reported by Hastie et al. (2009). The considered study was a multiclass problem (i.e. growth media and strain classes) and a LASSO model for each class was therefore developed to predict whether a sample belonged to the class (model value 1) or not (model value 0). Performance evaluation of the classification methods was carried out using a leave-one-out (LOO) procedure and confusion matrices (Cappellin et al., 2012a; Westerhuis et al., 2008).

VOC emission values, *Ph. infestans* colony diameters and *Lysobacter* cell numbers ($\log_{10}$-transformed) were analysed using Statistica 13.1 software (Dell, Round Rock, TX, USA) and a Kruskal-Wallis test with Bonferroni correction was applied to detect significant differences ($p \leq 0.05$) among *Lysobacter* type strains and growth media.

3. Results

3.1. Profiles of volatile organic compounds differed according to the Lysobacter *type strain and growth media*

VOC emission profiles measured by SPME/GC-MS analysis varied in *Lysobacter* type strains and growth media, with the first and sixth principal components (explaining 36.7 and 3.8% of variance respectively) of PCA analysis discriminating samples according to the growth medium (Fig. 1A). Moreover, marked similarities of VOC emission profiles occurred between HS vials belonging to the same *Lysobacter* type strain, independently of the growth medium (Fig. 1B). Specifically, the second and sixth principal components of PCA (explaining 18.6 and 3.8% of variance respectively) discriminated *Lysobacter* type strains, and HS vials of the same type strain grown on the two media clustered together.

A total of 77 VOCs were detected by the SPME/GC-MS analysis, and the emission profiles of 70 of them differed according to the growth medium and type strain (Fig. 2 and Table S1). No differences in bacterial growth were found between PDA and NA, except for *L. antibioticus* (Table 1), and VOC differences were mainly related to bacterial metabolism rather than to the growth rate. Specifically, the emission of 17 VOCs was higher for all *Lysobacter* type strains on PDA as compared with NA (PDA-specific VOCs, Cluster 1, Table S1), such as 3-methyl-2-buten-1-ol, 1-tridecanol, 1-tetradecanol, 1-pentadecanol, according to the Kruskal-Wallis test with Bonferroni correction ($p \leq 0.05$). PDA-specific profiles were also found for three ketones [delta-hexalactone (Fig. 3A), dihydro-5-pentyl-2(3H)-furanone and 2-hexadecanone], an organosulfur compound (methyl thiolacetate), a heterocyclic compound (indole; Fig. 3B) and five unknown compounds. Likewise, higher emission of methyl 2-methyl butanoate, 4-methyl-1-pentanol and (Z)-3-decen-1-ol was measured for all *Lysobacter* type strains grown on PDA as compared with NA. The emission profiles of PDA-specific VOCs differed for *Lysobacter* type strains, and the emission of 1-tridecanol, 1-tetradecanol, 1-

pentadecanol, delta-hexalactone, 2-hexadecanone, methyl thiolacetate, five unknown compounds, 4-methyl-1-pentanol and (Z)-3-decen-1-ol by *L. enzymogenes* was higher as compared with the other type strains on PDA. Moreover, 3-methyl-2-buten-1-ol and indole were emitted mainly by *L. gummosus* and *L. capsici* respectively, and dihydro-5-pentyl-2(3H)-furanone was mainly emitted by both *L. gummosus* and *L. capsici*.

The emission of 16 VOCs was higher for some *Lysobacter* type strains on PDA as compared with NA (Cluster 2, Table S1). For example, the emission of the n-undecanoic acid methyl ester was specific for three type strains grown on PDA (*L. capsici, L. enzymogenes* and *L. gummosus*) and it was not detected in other HS vials. These three type strains also showed higher emission of 1-propanol, 2-furanmethanol and 3-methyl-1-hexanol on PDA as compared with NA. The emission of 2-undecanol and methyl isobutyrate was higher on PDA as compared with NA for three type strains (*L. antibioticus*, *L. capsici* and *L. enzymogenes*) and two type strains (*L. antibioticus* and *L. enzymogenes*) respectively. On PDA, emission of 1-propanol by *L. capsici* and *L. enzymogenes* was higher as compared with *L. gummosus*, while that of methyl isobutyrate by *L. antibioticus* and *L. enzymogenes* was higher as compared with *L. capsici* and *L. gummosus.* Five compounds (2-tridecanone, acetone, 2-butanol and two unknown compounds) were emitted mainly by one PDA-grown *Lysobacter* type strain. Specifically, *L. enzymogenes* was characterised by the highest emission of 2-tridecanone and two unknown compounds, while *L. capsici* was characterised by the most significant emission of 2-butanol as compared with the other PDA-grown strains. Moreover, higher emission of isoamyl alcohol and phenyl ethyl alcohol by *L. enzymogenes*, ethanol by *L. capsici* and acetoin by *L. antibioticus* and *L. capsici* was found on PDA as compared with NA.

All the *Lysobacter* type strains showed higher emission of ten VOCs on NA as compared with PDA (NA-specific VOCs, Cluster 3, Table S1), such as 2,5-dimethyl pyrazine (Fig. 3C), 2,6-dimethyl pyrazine, 2,4,6-trimethyl pyridine, 1-(2-furanyl)-ethanone and an unknown compound, with consistent emission profiles for all NA-grown *Lysobacter* type strains. NA-specific profiles were also found for 2-butanone, pyrrole (Fig. 3D), 2-methoxy-3-(1-methyl-propyl) pyrazine and two unknown

335 compounds. Emission of these VOCs differed for NA-grown *Lysobacter* type strains: 2-butanone and
336 pyrrole were mainly emitted by *L. capsici*, while 2-methoxy-3-(1-methyl-propyl) pyrazine and two
337 unknown compounds were mainly emitted by *L. enzymogenes,* as compared with the other NA-grown
338 type strains.

339 The emission of 15 VOCs was higher on NA as compared with PDA for some type strains
340 (Cluster 4, Table S1), as in the case of 1-butanol and 2-nonanone emission by *L. antibioticus* and *L.*
341 *gummosus* respectively. Dihydro-3-methyl-2(3H)-furanone, decanal (Fig. 3E) and an unknown
342 compound were specifically emitted by more than two *Lysobacter* type strains grown on NA, with
343 the highest emission by *L. enzymogenes*. Emission of 3-methoxy-2,5-dimethyl pyrazine by *L. capsici*
344 and *L. gummosus* was higher on NA as compared with PDA, while its emission by *L. antibioticus* and
345 *L. enzymogenes* was comparable on NA and PDA medium. Moreover, 2-methoxy-3-methyl pyrazine
346 (Fig. 3F) and 2-methoxy-6-methyl pyrazine were emitted exclusively by *L. enzymogenes*, with lower
347 and no emission by *L. enzymogenes* on PDA respectively. Likewise, four unknown compounds
348 (named from 13 to 16) were mainly emitted by NA-grown *L. antibioticus* and *L. enzymogenes*.

349 The emission profiles differed for *Lysobacter* type strains on both media for 14 VOCs (Cluster
350 5, Table S1). For example, the emission of methyl 2-methyl butanoate and methyl 3-methyl butanoate
351 was higher by *L. antibioticus* was higher as compared with the other type strains on both growth
352 media. On NA, the emission of 2-methyl-1-propanol by *L. antibioticus* and *L. enzymogenes* was
353 higher as compared with *L. capsici* and 3-octanol emission by *L. gummosus* was higher as compared
354 with *L. antibioticus.* Moreover, 2-methoxy-3-(1-methylethyl) pyrazine was mainly emitted by *L.*
355 *enzymogenes* on both media and to a lower extent by *L. antibioticus* on NA, while methyl isobutyl
356 ketone was mainly emitted by *L. capsici* as compared with *L. antibioticus* and *L. gummosus* on PDA.
357 Consistent emission of seven VOCs (2-pentanone, dimethyl disulfide, 2-heptanone, 6-methyl-2-
358 heptanone, 5-methyl-2-heptanol, and two unknown compounds) was detected in *Lysobacter* type
359 strains and growth media (Cluster 6, Table S1) and they were possibly produced by constitutive
360 metabolic pathways.

3.2. Lysobacter *type strains and their growth media can be recognised by modelling the profiles of volatile organic compounds*

Differences in VOC emission among *Lysobacter* type strains grown on the two growth media were used to predict the medium on which the bacteria were grown. Optimisation of the LASSO model corresponded with a linear combination of the original variables (VOCs annotated by SPME/GC-MS analysis) with a coefficient of zero, except for the coefficient associated with the 2,4,6-trimethyl pyridine variable (Table S1). This result highlighted that a simple univariate model, built on the SPME/GC-MS emission data of 2,4,6-trimethyl pyridine alone, was sufficient to predict the growth substrate on the basis of only one bacterial VOC. The prediction performance was assessed with a LOO procedure and the success rate of growth media prediction using LASSO was 100%, meaning that the growth media could be predicted with high level of accuracy (Table 2).

PTR-ToF-MS data (Table S2) confirmed the marked differences in VOC emissions by *Lysobacter* type strains grown on PDA and NA. In agreement with the SPME/GC-MS analysis, the growth of *Lysobacter* type strains was comparable on PDA and NA (except for *L. antibioticus;* Table 1). LASSO modelling based on PTR-ToF-MS data resulted in prediction performance of the growth media comparable to that obtained with SPME/GC-MS data and cross-validation using a LOO procedure provided a prediction success rate of 100% (Table 2). The LASSO procedure was able to predict growth media on the basis of only two bacterial VOCs associated with peaks at *m/z* of 68.050 and 129.091 (Table S2). Although annotation of the compounds associated with PTR-ToF-MS spectral peaks is difficult (Cappellin et al., 2011a), the peak at *m/z* of 68.050 corresponds with the $C_4H_6N^+$ ion, which is consistent with a fragment ion of 2,4,6-trimethyl pyridine reaction with H_3O^+.

LASSO modelling was used for *Lysobacter* type strain prediction on the basis of VOC emission profiles. Since the medium prediction had a 100% success rate, the different growth media were modelled as separate classes and the success rate of strain prediction was 97 and 90% with LASSO modelling based on SPME/GC-MS and PTR-ToF-MS data respectively (Table 2). Specifically, HS

vials belonging to *L. enzymogenes* and *L. antibioticus* grown on both PDA and NA were correctly classified by SPME/GC-MS analysis, as well as *L. capsici* and *L. gummosus* grown on PDA. HS vials of *L. gummosus* were confused only once with *L. capsici* when grown on NA. Likewise, all *Lysobacter* type strains grown on PDA were correctly classified according to their volatilome assessed with PTR-ToF-MS analysis. On NA, HS vials of *L. gummosus* were confused only once with *L. antibioticus* and those of *L. enzymogenes* were confused twice with *L. capsici.* The LASSO modelling based on SPME/GC-MS and PTR-ToF-MS data associated non-zero coefficients with 11 VOCs (Table S1) and 12 peaks (Table S2) to distinguish *Lysobacter* type strains respectively, indicating that a linear model built using only these compounds was sufficient to discriminate the bacterial strains tested. Specifically, the emission profiles of methyl 2-methyl butanoate and methyl 3-methyl butanoate were characteristic for *L. antibioticus* on PDA, while those of 2-butanol, methyl thiolacetate and 3-methyl-2-buten-1-ol specified the emission of *L. capsici*, *L. enzymogenes* and *L. gummosus* respectively. On NA, the volatilome of *L. antibioticus* was characterised by the emission profiles of 2-furanmethanol and unknown compound 14, and *L. capsici*, *L. enzymogenes* and *L. gummosus* were specified by acetone, pyrazine (2-methoxy-3-methyl pyrazine and 2-methoxy-6-methyl pyrazine) and 3-octanol emission respectively.

3.3. Volatile organic compounds emitted by Lysobacter *type strains grown on nutrient agar and not on potato dextrose agar inhibit* Phytophthora infestans *growth*

VOCs emitted by *L. antibioticus*, *L. capsici*, *L. enzymogenes* and *L. gummosus* grown on NA inhibited the mycelial growth of *Ph. infestans* (Fig. 4A and 4B). Conversely, VOCs produced by the four *Lysobacter* type strains grown on PDA did not affect *Ph. infestans* growth. When transferred to new PAM dishes, the growth of *Ph. infestans* plugs previously exposed to VOCs produced by NA-grown *Lysobacter* type strains was compromised as compared with *Ph. infestans* plugs exposed to

413 uninoculated NA (Fig. 4C). Moreover, the growth of plugs exposed to VOCs produced by PDA-
414 grown *Lysobacter* type strains was comparable (Kruskal-Wallis test, $p > 0.05$) with those exposed to
415 uninoculated NA and PDA (data not shown).

416 Functional assays demonstrated that pure 2,5-dimethyl pyrazine, 2-methoxy-3-methyl
417 pyrazine, decanal and pyrrole inhibited the *Ph. infestans* growth (Table 3) and they were mainly
418 emitted by the NA-grown *Lysobacter* type strains. Conversely, pure delta-hexalactone and ethanol,
419 that were mainly emitted by the PDA-grown *Lysobacter* type strains, did not significantly inhibit the
420 *Ph. infestans* growth.

421

422

423 **4. Discussion**

424 In the last decade, increasing attention has been paid to the functional roles of bacterial VOCs in
425 soil microbial interactions (Effmert et al., 2012; Kai et al., 2009). Strains belonging to *L. antibioticus*,
426 *L. capsici* and *L. gummosus* play a major role in the soil suppressiveness against *R. solani* (Postma
427 and Schilder, 2015; Postma et al., 2008) and strains belonging to *L. enzymogenes* are involved in the
428 biocontrol of several phytopathogens (Hayward et al., 2010; Kobayashi and Yuen, 2007). The
429 incidence of *Lysobacter* spp. in soil is influenced by soil type, plant cover, seasonal factors and
430 organic amendments (Hayward et al., 2010; Postma et al., 2008), but little is known about the
431 ecological role of VOCs emitted by strains belonging to this genus. Although the synthesis of non-
432 volatile antimicrobial metabolites against phytopathogens has been widely studied (Puopolo et al.,
433 2014a; Xie et al., 2012), the possible contribution of *Lysobacter* VOCs to antagonistic processes has
434 been poorly investigated (Sang et al., 2011; Zou et al., 2007). In this work we analysed the VOC
435 profiles emitted by four *Lysobacter* type strains grown on PDA and NA using two types of headspace
436 analysis. The growth media had a different nutrient composition: PDA (sugar-rich media) contained
437 a high sugar content (20 g/l glucose), while NA (protein-rich media) mainly contained proteins (5 g/l
438 peptone and 2 g/l yeast extract) with a low sugar content (Fiddaman and Rossall, 1994). VOC

emission by the *Lysobacter* type strains changed radically according to the growth medium, and the comparable growth rate on both media indicated that volatilome differences were mainly related to metabolic changes instead of biomass formation. The composition and functional properties of the bacterial volatilome are known to be influenced by the growth substrate (Asari et al., 2016; Blom et al., 2011; Bruce et al., 2003; Garbeva et al., 2014; Weise et al., 2012), indicating metabolic adaptation of VOC production according to nutrient availability in the soil (Insam and Seewald, 2010). However, the composition of the bacterial bouquet is defined by genetic determinants (Peñuelas et al., 2014) and can be used to identify the four *Lysobacter* type strains grown on PDA with LASSO modelling. Specifically, butanoates (methyl 2-methyl butanoate, methyl 3-methyl butanoate), 2-butanol, methyl thiolacetate and 3-methyl-2-buten-1-ol specified the emission of *L. antibioticus*, *L. capsici*, *L. enzymogenes* and *L. gummosus* on PDA respectively. On NA, 2-furanmethanol and two pyrazines (2-methoxy-3-methyl pyrazine and 2-methoxy-6-methyl pyrazine) discriminated the emission of *L. antibioticus* and *L. enzymogenes* respectively. Interestingly, *Lysobacter* type strains emitted some strain-specific VOCs independently of the growth media. For example, *L. antibioticus* emitted higher amounts of two methyl esters (methyl 2-methyl butanoate and methyl 3-methyl butanoate) as compared with the other type on both media.

The functional properties of the *Lysobacter* volatilome changed radically according to the growth medium and the VOC-mediated biocontrol effects of the four *Lysobacter* type strains against *Ph. infestans* were enhanced on the protein-rich medium as compared with the sugar-rich medium. Likewise, a protein-rich medium (tryptone soya agar) increased the VOC-mediated antagonism of *Serratia* spp. against five sapstain fungi as compared with a sugar-rich medium (malt extract agar) (Bruce et al., 2003). In our experiments, higher emission of six pyrazines [2,5-dimethyl pyrazine, 2,6-dymethyl pyrazine, 2-methoxy-3-(1-methyl-propyl) pyrazine, 3-methoxy-2,5-dimethyl pyrazine, 2-methoxy-3-methyl pyrazine and 2-methoxy-6-methyl pyrazine] was found by NA-grown as compared with PDA-grown *Lysobacter* type strains and two pure pyrazines (2,5-dimethyl pyrazine, 2-methoxy-3-methyl pyrazine) inhibited the *Ph. infestans* growth. Pyrazines are synthesised by

alanine, valine, leucine and isoleucine (Dickschat et al., 2005) and addition of amino acids to the growth medium increased the bacterial production of pyrazines (Beck et al., 2003; Bungert et al., 2001), in agreement with higher emission by the NA-grown as compared with the PDA-grown *Lysobacter* type strains. Pyrazines and related heterocyclic compounds were involved in antimicrobial activities (Baldwin et al., 2013; Beck et al., 2003). Specifically, 2,5-dimethyl pyrazine and 2-ethyl-3,5-dimethyl pyrazine were emitted by a biocontrol strain of *Bacillus pumilus* and pure 2,5-dimethyl pyrazine showed antagonistic activity against *Ph. infestans* (De Vrieze et al., 2015) and *Phaeomoniella chlamydospora* (Haidar et al., 2016). Likewise, the VOC-mediated antimicrobial activity of the antagonist *B. megaterium* BP17 (Munjal et al., 2016) and *Pseudomonas putida* BP25 (Sheoran et al., 2015) was attributed to the emission of pyrazines, and four pure molecules (2,5-dimethyl pyrazine, 2-ethyl-3-methyl pyrazine, 2-ethyl pyrazine and 2-methyl pyrazine) showed inhibitory activities against *Ph. capsici*, *Ralstonia solanacearum* and *Magnaporthe oryzae* (Munjal et al., 2016). As shown for pyrazine emission by *Paenibacillus* spp. (Rybakova et al., 2016), three pyrazines [2-methoxy-3-(1-methyl-propyl) pyrazine, 2-methoxy-3-methyl pyrazine and 2-methoxy-6-methyl pyrazine] were species-specifically emitted, indicating the involvement of some species-specific biosynthetic pathways.

All the *Lysobacter* type strains showed higher emission of 2,4,6-trimethyl pyridine when grown on NA as compared to PDA and this VOC was also produced by the antagonistic strains *Collimonas fungivorans* Ter331 and *C. pratensis* Ter91 (Garbeva et al., 2014), suggesting its contribution to bacterial biocontrol processes. Pyrrole was also emitted by NA-grown *Lysobacter* type strains and inhibited the *Ph. infestans* growth. Likewise, pyrrole derivatives exhibited antagonistic activity towards phytopathogens, such as pyrrolnitrin [3-chloro-4-(20-nitro-30-chlorophenyl) pyrrole], which is a broad spectrum antifungal metabolite produced by several bacterial species (Saraf et al., 2014). The emission of 1-butanol by *L. antibioticus* was higher on NA as compared with PDA and the pure compound inhibited mycelial growth of *F. oxysporum* and *Moniliophthora perniciosa* (Chaves-López et al., 2015). Likewise, 1-butanol derivatives (3-methyl-1-butanol, 2-methyl-1-butanol and 1-butanol,

491 3-methyl-acetate) inhibited the mycelial growth of *Py. ultimum*, *R. solani* and *S. sclerotiorum* (Fialho
492 et al., 2011; Strobel et al., 2001), suggesting their contribution to the antagonistic activity against
493 phytopathogens. Dihydro-3-methyl-2(3H)-furanone and decanal were mainly emitted by the NA-
494 grown *L. enzymogenes* and the last one inhibited the *Ph. infestans* growth, indicating their potential
495 biocontrol activities as already shown for 3-(1-Hexenyl)-5-methyl-2-(5H)-furanone (Paulitz et al.,
496 2000) and decanal (Fernando et al., 2005). Nine VOCs specifically emitted by the NA-grown
497 *Lysobacter* type strains were found as unknown substances and more sensitive chromatographic
498 techniques are required to better characterise these compounds.
499 A blend of 17 VOCs was specifically emitted by all the *Lysobacter* type strains grown on PDA
500 and not on NA, such as three aliphatic alcohols (1-tridecanol, 1-tetradecanol and 1-pentadecanol). In
501 particular, 1-tridecanol and 1-tetradecanol showed no antifungal activity against *Saccharomyces*
502 *cerevisiae* (Kubo et al., 2003) and *S. sclerotiorum* (Giorgio et al., 2015) respectively, in agreement
503 with the absence of *Ph. infestans* inhibition with VOCs emitted by the PDA-grown *Lysobacter* type
504 strains. Delta-hexalactone and ethanol were mainly emitted by the PDA-grown *Lysobacter* type
505 strains and they did not show antagonistic activity against *P. infestans*. Likewise, ethanol was
506 produced by two *Serratia* spp. strains grown on the sugar-rich medium (malt extract agar) and not on
507 the protein-rich medium (tryptone soya agar) (Bruce et al., 2004) and did not seem to be implicated
508 in VOC-mediated biocontrol processes (Bruce et al., 2003). Indole emission was detected from the
509 PDA-grown *Lysobacter* type strains and low dosages of this VOC promoted *Arabidopsis thaliana*
510 growth (Blom et al., 2011). Likewise, acetoin, responsible for stimulation of *A. thaliana* growth (Ryu
511 et al., 2003), was mainly emitted by *L. antibioticus* and *L. capsici* on PDA, in agreement with higher
512 emission by *B. amyloliquefaciens* grown on a sugar-rich medium (M9 agar supplemented with
513 glucose) as compared with protein-rich media (tryptic soy agar and Luria-Bertani agar) (Asari et al.,
514 2016).
515 In conclusion, specific VOCs of *Lysobacter* spp. were identified and a tool for recognising four
516 *Lysobacter* type strains *in vitro* was developed according to VOC emission profiles, assessed using

SPME/GC-MS or PTR-ToF-MS analysis. The chemical profiles and functional properties of *Lysobacter* VOCs differed according to the growth medium, suggesting that appropriate nutrient sources should be preferred in dual culture assays in order to maximise biocontrol efficacy against phytopathogens. Bacterial VOC production in soil can differ according to community composition and nutrient availability (Insam and Seewald, 2010), suggesting a possible adaptation to the soil environment and inhabitants. Although our results were obtained from *in vitro*-grown bacteria, we hypothesized a possible scenario of *Lysobacter* VOCs that need further validation under soil conditions. Particularly, protein sources deriving from the lytic activities of phytopathogenic or saprophytic fungi may stimulate the production of antimicrobial VOCs by *Lysobacter* type strains (volatile pyrazines, pyrrole and decanal) to maximise antagonism to soil microbial inhabitants, such as *Ph. infestans*. Conversely, an increase in sugar availability due to root exudates in the rhizosphere (Jones et al., 2004) may change the volatilome of *Lysobacter* type strains, possibly to increase the production of plant growth stimulators (acetoin and indole) and non-antimicrobial compounds (1-tridecanol, 1-tetradecanol, delta-hexalactone and ethanol) to maximise beneficial interaction with the plant. However, further studies are required to investigate the volatilome shift and properties of *Lysobacter* spp. in soil conditions.

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Transparency declarations

All authors declare no conflict of interest.

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744

745

Table 1. Number of *Lysobacter* type strain cells developed during volatile organic compound assessment.

VOC analysis[1]	Media[2]	*Lysobacter* type strain concentration[3]			
		L. antibioticus	***L. capsici***	***L. enzymogenes***	***L. gummosus***
SPME/GC-MS	PDA	$7.75 \pm 0.32 \times 10^9$ ab	$4.77 \pm 0.38 \times 10^9$ bc	$7.23 \pm 0.49 \times 10^9$ ab	$1.12 \pm 0.03 \times 10^{10}$ a
	NA	$7.72 \pm 0.42 \times 10^8$ c	$5.82 \pm 1.30 \times 10^9$ abc	$5.86 \pm 0.92 \times 10^9$ abc	$4.14 \pm 2.09 \times 10^9$ abc
PTR-ToF-MS	PDA	$6.80 \pm 0.30 \times 10^9$ ab	$4.87 \pm 0.66 \times 10^9$ bc	$6.79 \pm 0.18 \times 10^9$ ab	$1.06 \pm 0.08 \times 10^{10}$ a
	NA	$1.40 \pm 0.09 \times 10^9$ c	$5.02 \pm 0.74 \times 10^9$ abc	$5.09 \pm 0.24 \times 10^9$ abc	$4.01 \pm 1.45 \times 10^9$ abc

[1] Headspace analysis of the volatile organic compounds (VOCs) emitted by *Lysobacter antibioticus* DSM 2044^T, *L. capsici* DSM 19286^T, *L. enzymogenes* DSM 2043^T and *L. gummosus* DSM 6980^T was carried out using solid-phase microextraction gas chromatography-mass spectrometry (SPME/GC-MS) and proton transfer reaction-time of flight-mass spectrometry (PTR-ToF-MS).

[2] The *Lysobacter* type strains were grown for ten days at 25°C on potato dextrose agar (PDA) or nutrient agar (NA) in headspace vials before VOC analysis.

[3] Growth of the *Lysobacter* type strains was measured one day after VOC assessment (11 days after inoculation). Bacterial cells were collected from the headspace vials and the number of *Lysobacter* cells for each vial was calculated by measuring optical density at 600 nm [optical density of 0.1 corresponds to 1×10^8 cells/ml according to Puopolo et al. (2016)]. Mean and standard deviation values of *Lysobacter* cells from four to five replicates are presented for each type strain and growth media. For each headspace VOC analysis, different letters indicate significant differences according to a Kruskal-Wallis test with Bonferroni correction ($p \leq 0.05$).

Table 2. Confusion matrix for bacteria strain prediction based on the least absolute shrinkage and selection operator method (LASSO) with a leave-one-out (LOO) procedure based on solid-phase microextraction gas chromatography-mass spectrometry (SPME/GC-MS) and proton transfer reaction-time of flight-mass spectrometry (PTR-ToF-MS) data.

			LASSO predicted class						
			PDA				NA		
			L. antibioticus	*L. capsici*	*L. enzymogenes*	*L. gummosus*	*L. antibioticus*	*L. capsici*	*L. enzymogenes*	*L. gummosus*
Real class	**SPME/GC-MS data**									
	PDA	*L. antibioticus*	**4**	0	0	0	0	0	0	0
		L. capsici	0	**4**	0	0	0	0	0	0
		L. enzymogenes	0	0	**5**	0	0	0	0	0
		L. gummosus	0	0	0	**4**	0	0	0	0
	NA	*L. antibioticus*	0	0	0	0	**4**	0	0	0
		L. capsici	0	0	0	0	0	**4**	0	0
		L. enzymogenes	0	0	0	0	0	0	**5**	0
		L. gummosus	0	0	0	0	0	**1**	0	**3**
	PTR-ToF-MS data									
	PDA	*L. antibioticus*	**5**	0	0	0	0	0	0	0
		L. capsici	0	**5**	0	0	0	0	0	0
		L. enzymogenes	0	0	**4**	0	0	0	0	0
		L. gummosus	0	0	0	**5**	0	0	0	0
	NA	*L. antibioticus*	0	0	0	0	**4**	0	0	0
		L. capsici	0	0	0	0	0	**4**	0	0
		L. enzymogenes	0	0	0	0	0	**2**	**2**	0
		L. gummosus	0	0	0	0	**1**	0	0	**4**

SPME/GC-MS and PTR-ToF-MS data were obtained from *Lysobacter antibioticus* DSM 2044^T, *L. capsici* DSM 19286^T, *L. enzymogenes* DSM 2043^T and *L. gummosus* DSM 6980^T grown on potato dextrose agar (PDA) or nutrient agar (NA).

Columns represent the class predicted with the LASSO method based on SPME/GC-MS or PTR-ToF-MS data and rows represent the real class. Diagonal entries of the matrix correspond to the number of samples correctly classified for each class and off-diagonal entries correspond to prediction errors.

Table 3. Antagonistic activity of pure volatile organic compounds (VOCs) on *Phytophthora infestans* growth.

Treatment	Inhibition (%) of *Phytophthora infestans* growth
control	0.00 ± 4.86 a
2,5-dimethyl pyrazine	93.66 ± 1.44 bc
2-methoxy-3-methyl pyrazine	97.03 ± 1.08 c
decanal	94.52 ± 0.82 bc
delta-hexalactone	8.55 ± 3.59 a
ethanol	29.33 ± 6.99 ab
pyrrole	96.58 ± 0.96 c

Each pure VOC was applied to a filter paper disk in split dishes at a concentration of 190 mg/l of air volume (VOC-treated) and distilled water was applied in control dishes (control). One plug of *Ph. infestans* was placed on the other side of each dish containing the pea agar medium (PAM) and colony diameter was measured seven days after incubation at 20°C. The inhibition of *Ph. infestans* growth (percentage) was calculated according to the following formula: (growth in control dishes — growth in VOC-treated dishes) / (growth in control dishes) × 100. Seven replicates (split dishes) were analysed for each treatment and the experiment was carried out twice. Mean and standard error values of 14 replicates pooled from two experiments are presented for each treatment. Different letters indicate significant differences according to the Kruskal-Wallis test with Bonferroni correction ($p \leq 0.05$).

Figure legends

Fig. 1. Principal component analysis (PCA) of volatile organic compounds (VOCs) emitted by *Lysobacter* type strains. PCA was based on VOCs measured using solid-phase microextraction gas chromatography-mass spectrometry (SPME/GC-MS) for *Lysobacter antibioticus* DSM 2044^T (red), *L. capsici* DSM 19286^T (blue), *L. enzymogenes* DSM 2043^T (black) and *L. gummosus* DSM 6980^T (green) grown for days on nutrient agar (triangles) or potato dextrose agar (circles). The percentage of variance explained by the principal components (PC) is reported in brackets for PC1 and PC6 **(A)** or PC6 and PC2 **(B)**.

Fig. 2. Profiles of volatile organic compounds (VOCs) emitted by *Lysobacter* type strains. Headspace VOC analysis was carried out using solid-phase microextraction gas chromatography-mass spectrometry (SPME/GC-MS) for *Lysobacter antibioticus* DSM 2044^T (La), *L. capsici* DSM 19286^T (Lc), *L. enzymogenes* DSM 2043^T (Le) and *L. gummosus* DSM 6980^T (Lg) grown for ten days on nutrient agar (NA) or potato dextrose agar (PDA). For each compound, the intensity of the colour gradient and letters are based on a Kruskal-Wallis test with Bonferroni correction ($p \leq 0.05$) on VOC emission data (Table S1). Compounds were grouped based on their emission profiles into: VOCs with higher emission by all *Lysobacter* type strains on PDA as compared with NA (Cluster 1), VOCs with higher emission by some *Lysobacter* type strains on PDA as compared with NA (Cluster 2), VOCs with higher emission by all *Lysobacter* type strains on NA as compared with PDA (Cluster 3), VOCs with higher emission by some *Lysobacter* type strains on NA as compared with PDA (Cluster 4), VOCs with different (Cluster 5) or consistent (Cluster 6) emission by *Lysobacter* type strains on both growth media.

Fig. 3. Profiles of selected volatile organic compounds (VOCs) emitted by *Lysobacter* type strains. Emission of delta-hexalactone (**A**), indole (**B**), 2,5-dimethyl pyrazine (**C**), pyrrole (**D**), decanal (**E**)

and 2-methoxy-3-methyl pyrazine (**F**) was measured using solid-phase microextraction gas chromatography-mass spectrometry (SPME/GC-MS) for *L. antibioticus* DSM 2044^T, *L. capsici* DSM 19286^T, *L. enzymogenes* DSM 2043^T and *L. gummosus* DSM 6980^T grown for ten days on nutrient agar (NA) or potato dextrose agar (PDA). For each compound, mean and standard error values of the absolute peak area from four to five replicates are reported for each *Lysobacter* type strain and growth medium. Different letters indicate significant differences according to the Kruskal-Wallis test with Bonferroni correction ($p \leq 0.05$). The structural formula is reported for each compound.

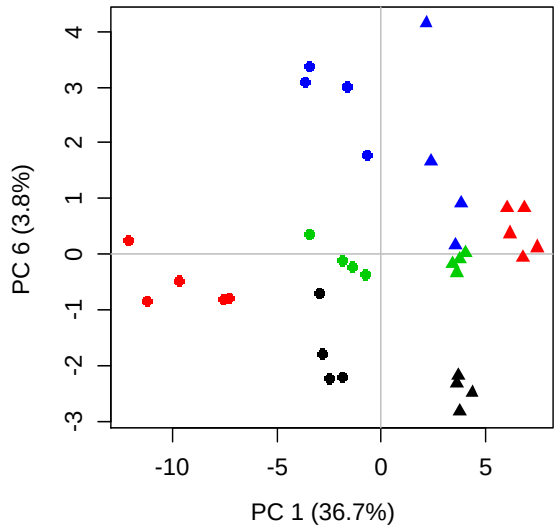
Fig. 4. Antagonistic activity of volatile organic compounds (VOCs) produced by *Lysobacter* type strains against *Phytophthora infestans*. *Lysobacter antibioticus* DSM 2044^T, *L. capsici* DSM 19286^T, *L. enzymogenes* DSM 2043^T and *L. gummosus* DSM 6980^T were grown for 72 h at 25°C on potato dextrose agar (PDA) or nutrient agar (NA) in split dishes and uninoculated dishes were used as controls (Uninoculated). One plug of *Ph. infestans* was placed on the other side of each dish containing the pea agar medium (PAM) and colony diameter was measured seven days after incubation at 20°C (**A**). Representative pictures of *Ph. infestans* growth (lower side of each dish) in split dishes with NA and PDA growth medium inoculated (*L. antibioticus*) or not (Uninoculated) with *L. antibioticus* (upper side of each dish) (**B**). Each *Ph. infestans* plug exposed to VOCs emitted by *Lysobacter* type strains grown on NA was then transferred to a fresh PAM dish and colony diameter was measured seven days after incubation at 20°C (**C**). Seven replicates (dishes) were analysed for each treatment and the experiment was carried out twice. Mean and standard error values of mycelium diameters obtained from 14 replicates pooled from two experiments are presented for each bacterial strain and growth media. Different letters indicate significant differences according to the Kruskal-Wallis test with Bonferroni correction ($p \leq 0.05$).

Appendix A. Supplementary data

Table S1. Volatile organic compounds (VOCs) emitted by the *Lysobacter* type strains and measured using solid-phase micro extraction gas chromatography-mass spectrometry (SPME/GC-MS) analysis.

Table S2. Volatile organic compounds (VOCs) emitted by *Lysobacter* type strains and measured using proton transfer reaction-time of flight-mass spectrometry (PTR-ToF-MS) analysis.

A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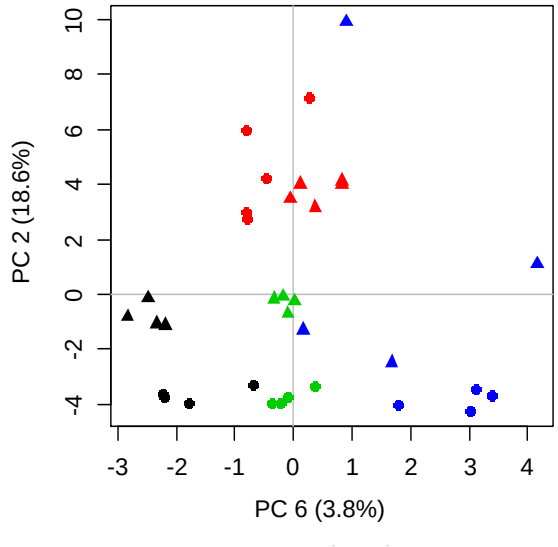
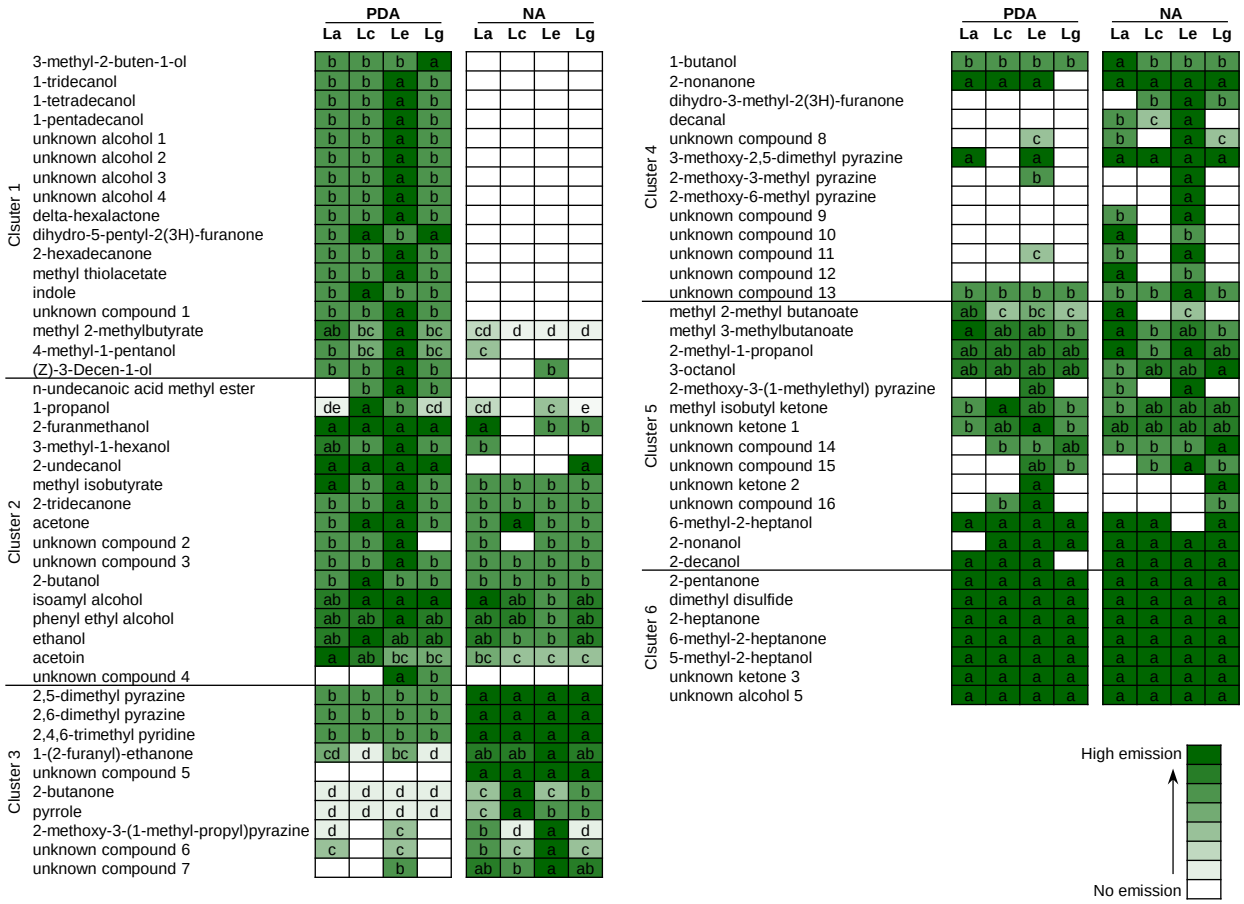
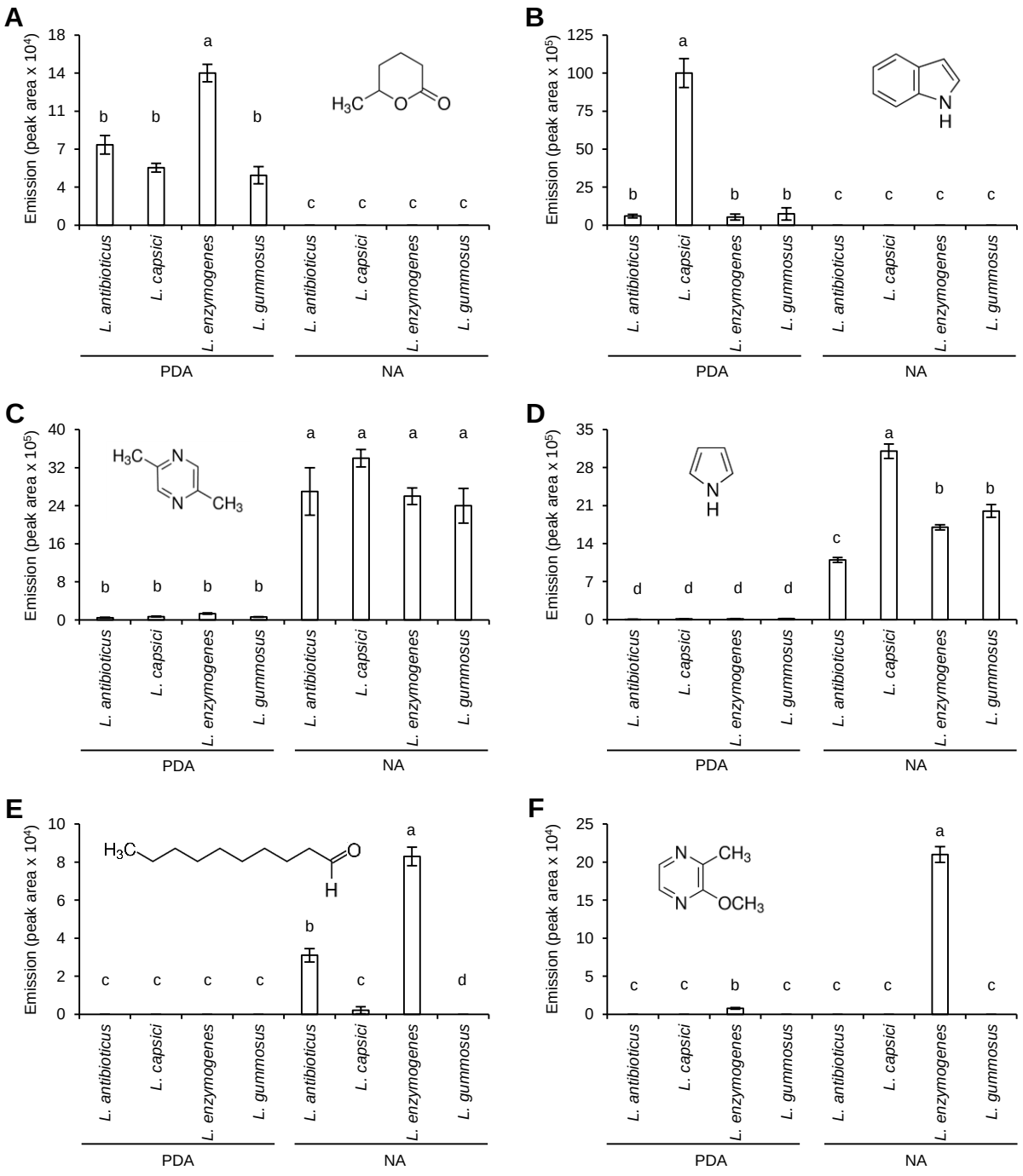
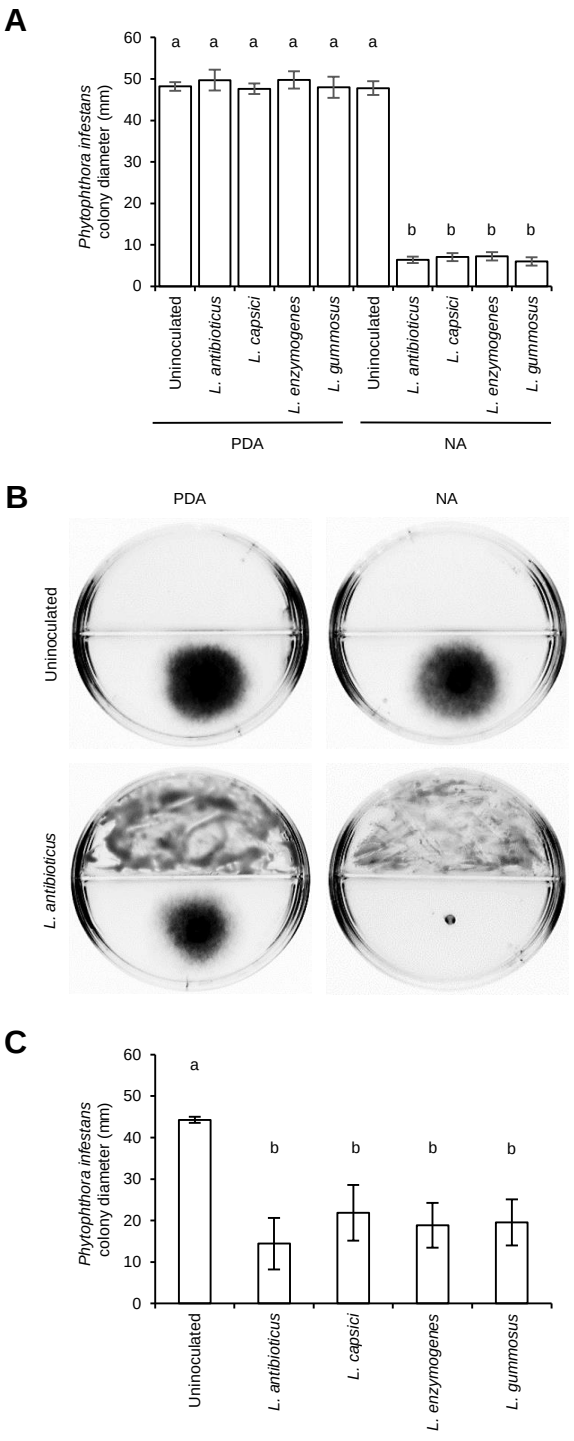
4
3
2
1
0
-1
-2
-3
-10
-5
0
5
PC 1 (36.7%)

B


PC 2 (18.6%)
10
8
6
4
2
0
-2
-4
-3
-2
-1
0
1
2
3
4
PC 6 (3.8%)


PDA
NA
La Lc Le Lg La Lc Le Lg
Clsuter 1
3-methyl-2-buten-1-ol b b b a
1-tridecanol b b a b
1-tetradecanol b b a b
1-pentadecanol b b a b
unknown alcohol 1 b b a b
unknown alcohol 2 b b a b
unknown alcohol 3 b b a b
unknown alcohol 4 b b a b
delta-hexalactone b b a b
dihydro-5-pentyl-2(3H)-furanone b a b a
2-hexadecanone b b a b
methyl thiolacetate b b a b
indole b a b b
unknown compound 1 b b a b
methyl 2-methylbutyrate ab bc a bc cd d d d
4-methyl-1-pentanol b bc a bc c
(Z)-3-Decen-1-ol b b a b b
Cluster 2
n-undecanoic acid methyl ester b a b
1-propanol de a b cd cd c e
2-furanmethanol a a a a a b b
3-methyl-1-hexanol ab b a b b
2-undecanol a a a a a
methyl isobutyrate a b a b b b b b
2-tridecanone b b a b b b b b
acetone b a a b b a b b
unknown compound 2 b b a b b
unknown compound 3 b b a b b b b b
2-butanol b a b b b b b b
isoamyl alcohol ab a a a a ab b ab
phenyl ethyl alcohol ab ab a ab ab ab b ab
ethanol ab a ab ab ab b b ab
acetoin a ab bc bc bc c c c
unknown compound 4 a b
Cluster 3
2,5-dimethyl pyrazine b b b b a a a a
2,6-dimethyl pyrazine b b b b a a a a
2,4,6-trimethyl pyridine b b b b a a a a
1-(2-furanyl)-ethanone cd d bc d ab ab a ab
unknown compound 5 a a a a
2-butanone d d d d c a c b
pyrrole d d d d c a b b
2-methoxy-3-(1-methyl-propyl)pyrazine d c b d a d
unknown compound 6 c c b c a c
unknown compound 7 b ab b a ab
PDA
NA
La Lc Le Lg La Lc Le Lg
Cluster 4
1-butanol b b b b a b b b
2-nonanone a a a a a a a
dihydro-3-methyl-2(3H)-furanone b a b
decanal b c a
unknown compound 8 c b a c
3-methoxy-2,5-dimethyl pyrazine a a a a a a
2-methoxy-3-methyl pyrazine b a
2-methoxy-6-methyl pyrazine a
unknown compound 9 b a
unknown compound 10 a b
unknown compound 11 c b a
unknown compound 12 a b
unknown compound 13 b b b b b b a b
Cluster 5
methyl 2-methyl butanoate ab c bc c a c
methyl 3-methylbutanoate a ab ab b a b ab b
2-methyl-1-propanol ab ab ab ab a b a ab
3-octanol ab ab ab ab b ab ab a
2-methoxy-3-(1-methylethyl) pyrazine ab b a
methyl isobutyl ketone b a ab b b ab ab ab
unknown ketone 1 b ab a b ab ab ab ab
unknown compound 14 b b ab b b b a
unknown compound 15 ab b a b
unknown ketone 2 a a
unknown compound 16 b a b
Clsuter 6
6-methyl-2-heptanol a a a a a a a
2-nonanol a a a a a a a
2-decanol a a a a a a a
2-pentanone a a a a a a a a
dimethyl disulfide a a a a a a a a
2-heptanone a a a a a a a a
6-methyl-2-heptanone a a a a a a a a
5-methyl-2-heptanol a a a a a a a a
unknown ketone 3 a a a a a a a a
unknown alcohol 5 a a a a a a a a
High emission
No emission


A
Emission (peak area x 10⁴)
18
14
11
7
4
0
b b a b c c c c
H3C O O
B
Emission (peak area x 10⁵)
125
100
75
50
25
0
b a b b c c c c
N H
C
Emission (peak area x 10⁵)
40
32
24
16
8
0
b b b b a a a a
H3C N N CH3
D
Emission (peak area x 10⁵)
35
28
21
14
7
0
d d d d c a b b
N H
E
Emission (peak area x 10⁴)
10
8
6
4
2
0
c c c c b c a d
H3C O H
F
Emission (peak area x 10⁴)
25
20
15
10
5
0
c c b c c c a c
N CH3 N OCH3
L. antibioticus
L. capsici
L. enzymogenes
L. gummosus
PDA
NA


A
Phytophthora infestans
colony diameter (mm)
60
50
40
30
20
10
0
a a a a a a
b b b b
Uninoculated
L. antibioticus
L. capsici
L. enzymogenes
L. gummosus
Uninoculated
L. antibioticus
L. capsici
L. enzymogenes
L. gummosus
PDA
NA
B
PDA
NA
Uninoculated
L. antibioticus
C
Phytophthora infestans
colony diameter (mm)
60
50
40
30
20
10
0
a
b b b b
Uninoculated
L. antibioticus
L. capsici
L. enzymogenes
L. gummosus

Supplementary Table S1. Volatile organic compounds (VOCs) emitted by the *Lysobacter* type strains and measured using solid-phase micro extraction gas chromatography-mass spectrometry (SPME/GC-MS) analysis.

	Compound	CAS number	Retention time	Retention index	NIST retention index	Potato dextrose agar				Nutrient agar				LASSO
						Lysobacter antibioticus	*Lysobacter capsici*	*Lysobacter enzymogenes*	*Lysobacter gummosus*	*Lysobacter antibioticus*	*Lysobacter capsici*	*Lysobacter enzymogenes*	*Lysobacter gummosus*	
Clsuter 1	3-methyl-2-buten-1-ol	556-82-1	14.5	1351	1320	$3.1 \pm 1.7 \times 10^4$ b	$1.6 \pm 1.5 \times 10^4$ b	$8.1 \pm 2.2 \times 10^4$ b	**$2.4 \pm 0.7 \times 10^5$ a ***	-	-	-	-	
	1-tridecanol	112-70-9	30.92	2056	2074	$1.9 \pm 1.4 \times 10^5$ b	$1.7 \pm 0.7 \times 10^5$ b	$1.5 \pm 0.5 \times 10^6$ a	$4.3 \pm 3.1 \times 10^5$ b	-	-	-	-	
	1-tetradecanol	112-72-1	33.83	2161	2165	$5.6 \pm 3.3 \times 10^4$ b	$5.6 \pm 2.3 \times 10^4$ b	$4.1 \pm 1.6 \times 10^5$ a	$8.5 \pm 5.0 \times 10^4$ b	-	-	-	-	
	1-pentadecanol	629-76-5	37.54	2297	2272	$7.4 \pm 0.1 \times 10^3$ b	$1.4 \pm 2.7 \times 10^4$ b	$1.9 \pm 0.4 \times 10^5$ a	$5.0 \pm 5.7 \times 10^4$ b	-	-	-	-	
	delta-hexalactone	823-22-3	26.12	1822	1791	$7.4 \pm 1.7 \times 10^4$ b	$5.3 \pm 0.8 \times 10^4$ b	$1.4 \pm 0.2 \times 10^5$ a	$4.6 \pm 1.6 \times 10^4$ b	-	-	-	-	
	dihydro-5-pentyl-2(3H)-furanone	104-61-0	31.08	2064	2024	$1.6 \pm 0.5 \times 10^5$ b	$3.0 \pm 0.3 \times 10^5$ a	$1.4 \pm 0.4 \times 10^5$ b	$2.9 \pm 0.7 \times 10^5$ a	-	-	-	-	
	2-hexadecanone	18787-63-8	31.97	2106	2121	$5.7 \pm 3.7 \times 10^4$ b	$4.6 \pm 1.5 \times 10^4$ b	$2.6 \pm 0.6 \times 10^5$ a	$2.9 \pm 3.4 \times 10^4$ b	-	-	-	-	
	methyl thiolacetate	1534-08-3	6.39	1078	1052	$9.1 \pm 0.7 \times 10^4$ b	$2.7 \pm 0.7 \times 10^5$ b	**$6.6 \pm 2.0 \times 10^6$ a ***	$1.2 \pm 0.7 \times 10^4$ b	-	-	-	-	
	indole	120-72-9	38.65	2342	2345	$6.0 \pm 2.4 \times 10^5$ b	$1.0 \pm 0.2 \times 10^7$ a	$5.3 \pm 4.4 \times 10^5$ b	$7.4 \pm 8.1 \times 10^5$ b	-	-	-	-	
	unknown compound 1		32.91	2134		$6.6 \pm 4.1 \times 10^4$ b	$2.1 \pm 1.4 \times 10^4$ b	$2.0 \pm 0.6 \times 10^5$ a	$6.9 \pm 4.1 \times 10^4$ b	-	-	-	-	
	unknown compound 2		34.43	2179		$9.1 \pm 0.1 \times 10^3$ b	$5.2 \pm 9.7 \times 10^3$ b	$1.3 \pm 0.7 \times 10^5$ a	$2.1 \pm 2.4 \times 10^4$ b	-	-	-	-	
	unknown compound 3		34.82	2190		$2.9 \pm 2.5 \times 10^5$ b	$2.4 \pm 1.3 \times 10^5$ b	$3.3 \pm 0.8 \times 10^6$ a	$7.3 \pm 5.8 \times 10^5$ b	-	-	-	-	
	unknown compound 4		35.11	2199		$2.3 \pm 3.4 \times 10^4$ b	$3.8 \pm 1.8 \times 10^4$ b	$2.5 \pm 0.4 \times 10^5$ a	$1.0 \pm 1.1 \times 10^5$ b	-	-	-	-	
	unknown compound 5		29.55	1987		$6.3 \pm 4.3 \times 10^3$ b	$1.7 \pm 0.3 \times 10^4$ b	$5.3 \pm 0.9 \times 10^4$ a	$1.4 \pm 0.2 \times 10^4$ b	-	-	-	-	
	methyl 2-methyl butanoate	868-57-5	5.27	1032	1009	$2.0 \pm 0.1 \times 10^7$ ab	$1.2 \pm 0.1 \times 10^7$ bc	$2.7 \pm 0.3 \times 10^7$ a	$1.3 \pm 0.6 \times 10^7$ bc	$4.7 \pm 3.2 \times 10^6$ cd	$1.7 \pm 1.4 \times 10^6$ d	$3.8 \pm 3.5 \times 10^5$ d	$4.3 \pm 3.2 \times 10^5$ d	
	4-methyl-1-pentanol	626-89-1	14.28	1343	1314	$4.9 \pm 1.8 \times 10^4$ b	$3.7 \pm 0.9 \times 10^4$ bc	$9.2 \pm 1.6 \times 10^4$ a	$4.2 \pm 0.9 \times 10^4$ bc	$1.1 \pm 0.9 \times 10^4$ c	-	-	-	
	(Z)-3-decen-1-ol	10340-22-4	25.97	1815	1789	$3.0 \pm 5.6 \times 10^3$ b	$9.5 \pm 6.3 \times 10^3$ b	$1.0 \pm 0.2 \times 10^5$ a	$6.9 \pm 8.3 \times 10^3$ b	-	-	$1.7 \pm 3.7 \times 10^4$ b	-	
Cluster 2	n-undecanoic acid methyl ester	1731-86-8	22.88	1678	1704	-	$2.7 \pm 5.1 \times 10^3$ b	$2.1 \pm 0.6 \times 10^5$ a	$1.2 \pm 1.3 \times 10^4$ b	-	-	-	-	
	1-propanol	71-23-8	6.11	1066	1036	$1.1 \pm 0.1 \times 10^5$ de	$6.5 \pm 0.7 \times 10^5$ a	$4.4 \pm 0.3 \times 10^5$ b	$2.4 \pm 0.2 \times 10^5$ cd	$1.7 \pm 0.1 \times 10^5$ cd	-	$2.5 \pm 0.5 \times 10^5$ c	$2.1 \pm 4.1 \times 10^4$ e	
	2-furanmethanol	98-00-0	23.17	1690	1660	$5.8 \pm 2.1 \times 10^5$ a	$4.6 \pm 0.8 \times 10^5$ a	$7.2 \pm 1.7 \times 10^5$ a	$6.4 \pm 1.5 \times 10^5$ a	**$4.6 \pm 0.3 \times 10^5$ a ***	-	$1.6 \pm 3.6 \times 10^4$ b	$2.0 \pm 3.9 \times 10^4$ b	
	3-methyl-1-hexanol	13231-81-7	16.95	1440	1413	$1.0 \pm 0.5 \times 105$ ab	$7.3 \pm 1.9 \times 10^4$ b	$1.7 \pm 0.2 \times 10^5$ a	$6.1 \pm 2.2 \times 10^4$ b	$4.6 \pm 4.5 \times 10^4$ b	-	-	-	
	2-undecanol	1653-30-1	24.38	1744	1717	$1.0 \pm 1.2 \times 10^4$ a	$8.4 \pm 1.9 \times 10^4$ a	$1.9 \pm 0.4 \times 10^5$ a	$1.1 \pm 1.3 \times 10^4$ a	-	-	-	$1.3 \pm 2.0 \times 10^5$ a	
	methyl isobutyrate	547-63-7	3.25	933	922	$3.8 \pm 0.7 \times 10^5$ a	$8.8 \pm 2.2 \times 10^4$ b	$3.3 \pm 0.5 \times 10^5$ a	$5.3 \pm 2.1 \times 10^4$ b	$5.8 \pm 6.1 \times 10^4$ b	$1.6 \pm 2.6 \times 10^3$ b	$4.0 \pm 3.2 \times 10^4$ b	$5.8 \pm 9.1 \times 10^4$ b	
	2-tridecanone	593-08-8	26.41	1836	1809	$4.2 \pm 3.7 \times 10^4$ b	$1.0 \pm 0.2 \times 10^5$ b	$5.4 \pm 1.6 \times 10^5$ a	$3.7 \pm 3.2 \times 10^4$ b	$3.8 \pm 0.8 \times 10^4$ b	$2.6 \pm 4.7 \times 10^3$ b	$1.1 \pm 1.0 \times 10^4$ b	$1.0 \pm 1.1 \times 10^5$ b	
	acetone	67-64-1	1.96	822	819	$1.4 \pm 0.2 \times 10^6$ b	$2.9 \pm 0.2 \times 10^6$ a	$3.2 \pm 0.7 \times 10^6$ a	$1.4 \pm 0.3 \times 10^6$ b	$9.3 \pm 1.1 \times 10^5$ b	**$3.6 \pm 0.3 \times 10^6$ a ***	$1.2 \pm 0.1 \times 10^6$ b	$1.4 \pm 0.7 \times 10^6$ b	
	unknown compound 6		11.65	1255		$1.1 \pm 1.5 \times 10^3$ b	$3.8 \pm 4.4 \times 10^3$ b	$3.6 \pm 1.8 \times 10^5$ a	-	$7.0 \pm 7.9 \times 10^3$ b	-	$3.4 \pm 5.5 \times 10^3$ b	$3.3 \pm 3.8 \times 10^4$ b	
	unknown compound 7		27.6	1892		$1.1 \pm 0.6 \times 10^5$ b	$1.6 \pm 0.7 \times 10^5$ b	$1.3 \pm 0.4 \times 10^6$ a	$1.2 \pm 0.5 \times 10^5$ b	$1.2 \pm 0.2 \times 10^5$ b	$8.1 \pm 0.4 \times 10^4$ b	$1.0 \pm 0.3 \times 10^5$ b	$2.0 \pm 0.9 \times 10^5$ b	
	2-butanol	78-92-2	3.31	937	927	$1.4 \pm 0.7 \times 10^4$ b	**$1.6 \pm 0.2 \times 10^6$ a ***	$1.6 \pm 0.2 \times 10^4$ b	$6.1 \pm 2.1 \times 10^4$ b	$3.1 \pm 4.7 \times 10^3$ b	$1.1 \pm 0.8 \times 10^4$ b	$2.9 \pm 3.6 \times 10^3$ b	$2.2 \pm 1.6 \times 10^4$ b	
	isoamyl alcohol	123-51-3	11.35	1246	1209	$1.2 \pm 0.5 \times 10^7$ ab	$2.0 \pm 0.6 \times 10^7$ a	$2.0 \pm 0.3 \times 10^7$ a	$2.2 \pm 0.4 \times 10^7$ a	$1.9 \pm 0.1 \times 10^7$ a	$4.6 \pm 0.4 \times 10^6$ ab	$2.4 \pm 1.9 \times 10^6$ b	$1.5 \pm 1.0 \times 10^7$ ab	
	phenylethyl alcohol	60-12-8	28.68	1944	1906	$1.8 \pm 0.6 \times 10^6$ ab	$2.2 \pm 0.3 \times 10^6$ ab	$2.4 \pm 0.5 \times 10^6$ a	$2.1 \pm 0.6 \times 10^6$ ab	$7.4 \pm 2.9 \times 10^5$ ab	$7.0 \pm 4.9 \times 10^5$ ab	$5.5 \pm 3.7 \times 10^5$ b	$1.0 \pm 0.8 \times 10^6$ ab	
	ethanol	64-17-5	3.45	944	932	$1.3 \pm 0.1 \times 10^6$ ab	$2.2 \pm 0.3 \times 10^6$ a	$1.4 \pm 0.1 \times 10^6$ ab	$1.5 \pm 0.2 \times 10^6$ ab	$3.9 \pm 0.3 \times 10^5$ ab	$5.2 \pm 3.6 \times 10^3$ b	$3.0 \pm 0.2 \times 10^5$ b	$7.3 \pm 1.4 \times 10^5$ ab	
	acetoin	513-86-0	13.43	1313	1284	$1.5 \pm 0.4 \times 10^6$ a	$1.4 \pm 0.5 \times 10^6$ ab	$8.0 \pm 5.3 \times 10^5$ abc	$5.3 \pm 5.1 \times 10^5$ abc	$1.8 \pm 0.2 \times 10^5$ bc	$1.8 \pm 2.2 \times 10^4$ c	$1.1 \pm 0.2 \times 10^5$ c	$9.5 \pm 6.0 \times 10^4$ c	
	unknown compound 8		27.12	1869		-	-	$8.8 \pm 2.9 \times 10^4$ a	$1.3 \pm 2.6 \times 10^4$ b	-	-	-	-	
Cluster 3	2,5-dimethyl pyrazine	123-32-0	14.33	1345	1320	$4.5 \pm 1.9 \times 10^4$ b	$6.9 \pm 1.4 \times 10^4$ b	$1.3 \pm 0.3 \times 10^5$ b	$6.1 \pm 1.6 \times 10^4$ b	$2.7 \pm 1.0 \times 10^6$ a	$3.4 \pm 0.4 \times 10^6$ a	$2.6 \pm 0.4 \times 10^6$ a	$2.4 \pm 0.7 \times 10^6$ a	
	2,6-dimethyl pyrazine	108-50-9	14.53	1352	1328	$4.0 \pm 2.2 \times 10^4$ b	$6.3 \pm 1.6 \times 10^4$ b	$1.3 \pm 0.4 \times 10^5$ b	$5.9 \pm 1.2 \times 10^4$ b	$3.7 \pm 1.4 \times 10^6$ a	$4.2 \pm 0.6 \times 10^6$ a	$3.4 \pm 1.1 \times 10^6$ a	$3.0 \pm 1.4 \times 10^6$ a	
	2,4,6-trimethyl pyridine	108-75-8	15.59	1389	1371	$6.2 \pm 4.5 \times 10^3$ b	$9.5 \pm 4.7 \times 10^3$ b	$1.7 \pm 0.9 \times 10^4$ b	$1.1 \pm 0.5 \times 10^4$ b	$5.2 \pm 0.8 \times 10^5$ a	$5.6 \pm 0.7 \times 10^5$ a	$5.8 \pm 0.6 \times 10^5$ a	$5.7 \pm 0.6 \times 10^5$ a	*
	1-(2-furanyl)-ethanone	1192-62-7	19.28	1530	1499	$1.4 \pm 0.6 \times 10^5$ cd	$9.5 \pm 1.8 \times 10^4$ d	$2.9 \pm 0.8 \times 10^5$ bc	$6.2 \pm 1.7 \times 10^4$ d	$4.3 \pm 0.2 \times 10^5$ ab	$4.2 \pm 0.3 \times 10^5$ ab	$4.5 \pm 0.2 \times 10^5$ a	$4.0 \pm 0.6 \times 10^5$ ab	
	unknown compound 9		16.87	1437		-	-	-	-	$1.6 \pm 0.2 \times 10^5$ a	$1.8 \pm 0.1 \times 10^5$ a	$1.6 \pm 0.1 \times 10^5$ a	$1.7 \pm 0.1 \times 10^5$ a	
	2-butanone	78-93-3	2.86	913	907	$2.9 \pm 0.2 \times 10^5$ d	$3.2 \pm 0.2 \times 10^5$ d	$3.9 \pm 2.2 \times 10^5$ d	$3.9 \pm 0.5 \times 10^5$ d	$1.2 \pm 0.4 \times 10^6$ c	$2.1 \pm 0.1 \times 10^6$ a	$1.4 \pm 0.1 \times 10^6$ c	$1.8 \pm 0.2 \times 10^6$ b	
	pyrrole	109-97-7	19.52	1539	1514	$4.8 \pm 6.3 \times 10^3$ d	$1.3 \pm 0.1 \times 10^4$ d	$1.5 \pm 0.9 \times 10^4$ d	$1.9 \pm 0.4 \times 10^4$ d	$1.1 \pm 0.1 \times 10^6$ c	$3.1 \pm 0.3 \times 10^6$ a	$1.7 \pm 0.1 \times 10^6$ b	$2.0 \pm 0.2 \times 10^6$ b	
	2-methoxy-3-(1-methyl-propyl) pyrazine	24168-70-5	19.23	1528	1500	$1.1 \pm 0.8 \times 10^4$ d	-	$1.6 \pm 0.4 \times 10^5$ c	-	$3.5 \pm 0.2 \times 10^5$ b	$3.6 \pm 2.3 \times 10^4$ d	$7.4 \pm 0.3 \times 10^5$ a	$3.0 \pm 5.9 \times 10^4$ d	
	unknown compound 10		20.41	1575		$1.5 \pm 2.5 \times 10^3$ c	-	$7.5 \pm 1.9 \times 10^4$ c	-	$3.4 \pm 0.7 \times 10^5$ b	$2.9 \pm 1.5 \times 10^4$ c	$8.8 \pm 0.4 \times 10^5$ a	$2.3 \pm 2.0 \times 10^4$ c	
	unknown compound 11		18.05	1482		-	-	$8.0 \pm 1.9 \times 10^4$ b	-	$2.9 \pm 2.4 \times 10^5$ ab	$9.5 \pm 0.2 \times 10^4$ b	$8.7 \pm 2.8 \times 10^5$ a	$2.5 \pm 0.4 \times 10^5$ ab	
Cluster 4	1-butanol	71-36-3	9.19	1175	1142	$6.5 \pm 2.8 \times 10^5$ b	$6.1 \pm 1.8 \times 10^5$ b	$7.8 \pm 2.2 \times 10^5$ b	$9.1 \pm 1.7 \times 10^5$ b	$5.9 \pm 0.6 \times 10^6$ a	$1.5 \pm 0.6 \times 10^4$ b	$1.7 \pm 1.3 \times 10^6$ b	$2.2 \pm 0.5 \times 10^5$ b	
	2-nonanone	821-55-6	16.24	1413	1390	$3.7 \pm 1.8 \times 10^4$ a	$7.1 \pm 0.9 \times 10^4$ a	$2.0 \pm 0.5 \times 10^5$ a	-	$9.6 \pm 3.4 \times 10^4$ a	$1.5 \pm 0.2 \times 10^5$ a	$1.8 \pm 0.4 \times 10^5$ a	$4.9 \pm 5.1 \times 10^5$ a	
	dihydro-3-methyl-2(3H)-furanone	1679-47-6	21.34	1612	1585	-	-	-	-	-	$1.9 \pm 2.2 \times 10^4$ b	$1.3 \pm 0.1 \times 10^5$ a	$1.6 \pm 1.9 \times 10^4$ b	
	decanal	112-31-2	19.14	1524	1498	-	-	-	-	$3.1 \pm 0.7 \times 10^4$ b	$2.1 \pm 3.9 \times 10^3$ c	$8.3 \pm 1.1 \times 10^4$ a	-	
	unknown compound 12		19.53	1540		-	-	$7.2 \pm 1.3 \times 10^4$ c	-	$2.0 \pm 0.2 \times 10^5$ b	-	$1.0 \pm 0.1 \times 10^6$ a	$2.7 \pm 5.4 \times 10^4$ c	
	3-methoxy-2,5-dimethyl pyrazine	19846-22-1	17.36	1456	1419	$9.3 \pm 4.0 \times 10^3$ a	-	$1.2 \pm 0.4 \times 10^5$ a	-	$1.2 \pm 0.1 \times 10^6$ a	$4.5 \pm 6.6 \times 10^5$ a	$1.9 \pm 1.2 \times 10^6$ a	$9.2 \pm 1.4 \times 10^5$ a	
	2-methoxy-3-methyl pyrazine	2847-30-5	15.81	1396	1339	-	-	$7.7 \pm 2.4 \times 10^3$ b	-	-	-	**$2.1 \pm 0.2 \times 10^5$ a ***	-	

	2-methoxy-6-methyl pyrazine	2882-21-5	16.49	1422	1371	-	-	-	-	-	-	**$3.1 \pm 0.3 \times 10^5$ a ***	-
	unknown compound 13		19.13	1524		-	-	-	-	$2.0 \pm 0.8 \times 10^5$ b	-	$4.2 \pm 0.3 \times 10^5$ a	-
	unknown compound 14		20.25	1568		-	-	-	-	**$1.8 \pm 0.1 \times 10^5$ a ***	-	$2.3 \pm 0.4 \times 10^4$ b	-
	unknown compound 15		19.6	1543		-	-	$1.1 \pm 0.6 \times 10^4$ c	-	$1.3 \pm 0.3 \times 10^5$ b	-	$1.8 \pm 0.2 \times 10^5$ a	-
	unknown compound 16		18.87	1514		-	-	-	-	$6.3 \pm 3.4 \times 10^5$ a	-	$7.3 \pm 1.7 \times 10^4$ b	-
	unknown compound 17		4.4	995		$2.6 \pm 1.2 \times 10^4$ b	$1.9 \pm 1.5 \times 10^4$ b	$2.2 \pm 0.2 \times 10^5$ b	$3.7 \pm 2.0 \times 10^4$ b	$7.9 \pm 0.3 \times 10^3$ b	$2.7 \pm 2.3 \times 10^4$ b	$2.4 \pm 0.4 \times 10^6$ a	$2.7 \pm 1.8 \times 10^5$ b
Cluster 5	methyl 2-methyl butanoate	868-57-5	10.65	1223	1229	**$5.0 \pm 2.0 \times 10^5$ ab ***	$3.2 \pm 1.4 \times 10^4$ c	$1.8 \pm 0.4 \times 10^5$ bc	$5.9 \pm 4.7 \times 10^4$ c	$7.1 \pm 2.7 \times 10^5$ a	-	$6.8 \pm 6.3 \times 10^4$ c	-
	methyl 3-methyl butanoate	556-24-1	5.54	1043	1018	**$1.2 \pm 0.1 \times 10^6$ a ***	$8.5 \pm 1.0 \times 10^5$ ab	$8.7 \pm 2.5 \times 10^5$ ab	$1.0 \pm 0.3 \times 10^5$ b	$1.2 \pm 0.6 \times 10^6$ a	$6.3 \pm 3.0 \times 10^4$ b	$5.0 \pm 3.2 \times 10^5$ ab	$1.9 \pm 1.3 \times 10^5$ b
	2-methyl-1-propanol	78-83-1	7.69	1125	1092	$1.4 \pm 0.1 \times 10^6$ ab	$1.5 \pm 0.1 \times 10^6$ ab	$1.9 \pm 0.1 \times 10^6$ ab	$1.6 \pm 0.2 \times 10^6$ ab	$2.2 \pm 0.1 \times 10^6$ a	$7.8 \pm 0.7 \times 10^5$ b	$2.2 \pm 0.4 \times 10^6$ a	$1.4 \pm 0.9 \times 10^6$ ab
	3-octanol	589-98-0	16.33	1416	1393	$1.6 \pm 0.9 \times 10^4$ ab	$4.0 \pm 0.7 \times 10^4$ ab	$1.6 \pm 2.1 \times 10^4$ ab	$4.7 \pm 1.6 \times 10^4$ ab	$6.0 \pm 4.3 \times 10^3$ b	$2.4 \pm 1.4 \times 10^4$ ab	$1.1 \pm 0.5 \times 10^4$ ab	**$5.3 \pm 1.6 \times 10^4$ a ***
	2-methoxy-3-(1-methylethyl) pyrazine	25773-40-4	17.51	1461	1427	-	-	$2.9 \pm 0.9 \times 10^4$ ab	-	$7.6 \pm 5.2 \times 10^3$ b	-	$7.9 \pm 4.4 \times 10^4$ a	-
	methyl isobutyl ketone	108-10-1	5.16	1027	1010	$1.4 \pm 0.3 \times 10^4$ b	$1.5 \pm 0.2 \times 10^5$ a	$6.7 \pm 0.9 \times 10^4$ ab	$9.4 \pm 1.3 \times 10^3$ b	$3.8 \pm 2.0 \times 10^4$ b	$5.5 \pm 1.6 \times 10^4$ ab	$6.0 \pm 0.9 \times 10^4$ ab	$6.7 \pm 7.9 \times 10^4$ ab
	unknown compound 18		22.93	1680		$8.2 \pm 6.3 \times 10^4$ b	$2.4 \pm 0.9 \times 10^5$ ab	$1.6 \pm 0.6 \times 10^6$ a	$9.4 \pm 5.2 \times 10^4$ b	$5.4 \pm 0.7 \times 10^5$ ab	$3.0 \pm 0.7 \times 10^5$ ab	$5.4 \pm 1.1 \times 10^5$ ab	$1.4 \pm 1.0 \times 10^6$ ab
	unknown compound 19		12.25	1274		-	$6.6 \pm 0.1 \times 10^3$ b	$9.5 \pm 0.1 \times 10^3$ b	$5.9 \pm 4.2 \times 10^4$ ab	$2.5 \pm 0.2 \times 10^4$ b	$2.8 \pm 0.6 \times 10^4$ b	$8.2 \pm 6.3 \times 10^3$ b	$1.6 \pm 0.9 \times 10^5$ a
	unknown compound 20		15.14	1373		-	-	$2.9 \pm 0.4 \times 10^5$ ab	$7.8 \pm 1.4 \times 10^3$ b	-	$7.9 \pm 6.2 \times 10^3$ b	$4.3 \pm 2.7 \times 10^5$ a	$1.9 \pm 1.6 \times 10^4$ b
	unknown compound 21		25.32	1786		-	-	$1.8 \pm 0.5 \times 10^5$ a	-	-	-	-	$1.2 \pm 2.1 \times 10^5$ a
	unknown compound 22		26.88	1858		-	$9.5 \pm 1.9 \times 10^3$ b	$2.0 \pm 0.7 \times 10^5$ a	-	-	-	-	$2.0 \pm 2.1 \times 10^4$ b
	6-methyl-2-heptanol	4730-22-7	15.81	1396	1372	$2.1 \pm 0.9 \times 10^4$ a	$1.0 \pm 0.2 \times 10^5$ a	$6.7 \pm 1.7 \times 10^4$ a	$2.0 \pm 1.4 \times 10^4$ a	$9.0 \pm 3.1 \times 10^4$ a	$3.1 \pm 3.6 \times 10^4$ a	-	$1.6 \pm 2.0 \times 10^5$ a
	2-nonanol	628-99-9	19.6	1543	1521	-	$7.5 \pm 1.2 \times 10^4$ a	$1.4 \pm 0.3 \times 10^5$ a	$9.2 \pm 1.8 \times 10^4$ a	$3.8 \pm 1.8 \times 10^4$ a	$1.1 \pm 1.4 \times 10^4$ a	$6.3 \pm 5.3 \times 10^4$ a	$5.4 \pm 7.1 \times 10^5$ a
	2-decanol	1120-06-5	20.96	1596	1601	$1.9 \pm 1.7 \times 10^4$ a	$1.6 \pm 0.2 \times 10^5$ a	$3.3 \pm 0.8 \times 10^5$ a	-	$6.1 \pm 1.6 \times 10^4$ a	$3.4 \pm 2.8 \times 10^4$ a	$1.1 \pm 0.9 \times 10^5$ a	$1.8 \pm 2.3 \times 10^6$ a
Clsuter 6	2-pentanone	107-87-9	4.4	995	981	$2.6 \pm 0.6 \times 10^4$ a	$4.9 \pm 0.4 \times 10^4$ a	$7.7 \pm 0.7 \times 10^4$ a	$7.0 \pm 8.2 \times 10^3$ a	$1.2 \pm 0.4 \times 10^5$ a	$1.1 \pm 0.4 \times 10^5$ a	$4.6 \pm 1.3 \times 10^4$ a	$5.9 \pm 1.1 \times 10^5$ a
	dimethyl disulfide	624-92-0	7.01	1103	1077	$1.0 \pm 0.5 \times 10^5$ a	$4.8 \pm 7.3 \times 10^5$ a	$2.2 \pm 0.6 \times 10^6$ a	$2.0 \pm 0.6 \times 10^6$ a	$2.7 \pm 0.7 \times 10^5$ a	$4.3 \pm 0.8 \times 10^5$ a	$1.3 \pm 1.9 \times 10^6$ a	$6.5 \pm 4.6 \times 10^5$ a
	2-heptanone	110-43-0	10.28	1211	1182	$1.6 \pm 0.6 \times 10^5$ a	$2.4 \pm 0.3 \times 10^5$ a	$7.0 \pm 1.9 \times 10^5$ a	$5.3 \pm 2.1 \times 10^4$ a	$5.6 \pm 2.6 \times 10^5$ a	$8.1 \pm 1.2 \times 10^5$ a	$7.2 \pm 0.8 \times 10^5$ a	$1.5 \pm 2.4 \times 10^6$ a
	6-methyl-2-heptanone	928-68-7	11.99	1265	1237	$2.3 \pm 1.2 \times 10^5$ a	$2.7 \pm 0.4 \times 10^5$ a	$8.0 \pm 1.7 \times 10^5$ a	$1.7 \pm 0.5 \times 10^4$ a	$9.5 \pm 3.7 \times 10^5$ a	$8.7 \pm 1.7 \times 10^5$ a	$1.2 \pm 0.2 \times 10^6$ a	$9.3 \pm 1.3 \times 10^5$ a
	5-methyl-2-heptanol	54630-50-1	15.93	1401	1395	$2.2 \pm 4.1 \times 10^3$ a	$3.6 \pm 0.5 \times 10^4$ a	$1.7 \pm 0.5 \times 10^4$ a	$5.3 \pm 6.6 \times 10^3$ a	$7.0 \pm 8.0 \times 10^3$ a	$4.2 \pm 7.9 \times 10^3$ a	$6.5 \pm 1.4 \times 10^3$ a	$4.5 \pm 5.7 \times 10^4$ a
	unknown compound 23		17.79	1472		$1.3 \pm 0.7 \times 10^5$ a	$1.3 \pm 0.3 \times 10^5$ a	$4.0 \pm 0.9 \times 10^5$ a	$6.8 \pm 8.5 \times 10^3$ a	$3.5 \pm 0.6 \times 10^5$ a	$2.1 \pm 0.5 \times 10^5$ a	$3.7 \pm 0.7 \times 10^5$ a	$1.6 \pm 1.6 \times 10^6$ a
	unknown compound 24		25.58	1797		$1.0 \pm 1.3 \times 10^4$ a	$7.3 \pm 1.9 \times 10^4$ a	$2.2 \pm 0.4 \times 10^5$ a	$1.8 \pm 1.4 \times 10^4$ a	$9.4 \pm 4.1 \times 10^4$ a	$1.0 \pm 0.1 \times 10^5$ a	$1.2 \pm 0.2 \times 10^5$ a	$3.4 \pm 4.4 \times 10^5$ a

Headspace volatile organic compound (VOC) analysis was carried out by solid-phase microextraction gas chromatography-mass spectrometry (SPME/GC-MS) for *Lysobacter antibioticus* DSM 2044^T, *L. capsici* DSM 19286^T, *L. enzymogenes* DSM 2043^T and *L. gummosus* DSM 6980^T grown for days on nutrient agar (NA) or potato dextrose agar (PDA).

CAS registry numbers of compound annotation are reported (http://webbook.nist.gov/chemistry/). Mean ± standard deviation values of the absolute peak area from four to five replicates are reported for each compound, *Lysobacter* type strain and growth media. For each compound, different letters indicate significant differences according to Kruskal-Wallis test with Bonferroni correction ($p \leq 0.05$). Only compounds with a background-corrected headspace concentration significantly emitted (Kruskal-Wallis with Bonferroni correction, $p \leq 0.05$) in *Lysobacter*-inoculated headspace vials as compared with uninoculated vials for at least one strain and growth medium are reported.

VOCs were grouped based on their emission profiles in: VOCs with higher emission by all *Lysobacter* type strains on PDA as compared with NA (Cluster 1), VOCs with higher emission by some *Lysobacter* type strains on PDA as compared with NA (Cluster 2), VOCs with higher emission by all *Lysobacter* type strains on NA as compared with PDA (Cluster 3), VOCs with higher emission by some *Lysobacter* type strains on NA as compared with PDA (Cluster 4), VOCs with different (Cluster 5) or consistent (Cluster 6) emission by *Lysobacter* type strains on both growth media.

Asterisks in bold (*) indicate VOC emission values associated to non-zero coefficients of the least absolute shrinkage and selection operator (LASSO) model calculated for the growth media prediction (column LASSO) and *Lysobacter* type strain prediction on PDA (columns Potato dextrose agar) and NA (columns Nutrient agar). Non-zero coefficients specify VOCs that can be used to predict the growth media and the *Lysobacter* type strain, respectively.

Supplementary Table S2. Volatile organic compounds (VOCs) emitted by *Lysobacter* type strains and measured using proton transfer reaction-time of flight-mass spectrometry (PTR-ToF-MS) analysis.

	***m/z* value**	**Potato dextrose agar**				**Nutrient agar**				**LASSO**
		Lysobacter antibioticus	***Lysobacter capsici***	***Lysobacter enzymogenes***	***Lysobacter gummosus***	***Lysobacter antibioticus***	***Lysobacter capsici***	***Lysobacter enzymogenes***	***Lysobacter gummosus***	
Cluster 1	49.023	0.213 ± 0.069 b	0.158 ± 0.019 b	4.637 ± 2.041 a	0.123 ± 0.009 b	-	-	-	-	
	49.054	0.193 ± 0.049 b	0.254 ± 0.02 b	0.542 ± 0.147 a	0.161 ± 0.025 b	-	-	-	-	
	61.054	0.763 ± 0.168 c	1.998 ± 0.4 a	1.66 ± 0.133 ab	0.994 ± 0.136 bc	-	-	-	-	
	62.057	0.024 ± 0.007 b	0.056 ± 0.012 a	0.05 ± 0.002 ab	0.033 ± 0.004 ab	-	-	-	-	
	63.984	0.034 ± 0.008 b	0.03 ± 0.008 b	0.097 ± 0.01 a	0.081 ± 0.007 a	-	-	-	-	
	64.007	0.063 ± 0.007 a	0.042 ± 0.008 a	0.064 ± 0.004 a	0.042 ± 0.011 a	-	-	-	-	
	68.050	2.712 ± 0.226 a	3.235 ± 0.874 a	2.293 ± 0.229 a	2.672 ± 0.49 a	-	-	-	-	*
	79.074	0.023 ± 0.006 b	0.07 ± 0.006 a	0.037 ± 0.006 b	0.028 ± 0.004 b	-	-	-	-	
	84.004	0.064 ± 0.015 ab	0.094 ± 0.009 a	0.053 ± 0.004 b	0.088 ± 0.009 ab	-	-	-	-	
	85.016	1.331 ± 0.284 b	2.075 ± 0.092 a	1.283 ± 0.098 b	1.786 ± 0.131 ab	-	-	-	-	
	89.045	0.129 ± 0.021 b	0.231 ± 0.029 a	0.136 ± 0.024 b	0.106 ± 0.017 b	-	-	-	-	
	92.989	0.012 ± 0.005 b	0.016 ± 0.009 b	0.125 ± 0.026 a	0.015 ± 0.004 b	-	-	-	-	
	93.022	0.107 ± 0.035 b	0.097 ± 0.009 b	0.302 ± 0.03 a	0.094 ± 0.032 b	-	-	-	-	
	110.949	0.01 ± 0.004 b	0.009 ± 0.002 b	0.117 ± 0.017 a	0.016 ± 0.007 b	-	-	-	-	
	114.065	0.033 ± 0.003 a	0.021 ± 0.002 b	0.022 ± 0.003 b	0.022 ± 0.003 b	-	-	-	-	
	116.913	0.05 ± 0.009 a	0.05 ± 0.004 a	0.05 ± 0.009 a	0.032 ± 0.004 a	-	-	-	-	
	116.964	0.082 ± 0.026 a	0.071 ± 0.013 a	0.091 ± 0.019 a	0.03 ± 0.007 a	-	-	-	-	
	117.076	3.083 ± 0.694 a	2.909 ± 0.474 ab	3.467 ± 0.605 a	1.085 ± 0.362 b	-	-	-	-	
	118.053	0.002 ± 0.002 b	0.152 ± 0.066 a	0.023 ± 0.024 ab	0.005 ± 0.004 b	-	-	-	-	
	119.059	0.035 ± 0.008 b	0.073 ± 0.019 b	0.36 ± 0.024 a	0.025 ± 0.006 b	-	-	-	-	
	129.046	0.066 ± 0.007 b	0.064 ± 0.006 b	0.452 ± 0.038 a	0.082 ± 0.006 b	-	-	-	-	
	129.091	0.116 ± 0.011 a	0.085 ± 0.006 b	0.09 ± 0.002 ab	0.07 ± 0.01 b	-	-	-	-	*
	129.132	0.086 ± 0.008 b	0.065 ± 0.008 b	0.125 ± 0.007 a	0.026 ± 0.004 c	-	-	-	-	
	135.049	0.024 ± 0.002 b	0.025 ± 0.002 b	0.046 ± 0.004 a	0.025 ± 0.005 b	-	-	-	-	
	135.086	0.043 ± 0.005 b	0.038 ± 0.004 b	0.061 ± 0.002 a	0.03 ± 0.003 b	-	-	-	-	
	139.086	0.103 ± 0.009 b	0.078 ± 0.01 bc	0.149 ± 0.011 a	0.058 ± 0.007 c	-	-	-	-	
	141.927	0.018 ± 0.01 b	0.002 ± 0.002 b	0.049 ± 0.007 a	0.066 ± 0.006 a	-	-	-	-	
	143.112	0.062 ± 0.007 ab	0.041 ± 0.009 b	0.106 ± 0.025 a	0.055 ± 0.008 b	-	-	-	-	
	144.151	0.006 ± 0.003 b	0.006 ± 0.002 b	0.018 ± 0.004 a	0.002 ± 0.002 b	-	-	-	-	
	153.101	0.069 ± 0.006 ab	0.078 ± 0.013 ab	0.1 ± 0.015 a	0.046 ± 0.005 b	-	-	-	-	
	159.096	0.02 ± 0.005 b	0.016 ± 0.003 b	0.049 ± 0.004 a	0.011 ± 0.004 b	-	-	-	-	
	163.150	0.02 ± 0.004 b	0.017 ± 0.002 b	0.018 ± 0 b	0.063 ± 0.008 a	-	-	-	-	
	167.158	0.021 ± 0.003 a	0.009 ± 0.002 b	0.02 ± 0.003 a	0.006 ± 0.001 b	-	-	-	-	
	171.182	0.04 ± 0.012 b	0.048 ± 0.005 b	0.177 ± 0.015 a	0.015 ± 0.003 b	-	-	-	-	
	172.170	0.009 ± 0.002 b	0.009 ± 0.003 b	0.025 ± 0.005 a	0.003 ± 0.001 b	-	-	-	-	
	181.144	0.027 ± 0.003 b	0.019 ± 0.002 b	0.087 ± 0.009 a	0.015 ± 0.002 b	-	-	-	-	
	185.157	0.026 ± 0.004 ab	0.022 ± 0.005 b	0.046 ± 0.008 a	0.018 ± 0.003 b	-	-	-	-	
	185.199	0.02 ± 0.008 b	0.039 ± 0.008 b	0.381 ± 0.052 a	0.02 ± 0.009 b	-	-	-	-	
	197.211	0.009 ± 0.002 b	0.009 ± 0.001 b	0.03 ± 0.004 a	0.011 ± 0.002 b	-	-	-	-	
	199.106	0.032 ± 0.003 a	0.021 ± 0.002 b	0.017 ± 0.002 b	0.015 ± 0.003 b	-	-	-	-	
	199.170	0.236 ± 0.031 a	0.014 ± 0.006 b	0.003 ± 0.004 b	0.011 ± 0.004 b	-	-	-	-	
	200.186	0.047 ± 0.006 a	0.005 ± 0.002 b	0.01 ± 0.002 b	0.007 ± 0.002 b	-	-	-	-	
	219.217	0.014 ± 0.002 b	0.012 ± 0.002 b	0.01 ± 0.002 b	**0.442 ± 0.06 a ***	-	-	-	-	
	220.219	0.005 ± 0.002 b	0.004 ± 0.002 b	0.004 ± 0.001 b	**0.08 ± 0.01 a ***	-	-	-	-	
	45.992	3.502 ± 0.256 a	3.924 ± 0.147 a	3.561 ± 0.225 a	3.851 ± 0.105 a	1.82 ± 0.056 b	1.879 ± 0.077 b	1.887 ± 0.165 b	2.181 ± 0.548 b	
	149.137	0.041 ± 0.006 b	0.024 ± 0.008 b	0.022 ± 0.002 b	0.063 ± 0.004 a	-	-	-	-	

Cluster 2	34.995	0.011 ± 0.008 b	0.018 ± 0.008 b	11.398 ± 3.371 a	0.023 ± 0.007 b	0.025 ± 0.026 b	1.716 ± 3.631 b	1.758 ± 2.588 b	0.028 ± 0.038 b	
	48.053	1.777 ± 0.427 ab	2.386 ± 0.253 a	1.925 ± 0.227 a	1.446 ± 0.221 abc	0.495 ± 0.042 c	0.448 ± 0.478 c	0.713 ± 0.347 bc	0.515 ± 0.311 c	
	81.036	0.932 ± 0.063 ab	0.851 ± 0.043 abc	0.999 ± 0.048 a	0.84 ± 0.06 abc	0.75 ± 0.051 bc	0.697 ± 0.085 c	0.696 ± 0.109 c	0.64 ± 0.056 c	
	126.973	0.026 ± 0.008 b	0.022 ± 0.005 b	0.125 ± 0.015 a	0.029 ± 0.004 b	0.033 ± 0.005 b	0.042 ± 0.018 b	0.061 ± 0.015 b	0.053 ± 0.016 b	
Cluster 3	51.044	0.754 ± 0.032 b	0.681 ± 0.042 b	0.748 ± 0.077 b	0.608 ± 0.038 b	1.545 ± 0.034 a	1.831 ± 0.456 a	1.839 ± 0.266 a	1.753 ± 0.185 a	
	38.034	16.683 ± 0.349 b	16.546 ± 0.184 b	17.102 ± 0.892 b	16.555 ± 0.294 b	30.777 ± 0.35 a	29.219 ± 3.998 a	31.01 ± 0.384 a	31.713 ± 0.886 a	
	39.033	48.288 ± 1.058 b	47.781 ± 0.359 b	48.731 ± 2.21 b	47.63 ± 1.055 b	101.93 ± 1.087 a	94.976 ± 17.224 a	104.084 ± 2.246 a	104.764 ± 2.061 a	
	102.097	0.026 ± 0.005 d	0.051 ± 0.003 bcd	0.035 ± 0.002 cd	0.021 ± 0.003 d	0.091 ± 0.013 ab	0.112 ± 0.017 a	0.118 ± 0.031 a	0.079 ± 0.023 abc	
	115.114	0.161 ± 0.017 b	0.093 ± 0.009 b	0.335 ± 0.016 ab	0.031 ± 0.005 b	0.812 ± 0.047 a	0.677 ± 0.248 a	0.768 ± 0.328 a	0.134 ± 0.028 b	
	116.116	0.014 ± 0.003 c	0.011 ± 0.003 c	0.027 ± 0.003 bc	0.003 ± 0.002 c	0.063 ± 0.016 a	0.052 ± 0.003 ab	0.065 ± 0.022 a	**0.011 ± 0.007 c ***	
	123.948	0.572 ± 0.019 b	0.525 ± 0.012 b	0.517 ± 0.019 b	0.491 ± 0.017 b	0.79 ± 0.073 a	0.81 ± 0.046 a	0.792 ± 0.032 a	0.842 ± 0.05 a	
	147.085	0.018 ± 0.001 cd	0.017 ± 0.003 cd	0.029 ± 0.002 bcd	0.012 ± 0.001 d	0.083 ± 0.009 ab	0.093 ± 0.028 a	0.105 ± 0.038 a	0.073 ± 0.016 abc	
	157.165	0.074 ± 0.018 bc	0.074 ± 0.008 bc	0.241 ± 0.012 bc	0.029 ± 0.009 c	**0.615 ± 0.047 a ***	0.333 ± 0.119 ab	0.365 ± 0.206 ab	0.079 ± 0.004 bc	
	158.160	0.013 ± 0.002 bc	0.014 ± 0.003 bc	0.037 ± 0.004 abc	0.006 ± 0.001 c	0.073 ± 0.006 a	0.047 ± 0.015 ab	0.049 ± 0.03 ab	0.016 ± 0.004 bc	
	161.100	0.039 ± 0.004 b	0.037 ± 0.005 b	0.076 ± 0.004 ab	0.029 ± 0.003 b	0.087 ± 0.01 ab	0.121 ± 0.045 a	0.133 ± 0.043 a	0.07 ± 0.013 ab	
	252.1681	0.005 ± 0.002 c	0.011 ± 0.003 c	0.013 ± 0.001 c	0.014 ± 0.001 bc	0.03 ± 0.005 a	0.035 ± 0.005 a	0.028 ± 0.004 ab	0.03 ± 0.008 a	
Cluster 4	33.034	25.699 ± 2.406 abc	23.228 ± 0.934 bc	23.886 ± 1.368 bc	21.03 ± 1.429 c	26.261 ± 1.46 abc	31.213 ± 1.31 a	31.291 ± 2.834 a	27.634 ± 2.437 ab	
	44.010	0.189 ± 0.022 b	0.192 ± 0.015 b	0.202 ± 0.022 b	0.197 ± 0.012 b	0.26 ± 0.006 ab	0.336 ± 0.071 a	0.245 ± 0.017 ab	0.271 ± 0.059 ab	
	73.065	14.243 ± 1.079 c	12.753 ± 1.788 c	17.131 ± 1.065 c	15.091 ± 1.186 c	40.759 ± 3.528 bc	48.153 ± 11.972 b	42.231 ± 5.577 bc	79.89 ± 21.757 a	
	74.068	0.621 ± 0.043 de	0.554 ± 0.066 e	0.733 ± 0.033 cde	0.668 ± 0.046 cde	1.973 ± 0.133 bcd	2.316 ± 0.598 b	2.009 ± 0.274 bc	3.731 ± 0.935 a	
	143.148	0.052 ± 0.006 c	0.05 ± 0.008 c	0.154 ± 0.015 bc	0.022 ± 0.001 c	0.499 ± 0.051 a	0.4 ± 0.085 ab	0.406 ± 0.182 ab	0.143 ± 0.07 bc	
Cluster 5	214.096	0.014 ± 0.003 b	0.016 ± 0.003 ab	0.021 ± 0.004 ab	0.024 ± 0.001 a	0.014 ± 0.003 b	0.016 ± 0.003 ab	0.021 ± 0.004 ab	0.024 ± 0.001 a	
	68.060	0.392 ± 0.02 b	0.369 ± 0.03 b	0.497 ± 0.019 a	0.561 ± 0.018 a	0.392 ± 0.02 b	0.369 ± 0.03 b	0.497 ± 0.019 a	0.561 ± 0.018 a	
	27.025	0.047 ± 0.005 b	0.155 ± 0.008 ab	0.07 ± 0.008 ab	0.058 ± 0.011 b	0.121 ± 0.008 ab	0.198 ± 0.154 ab	0.309 ± 0.072 a	0.198 ± 0.091 ab	
	34.037	0.373 ± 0.031 ab	0.337 ± 0.01 ab	0.359 ± 0.022 ab	0.31 ± 0.026 b	0.36 ± 0.036 ab	0.454 ± 0.034 a	0.412 ± 0.068 ab	0.394 ± 0.045 ab	
	44.058	0.416 ± 0.035 b	1.808 ± 0.111 a	0.759 ± 0.036 ab	0.537 ± 0.066 ab	0.795 ± 0.054 ab	1.068 ± 0.883 ab	1.72 ± 0.282 ab	1.273 ± 0.548 ab	
	57.070	17.593 ± 0.508 b	22.8 ± 0.816 ab	21.695 ± 1.28 ab	14.996 ± 1.781 b	53.129 ± 3.529 ab	33.799 ± 33.535 ab	75.832 ± 21.326 a	46.001 ± 21.77 ab	
	58.073	0.8 ± 0.027 b	1.042 ± 0.061 ab	1.001 ± 0.065 ab	0.672 ± 0.078 b	2.426 ± 0.116 ab	1.583 ± 1.552 ab	3.421 ± 0.974 a	2.128 ± 0.972 ab	
	65.023	0.166 ± 0.012 b	0.214 ± 0.013 ab	0.188 ± 0.005 ab	0.174 ± 0.01 b	0.407 ± 0.068 ab	0.466 ± 0.285 ab	0.94 ± 0.445 a	0.677 ± 0.342 ab	
	72.090	0.264 ± 0.04 b	0.478 ± 0.029 ab	0.395 ± 0.043 ab	0.308 ± 0.047 ab	0.436 ± 0.033 ab	0.526 ± 0.447 ab	**1.035 ± 0.329 a ***	0.614 ± 0.193 ab	
	77.060	0.19 ± 0.047 c	0.475 ± 0.112 abc	0.457 ± 0.057 abc	0.257 ± 0.037 bc	0.525 ± 0.057 abc	0.925 ± 0.247 a	0.755 ± 0.143 ab	0.575 ± 0.254 abc	
	101.097	0.126 ± 0.017 bc	0.467 ± 0.041 abc	0.287 ± 0.007 bc	0.067 ± 0.005 c	0.939 ± 0.096 ab	0.838 ± 0.453 abc	1.234 ± 0.323 a	0.622 ± 0.363 abc	
	118.073	0.188 ± 0.031 ab	0.609 ± 0.242 a	0.266 ± 0.058 ab	0.085 ± 0.022 b	0.188 ± 0.031 ab	0.609 ± 0.242 a	0.266 ± 0.058 ab	0.085 ± 0.022 b	
	127.968	0.004 ± 0.001 b	0.006 ± 0.001 ab	0.012 ± 0.002 a	0.004 ± 0.003 ab	0.004 ± 0.001 b	0.006 ± 0.001 ab	0.012 ± 0.002 a	0.004 ± 0.003 ab	
	130.130	0.011 ± 0.003 ab	0.008 ± 0.001 ab	0.015 ± 0.002 a	0.007 ± 0.001 b	0.011 ± 0.003 ab	0.008 ± 0.001 ab	0.015 ± 0.002 a	0.007 ± 0.001 b	
	131.054	0.012 ± 0.002 b	0.01 ± 0.006 b	0.036 ± 0.004 a	0.008 ± 0.003 b	0.012 ± 0.002 b	0.01 ± 0.006 b	0.036 ± 0.004 a	0.008 ± 0.003 b	
	151.116	0.116 ± 0.01 a	0.094 ± 0.003 ab	0.044 ± 0.003 b	0.069 ± 0.007 ab	0.112 ± 0.007 a	0.11 ± 0.038 a	0.093 ± 0.009 ab	0.108 ± 0.006 a	
	186.199	0.004 ± 0.002 bc	0.007 ± 0.002 bc	0.06 ± 0.01 a	0.004 ± 0.002 c	0.019 ± 0.002 bc	0.025 ± 0.007 b	0.021 ± 0.013 bc	0.017 ± 0.005 bc	
	199.200	**0.078 ± 0.018 a ***	0.02 ± 0.005 b	0.072 ± 0.011 a	0.023 ± 0.01 b	0.043 ± 0.014 ab	0.054 ± 0.017 ab	0.038 ± 0.007 ab	0.039 ± 0.011 ab	
	225.053	0.217 ± 0.015 b	0.223 ± 0.023 b	0.23 ± 0.056 b	0.473 ± 0.121 a	0.35 ± 0.019 ab	0.345 ± 0.078 ab	0.431 ± 0.038 ab	0.34 ± 0.042 ab	
	226.053	0.045 ± 0.005 b	0.043 ± 0.006 b	0.043 ± 0.013 b	0.096 ± 0.024 a	0.076 ± 0.008 ab	0.078 ± 0.022 ab	0.09 ± 0.006 ab	0.068 ± 0.017 ab	
	227.0403	0.051 ± 0.004 b	0.05 ± 0.002 b	0.052 ± 0.008 b	0.105 ± 0.025 a	0.051 ± 0.004 b	0.05 ± 0.002 b	0.052 ± 0.008 b	0.105 ± 0.025 a	
Cluster 6	50.013	0.148 ± 0.089 a	0.056 ± 0.026 a	7.555 ± 0.585 a	0.076 ± 0.012 a	2.197 ± 0.285 a	12.166 ± 26.192 a	54.394 ± 44.594 a	7.213 ± 13.255 a	
	51.007	0.472 ± 0.187 a	0.221 ± 0.058 a	20.17 ± 1.49 a	0.27 ± 0.015 a	4.726 ± 0.776 a	28.648 ± 62.18 a	95.337 ± 98.17 a	16.76 ± 31.107 a	
	52.007	0.042 ± 0.006 a	0.043 ± 0.004 a	0.252 ± 0.022 a	0.036 ± 0.006 a	0.072 ± 0.035 a	0.37 ± 0.774 a	1.454 ± 1.198 a	0.211 ± 0.373 a	
	53.002	0.081 ± 0.011 a	0.124 ± 0.019 a	0.185 ± 0.007 a	0.088 ± 0.01 a	0.085 ± 0.013 a	0.167 ± 0.194 a	**0.556 ± 0.359 a ***	0.135 ± 0.123 a	
	59.049	247.689 ± 60.016 a	649.633 ± 160.071 a	587.059 ± 52.154 a	341.874 ± 56.624 a	342.242 ± 27.044 a	**720.223 ± 360.911 a ***	482.783 ± 113.029 a	344.305 ± 144.231 a	
	60.053	8.366 ± 1.986 a	21.807 ± 5.327 a	19.649 ± 1.712 a	11.536 ± 1.791 a	12.153 ± 1.04 a	24.689 ± 14.167 a	17.055 ± 3.959 a	12.132 ± 4.928 a	
	63.008	3.743 ± 0.347 a	3.223 ± 0.235 a	3 ± 0.066 a	3.057 ± 0.132 a	4.017 ± 0.162 a	3.028 ± 2.575 a	3.353 ± 0.459 a	**5.368 ± 1.109 a ***	
	63.026	1.086 ± 0.083 a	2.068 ± 0.08 a	2.152 ± 0.093 a	1.695 ± 0.038 a	2.169 ± 0.041 a	4.626 ± 4.577 a	15.604 ± 12.076 a	8.598 ± 9.076 a	
	64.023	0.018 ± 0.011 a	0.052 ± 0.011 a	0.098 ± 0.007 a	0.046 ± 0.009 a	0.077 ± 0.021 a	0.159 ± 0.16 a	0.505 ± 0.422 a	0.286 ± 0.296 a	

65.060	2.232 ± 0.515 a	2.922 ± 0.342 a	2.413 ± 0.38 a	1.808 ± 0.285 a	1.144 ± 0.14 a	0.987 ± 1.109 a	1.463 ± 0.747 a	1.149 ± 0.745 a
67.022	0.013 ± 0.006 a	0.009 ± 0.005 a	0.108 ± 0.012 a	0.013 ± 0.007 a	0.034 ± 0.004 a	0.193 ± 0.392 a	0.821 ± 0.665 a	0.112 ± 0.191 a
71.086	4.792 ± 0.747 a	8.483 ± 0.524 a	6.946 ± 0.773 a	5.426 ± 0.709 a	7.7 ± 0.561 a	9.334 ± 8.077 a	17.805 ± 6.239 a	11.087 ± 3.709 a
73.250	0.069 ± 0.005 a	0.077 ± 0.032 a	0.077 ± 0.012 a	0.147 ± 0.024 a	0.069 ± 0.005 a	0.077 ± 0.032 a	0.077 ± 0.012 a	0.147 ± 0.024 a
77.998	0.022 ± 0.008 a	0.022 ± 0.006 a	0.084 ± 0.04 a	0.017 ± 0.004 a	0.022 ± 0.008 a	0.022 ± 0.006 a	0.084 ± 0.04 a	0.017 ± 0.004 a
80.986	0.04 ± 0.022 a	0.156 ± 0.073 a	0.185 ± 0.045 a	0.075 ± 0.041 a	0.04 ± 0.022 a	0.156 ± 0.073 a	0.185 ± 0.045 a	0.075 ± 0.041 a
88.053	0.624 ± 0.232 a	0.516 ± 0.11 a	0.704 ± 0.133 a	0.232 ± 0.068 a	0.196 ± 0.029 a	0.257 ± 0.22 a	0.445 ± 0.137 a	0.246 ± 0.094 a
89.061	1.194 ± 0.14 a	2.271 ± 0.193 a	1.073 ± 0.307 a	0.785 ± 0.051 a	0.913 ± 0.512 a	1.259 ± 1.154 a	0.805 ± 0.382 a	0.687 ± 0.499 a
90.064	0.068 ± 0.007 a	0.114 ± 0.009 a	0.06 ± 0.018 a	0.042 ± 0.005 a	0.054 ± 0.022 a	0.088 ± 0.063 a	0.06 ± 0.015 a	0.034 ± 0.024 a
91.024	0.093 ± 0.036 a	0.185 ± 0.044 a	4.541 ± 0.58 a	0.053 ± 0.005 a	0.938 ± 0.071 a	3.365 ± 7.038 a	9.482 ± 7.199 a	0.18 ± 0.276 a
92.028	0.007 ± 0.005 a	0.009 ± 0.004 a	0.2 ± 0.023 a	0.005 ± 0.002 a	0.043 ± 0.009 a	0.157 ± 0.303 a	0.423 ± 0.318 a	0.01 ± 0.017 a
101.027	0.23 ± 0.014 a	0.242 ± 0.001 a	0.242 ± 0.003 a	0.215 ± 0.009 a	0.233 ± 0.029 a	0.268 ± 0.077 a	0.348 ± 0.086 a	0.222 ± 0.031 a
103.078	1.86 ± 0.318 a	0.828 ± 0.123 a	0.986 ± 0.171 a	0.439 ± 0.187 a	2.651 ± 0.286 a	1.467 ± 1.535 a	2.661 ± 1.752 a	10.323 ± 19.343 a
104.074	0.141 ± 0.02 a	0.084 ± 0.01 a	0.088 ± 0.013 a	0.065 ± 0.023 a	0.205 ± 0.026 a	0.149 ± 0.095 a	0.218 ± 0.083 a	0.689 ± 1.173 a
115.042	0.096 ± 0.006 a	0.087 ± 0.007 a	0.08 ± 0.005 a	0.073 ± 0.009 a	0.081 ± 0.018 a	0.082 ± 0.009 a	0.107 ± 0.013 a	0.08 ± 0.021 a
115.078	0.364 ± 0.089 a	0.141 ± 0.02 a	0.249 ± 0.038 a	0.146 ± 0.021 a	0.241 ± 0.032 a	0.218 ± 0.167 a	0.376 ± 0.181 a	0.299 ± 0.212 a
117.009	0.103 ± 0.02 a	0.114 ± 0.049 a	0.111 ± 0.022 a	0.039 ± 0.011 a	0.103 ± 0.02 a	0.114 ± 0.049 a	0.111 ± 0.022 a	0.039 ± 0.011 a
117.094	30.884 ± 10.018 a	26.295 ± 4.444 a	33.94 ± 5.697 a	10.929 ± 3.005 a	21.92 ± 1.579 a	26.245 ± 36.166 a	57.939 ± 26.697 a	25.151 ± 12.459 a
117.327	0.068 ± 0.027 a	0.059 ± 0.013 a	0.071 ± 0.013 a	0.025 ± 0.007 a	0.068 ± 0.027 a	0.059 ± 0.013 a	0.071 ± 0.013 a	0.025 ± 0.007 a
118.098	2.093 ± 0.693 a	1.8 ± 0.324 a	2.297 ± 0.377 a	0.754 ± 0.21 a	1.485 ± 0.126 a	1.825 ± 2.527 a	3.863 ± 1.768 a	1.711 ± 0.865 a
119.095	0.281 ± 0.065 a	0.275 ± 0.032 a	0.286 ± 0.04 a	0.156 ± 0.026 a	0.267 ± 0.032 a	0.293 ± 0.215 a	0.488 ± 0.146 a	0.42 ± 0.342 a
120.052	0.018 ± 0.004 a	0.013 ± 0.001 a	0.03 ± 0.005 a	0.011 ± 0.002 a	0.011 ± 0.007 a	0.02 ± 0.005 a	0.046 ± 0.032 a	0.308 ± 0.599 a
125.635	0 ± 0 a	0.009 ± 0.004 a	0.008 ± 0.001 a	0.002 ± 0.003 a	0 ± 0 a	0.009 ± 0.004 a	0.008 ± 0.001 a	0.002 ± 0.003 a
130.040	0.009 ± 0.001 a	0.008 ± 0.002 a	0.042 ± 0.004 a	0.011 ± 0.002 a	0.02 ± 0.003 a	0.091 ± 0.125 a	0.237 ± 0.149 a	0.035 ± 0.004 a
131.034	0.005 ± 0.003 a	0.006 ± 0.001 a	0.019 ± 0.004 a	0.006 ± 0.002 a	0.014 ± 0.006 a	0.074 ± 0.108 a	0.159 ± 0.101 a	0.041 ± 0.033 a
133.072	0.038 ± 0.005 a	0.051 ± 0.006 a	0.842 ± 0.065 a	0.036 ± 0.004 a	0.736 ± 0.093 a	1.016 ± 2.049 a	5.284 ± 3.964 a	2.865 ± 5.569 a
134.073	0.01 ± 0.003 a	0.01 ± 0.002 a	0.075 ± 0.012 a	0.006 ± 0.002 a	0.073 ± 0.008 a	0.103 ± 0.161 a	0.435 ± 0.328 a	0.241 ± 0.454 a
149.055	0.045 ± 0.005 a	0.07 ± 0.011 a	0.074 ± 0.021 a	0.066 ± 0.015 a	0.045 ± 0.005 a	0.07 ± 0.011 a	0.074 ± 0.021 a	0.066 ± 0.015 a
167.118	0.101 ± 0.009 a	0.07 ± 0.005 a	0.16 ± 0.014 a	0.039 ± 0.007 a	0.07 ± 0.015 a	0.109 ± 0.072 a	0.166 ± 0.117 a	0.029 ± 0.007 a
169.043	0.08 ± 0.014 a	0.093 ± 0.008 a	0.106 ± 0.012 a	0.099 ± 0.009 a	0.12 ± 0.017 a	0.139 ± 0.049 a	0.137 ± 0.025 a	0.111 ± 0.015 a
186.917	0.037 ± 0.008 a	0.031 ± 0.006 a	0.036 ± 0.009 a	0.047 ± 0.004 a	0.037 ± 0.008 a	0.031 ± 0.006 a	0.036 ± 0.009 a	0.047 ± 0.004 a
223.071	0.306 ± 0.047 a	0.293 ± 0.047 a	0.3 ± 0.088 a	0.606 ± 0.126 a	0.432 ± 0.03 a	0.495 ± 0.206 a	0.526 ± 0.104 a	0.417 ± 0.074 a
224.072	0.065 ± 0.013 a	0.068 ± 0.012 a	0.064 ± 0.021 a	0.136 ± 0.03 a	0.1 ± 0.013 a	0.118 ± 0.063 a	0.123 ± 0.034 a	0.101 ± 0.02 a
43.054	11.958 ± 1.197 a	**52.83 ± 3.456 a ***	21.216 ± 0.946 a	15.492 ± 1.735 a	21.484 ± 1 a	32.341 ± 27.711 a	51.222 ± 10.703 a	35.167 ± 16.705 a
44.998	30.733 ± 2.431 a	26.507 ± 1.446 a	24.363 ± 0.928 a	25.237 ± 1.081 a	49.036 ± 1.001 a	35.609 ± 29.4 a	47.339 ± 8.195 a	63.426 ± 13.638 a
46.995	0.38 ± 0.078 a	0.366 ± 0.04 a	**9.6 ± 0.509 a ***	0.315 ± 0.022 a	0.928 ± 0.185 a	4.572 ± 9.753 a	21.468 ± 17.341 a	3.093 ± 5.477 a
48.004	0.724 ± 0.139 a	0.597 ± 0.051 a	**15.599 ± 0.745 a ***	0.66 ± 0.024 a	1.706 ± 0.216 a	7.359 ± 15.108 a	32.77 ± 26.3 a	4.654 ± 7.948 a
49.011	8.302 ± 4.011 a	2.959 ± 1.203 a	314.259 ± 129.406 a	4.045 ± 0.163 a	101.948 ± 17.028 a	634.38 ± 1387.185 a	2747.29 ± 2248.65 a	364.65 ± 683.445 a
142.936	0.009 ± 0.002 a	0.003 ± 0.001 a	0.031 ± 0.004 a	0.031 ± 0.002 a	0.007 ± 0.006 a	0.019 ± 0.024 a	0.039 ± 0.02 a	0.014 ± 0.007 a

Headspace VOC analysis was carried out by proton transfer reaction-time of flight-mass spectrometry (PTR-ToF-MS) analysis for *Lysobacter antibioticus* DSM 2044^T, *L. capsici* DSM 19286^T, *L. enzymogenes* DSM 2043^T and *L. gummosus* DSM 6980^T grown for ten days on nutrient agar (NA) or potato dextrose agar (PDA). VOCs were identified by the mass/charge ratio (*m/z*). Mean ± standard deviation values of the headspace VOC concentration (expressed as ppbv) from four to five replicates are reported for each compound, *Lysobacter* type strain and growth media. For each compound, different letters indicate significant differences according to Kruskal-Wallis test with Bonferroni correction ($p \leq 0.05$). Only compounds with a background-corrected headspace concentration significantly emitted (Kruskal-Wallis with Bonferroni correction, $p \leq 0.05$) in *Lysobacter*-inoculated headspace vials as compared with uninoculated vials for at least one strain and growth medium are reported.

VOCs were grouped based on their emission profiles in: VOCs with higher emission by all *Lysobacter* type strains on PDA as compared with NA (Cluster 1), VOCs with higher emission by some *Lysobacter* type strains on PDA as compared with NA (Cluster 2), VOCs with higher emission by all *Lysobacter* type strains on NA as compared with PDA (Cluster 3), VOCs with higher emission by some *Lysobacter* type strains on NA as compared with PDA (Cluster 4), VOCs with different (Cluster 5) or consistent (Cluster 6) emission by *Lysobacter* type strains on both growth media.

Asterisks in bold (*) indicate VOC emission values associated to non-zero coefficients of the least absolute shrinkage and selection operator (LASSO) model calculated for the growth media prediction (column LASSO) and *Lysobacter* type strain prediction on PDA (columns Potato dextrose agar) and NA (columns Nutrient agar). Non-zero coefficients specify VOCs that can be used to predict the growth media and the *Lysobacter* type strain, respectively.