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Discrimination of plant pathogenic bacteria using microbial volatile organic compounds (mVOCs) emitted from decaying vegetables

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Abstract

The odors of five types of vegetables (potato, cabbage, broccoli, onion, and Welsh onion) exhibiting rot symptoms caused by seven bacterial pathogens (*Pectobacterium carotovorum* subsp. *carotovorum*, *Erwinia persicina*, *Pseudomonas marginalis* pv. *marginalis*, *Pseudomonas viridiflava*, *Xanthomonas campestris* pv. *campestris*, *Burkholderia gladioli*, and *Burkholderia cepacia*) were analyzed using gas chromatography-mass spectrometry (GC-MS). A total of 39 compounds were detected across these samples, with each vegetable-pathogen combination exhibiting a distinct profile of microbial volatile organic compounds (mVOCs). These findings suggest that, in principle, phytopathogens can be discriminated based on olfactory information derived from their metabolites.

Full Text

Vegetables infected by plant pathogenic bacteria sometimes rot and emit characteristic odors. The smells of decaying vegetables vary depending on the causal pathogens. For example, the distinctive odor of soft rot disease enables farmers and researchers to distinguish it from other rot diseases, even when the symptoms are similar. The odors are composed of volatile substances derived not only from microbial metabolism but also from their host plants. Volatile substances produced by bacteria, fungi, and molds during metabolism are referred to as microbial volatile organic compounds (mVOCs), which are generated as by-products of both primary and secondary metabolism (Wang et al 2016). More than 1,000 mVOCs have been described (Audrain et al 2015; Kemmler et al 2025), including hydrocarbons, alcohols, acids, aldehydes, ketones, esters, sulfur-containing organic compounds, and others (Bos et al 2013). The purpose of bacterial production of mVOCs is considered to be the expression of pathogenicity and/or competition with other microorganisms (Bennet et al 2012; Schulz and Dickschat 2007; Schulz-Bohm et al 2017).

Numerous studies have focused on differences in mVOCs biosynthesis to discriminate among microbial species in medical, food, livestock, and architectural fields (Boer et al 2019; Cui et al 2022; Gilchrist et al 2013; Jünger et al 2012; Park 2003; Takeuchi et al 2013; Timm et al 2018; Wang et al 2016; Weiss 2017). In contrast, mVOCs research involving plant pathogenic bacteria remains limited. Weise et al (2012) reported that the volatile organic compounds (VOCs) produced by *Xanthomonas campestris* pv. *vesicatoria* inhibit the growth of *Rhizoctonia solani*. Almeida et al (2023) reported that the VOCs produced by *Serratia* spp. and *Achromobacter* sp. strains promote the growth of rice inducing metabolic changes. For rotten vegetables, Vikram et al (2005) analyzed the volatiles from onion inoculated with fungal pathogens and *Erwinia carotovora* subsp. *carotovora*, and Blasioli et al (2013) analyzed the volatile compounds from potatoes inoculated with *Ralstonia solanacearum* and *Clavibacter michiganensis* subsp.

sepedonicus. These studies provide insights into mVOCs associated with particular plant species and pathogenic bacteria.

To our knowledge, no comparative studies have chemically analyzed mVOCs associated with multiple plant pathogenic bacteria within the same host plant species. However, simple odor observations of decaying vegetables suggest that different pathogens infecting the same host may release distinct blends of mVOCs. For example, rot disease of onion caused by *Burkholderia cepacia* complex bacteria is associated with a vinegar-like odor (Burkholder 1950), scale rot by *Burkholderia gladioli* pv. *alliicola* with a sour smell (Lee et al 2005), and soft rot by *Pectobacterium carotovorum* subsp. *carotovorum* with a foul smell (Schwartz and Mohan 1995). If such odors are sufficiently specific to discriminate among plant pathogenic bacteria, rapid and practical diagnostic technologies for numerous samples will become feasible. The present study provides fundamental information toward the development of such future diagnostic technologies.

We analyzed rotten odors of representative spoilage-prone vegetables after harvest by gas chromatography-mass spectrometry (GC-MS) using potato tubers, cabbage leaves, flower buds of broccoli, onion bulbs, and pseudostem of Welsh onion, inoculated with pathogenic bacteria. Preparation of rotten vegetables was done as follows; after surface sterilization using 70% ethanol followed by sufficient air drying, vegetable materials are cut into one square centimeter sections with a sterilized knife, then 2 ± 0.1g of sections were placed into 40 ml EPA (United States Environmental Protection Agency) vials class2000 (LabLab Company Co., Ltd.). As the causal agent of rot diseases, we used seven well-known and wide-host-range bacterial species; *P. carotovorum* subsp. *carotovorum* (Pcc, TS20-127, Tsuji et al 2025), *Erwinia persicina* (Ep, TS22-125, Accession No. LC921183 and LC921184), *Pseudomonas marginalis* pv. *marginalis* (Pmar, MAFF301674), *Pseudomonas viridiflava* (Pvir, O-2, Tsuji and Fuji 2021, only on broccoli), *Xanthomonas campestris* pv. *campestris* (Xcc, MAFF106692), *B. gladioli* (Bgla, SUPP593, Sotokawa and Takikawa 2004), *B. cepacia* (Bcc, TS17-JN07, Tsuji and Kadota 2020). Detailed information on MAFF strains is available in the database of NARO Genebank (https://www.gene.affrc.go.jp/databases-micro_pl_diseases.php). Bacterial strains were cultured on potato-peptone-glucose agar (Nishiyama and Ezuka 1977) for 24 h at 28 °C, then suspended in sterilized distilled water (SDW) at approximately 10^8 cfu/ml and inoculated with their respective host plant, with the exception of potato. SDW was used as a negative control (NC). 100 µl of bacterial suspension or SDW was poured into each vial, then vegetable sections were stabbed several times using a sterilized bamboo skewer (12 cm) to promote bacterial infection (Fig. 1). The vials were incubated for 48 h at 28 °C and subsequently used for mVOCs analyses.

The mVOCs emitted from vegetables were collected by static headspace method with the technique of solid-phase micro extraction (SPME). A SPME fiber coated with 50/30 µm

DVB/CAR/PDMS (Supelco®, PA, USA) was used. A new fiber was conditioned according to the manufacturer's instructions, and the fiber was heated at 270 °C for 20 min immediately before each use. The heating process was performed using a Fiber Conditioner (GL Sciences Inc., Tokyo, Japan). The conditioned SPME fiber was then inserted into the vial and exposed to the headspace for 20 min in an incubator maintained at 28 °C (Fig. 2a).

Qualitative analysis of mVOCs were performed on a GCMS-QP2010 system (Shimadzu Co., Ltd., Kyoto, Japan) equipped with a fused silica capillary column DB-5MS (30 m length, 0.32 mm i.d., and 0.25 µm film thickness; Agilent Technologies Inc., WI, USA). The system was operated using GCMSsolution ver. 4.45 (Shimadzu Co., Ltd.). The SPME fiber was thermally desorbed in an injection port at 250 °C for 1 min in the splitless mode (Fig. 2b). The chromatographic conditions were as follows; helium was used as a carrier gas and a head pressure of 50 kPa (a flow rate of 2.65 mL/min at 40 °C); the GC oven was held at 40 °C for 2 min after injection, and increased to 230 °C at a rate of 5 °C /min and then to 300 °C at a rate of 25 °C /min, the temperature was held at 300 °C for 4 min. The column was directly coupled to a quadrupole mass spectrometer operated in electron ionization mode at 70 eV, with an ion source temperature of 200 °C and an interface temperature of 310 °C. Mass spectra were collected at a scan rate of 1111 amu/s from m/z 29 to 350, with a monitoring time is from 2.5 to 40 minutes. Compounds were tentatively identified by comparing the mass spectrometry data to those in the NIST/EPA/NIH spectral database (1998 edition for CLASS software, Shimadzu Co., Ltd.) using a similarity index (SI%) and subsequently confirmed with the linear retention index (LRI) of published data (NIST Chemistry WebBook, SRD 69, https://webbook.nist.gov/chemistry/).

A total of 39 compounds were identified in the present study. These compounds are numbered and listed in Table 1. Although Table 1 includes VOCs derived from vegetables in NC, we refer to all detected compounds as mVOCs in this context to avoid confusion. Total ion chromatograms of the mVOCs from vegetable samples are shown in Fig. 3. It should be noted that SPME fiber exhibits compound selectivity; therefore, quantitative comparisons among different compounds were not performed. The presence or absence of mVOCs in each sample are summarized in Table 2.

On potato (Fig. 3a), Pcc and Ep caused strong soft rot and showed similar chromatographic patterns. Pcc uniquely showed No. 7 (1-Butanol, 3-methyl-, acetate), whereas Ep alone showed a notable peak of No. 19 (Ethanone, 1-(2-pyridinyl)-) which has been described as having a popcorn-like odor. Both Pcc and Ep showed No. 25 (Phenylethyl Alcohol), which was absent in Pmar, Xcc, and Bgla. Pmar was characterized by the presence of No. 22 (1-Undecene) and No. 24 (2-Nonanol). Although Xcc and Bgla showed no species-specific peaks under the present analytical conditions, their mVOCs profiles were distinct from those of the other species.

On cabbage (Fig. 3b), Pcc, Pmar, and Xcc caused severe rot symptoms accompanied by marked dehydration. Pcc was characterized by the presence of esters, including No. 7 (1-Butanol, 3-methyl-, acetate) and No.18 (Acetic acid, hexyl ester). Ep caused weak water-soaked rot and released only a few non-species-specific compounds. Pmar was characterized by sulfur-containing compounds, such as No. 8 (Allyl isothiocyanate), No. 12 (Isobutyl isothiocyanate), and No. 14 (1-Butene, 4-isothiocyanato-). Xcc uniquely showed No.27 (Benzene, 1-ethenyl-4-methoxy-), which has been reported as an aggregation pheromone in locusts (Guo et al 2020).

On broccoli (Fig. 3c), Pcc and Pmar caused severe rot, whereas Ep, Xcc and Pvir caused weak water-soaked rot on the base of flower buds. Pcc and Pmar were characterized by the production of esters; No. 7(1-Butanol, 3-methyl-, acetate) and No. 23 (Butanoic acid, 3-methyl-, 3-methylbutyl ester) for Pcc, and No. 1 (Butanoic acid, ethyl ester), No. 2 (Acetic acid, butyl ester), No. 30 (Benzenepropanoic acid, methyl ester), No. 34 (Benzenepropanoic acid, ethyl ester), and a notable peak of No. 15 (Butanoic acid, butyl ester) for Pmar. In contrast, Ep, Xcc, and Pvir emitted different blends of mVOCs, although none of these compounds were species-specific.

On onion (Fig. 3d) and Welsh onion (Fig. 3e), Pcc, Bcc, and Bgla caused severe soft rot, while Pmar caused water-soaked rot, maintaining the shape of vegetable sections. The mVOCs profiles differed markedly depending on the combinations of plant and pathogen species (Table 2). However, Pcc and Pmar consistently released species-specific compounds in both onion and Welsh onion, namely No. 35 (1-Butanol, 3-methyl-, benzoate) and No. 22 (1-Undecene), respectively. Qualitative differences were also observed in the mVOCs profiles between Bcc and Bgla; specifically, No.17 (Hexanoic acid, ethyl ester) in onion, No. 21 (2-Nonanone) and No. 32 (2-Undecanol) in Welsh onion. The presence of No. 22 (1-Undecene) was characteristic in Pmar, same as on potato, cabbage and broccoli.

From the results obtained from GC-MS analysis, the seven bacterial species examined (Pcc, Ep, Pmar, Pvir, Xcc, Bcc, and Bgla) exhibited distinctive mVOCs profiles on each of vegetables tested (potato, cabbage, broccoli, onion, and Welsh onion). Although the composition of individual compounds varied depending on the vegetable used and disease symptoms, the overall diversity and structural characteristics of the mVOCs profiles were sufficiently distinct to allow odor-based discrimination of bacterial species tested. In the present study, we primarily focused on qualitative differences in mVOCs profiles, such as the presence or absence of clearly detectable marker compounds. Similarly, other key compounds may also be present but not fully considered in the present analysis, because the compounds with a short elution time (LRI<ca.777 with DB-5MS) were not detected. Furthermore, incorporation of quantitative information about the relative abundance ratios among these mVOCs components may provide additional information for discerning bacterial species.

The bacterial strains tested exhibited species- or strain-specific peaks in their mVOCs profiles. As described above, Pcc was characterized by the production of esters including No. 7 (1-Butanol, 3-methyl-, acetate) on potato, cabbage and broccoli, No. 18 (Acetic acid, hexyl ester) on cabbage, and No. 23 (Butanoic acid, 3-methyl-, 3-methylbutyl ester) on broccoli. Similarly, Pmar uniquely produced other ester compounds, such as No. 34 (Benzenepropanoic acid, ethyl ester) and No. 35 (1-Butanol, 3-methyl-, ethyl ester) on broccoli, onion, and Welsh onion. These results suggest that the repertoires of ester compounds provide an important cue to discern bacterial species. The production of ester volatiles by bacteria has also been reported in several human pathogenic species, including *Escherichia coli*, *Staphylococcus aureus*, *Pseudomonas aeruginosa* and others (Bos et al 2013). In plant pathogenic bacteria, Blasioli et al (2013) reported an ethyl ester from *R. solanacearum* and *C. michiganensis* subsp. *sepedonicus*.

We also identified additional compounds that strongly contributed to species- or strain-specific discrimination. In potato, Ep was characterized by No. 19 (Ethanone, 1-(2-pyridinyl)-) which was not detected in other bacterial species tested. Across all vegetables examined, the alkene compound No. 22 (1-Undecene) was consistently detected in Pmar and Pvir, but not in Xcc, Bcc, and Bgla which are former pseudomonads. The production of 1-Undecene was previously reported in *Ps. aeruginosa* (Bos et al 2013; Prakash et al 2021), *Pseudomonas fluorescens* (Dupont et al 2023), *Pseudomonas putida* (Sheoran et al 2015). These results suggest 1-Undecene to serve as a reliable indicator for distinguishing members of the genus *Pseudomonas*.

A single bacterial strain exhibited different mVOCs profiles on different vegetables, suggesting that host-specific metabolic substrates strongly influence volatile production. Additionally, difference in rot symptoms may also affect the resulting mVOCs profiles. For example, on onion and Welsh onion, Pcc, Bcc and Bgla caused severe rot symptoms and showed notable peaks of sulfur-containing compounds (No. 6, 11, 20, and 33), but not in Pmar which caused water-soaked rot. When bacterial inoculum was not pathogenic on a vegetable, such as Bgla on potato, mVOCs detection was markedly reduced, likely due to limited bacterial growth and metabolic activity. These results highlight the complex interplay among bacterial metabolism, biochemical composition of host tissue, and disease progression in shaping mVOCs profiles.

In the present study, comparisons of mVOCs profiles from five types of rotten vegetables enabled discrimination among bacterial species tested, providing sufficient specificity to differentiate them. These results suggest the potential for the use of mVOCs as a diagnostic tool for plant pathogenic bacteria in the future. In contrast, the present study suggested that the use of a uniform and standardized culture medium may be advantageous for the purpose of taxonomic discrimination, given the inherent variability of fresh vegetable tissues. While conventional methods of bacterial characterization evaluate

individual metabolic properties in the liquid phase, mVOCs represent integrated metabolic outputs expressed in the gaseous phase. The application of odor-based discrimination using culture media therefore remains an important topic for future research.

Declarations

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Conflict of interest

The authors declare that they have no conflict of interest.

Ethical approval

This article does not contain any studies with human participants or animals.

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Tables

Table 1 Identified compounds from all vegetable samples.

Peak No.	Compounds [1]	LRI[2]	SI%[3]
Alkane			
16	Decane	998	91
29	Dodecane	1196	93
Alkene			
22	1-Undecene	1089	94
Alcohol			
4	3-Hexen-1-ol	843	94
5	1-Hexanol	862	92
24	2-Nonanol	1099	94
25	Phenylethyl Alcohol	1103	94
32	2-Undecanol	1304	93
38	2-Tridecanol	1505	93
Ester			
1	Butanoic acid, ethyl ester	797	93
2	Acetic acid, butyl ester	805	95
7	1-Butanol, 3-methyl-, acetate	871	94
15	Butanoic acid, butyl ester	986	94
17	Hexanoic acid, ethyl ester	1003	93
18	Acetic acid, hexyl ester	1010	91
23	Butanoic acid, 3-methyl-, 3-methylbutyl ester	1095	94
30	Benzenepropanoic acid, methyl ester	1254	92
34	Benzenepropanoic acid, ethyl ester	1326	95
35	1-Butanol, 3-methyl-, benzoate	1430	95
Ketone			
9	2-Heptanone	885	91
21	2-Nonanone	1078	95
31	2-Undecanone	1287	94
37	2-Tridecanone	1489	95
36	3(2H)-Furanone, 2-hexyl-5-methyl-	1437	92
39	3(2H)-Furanone, 5-methyl-2-octyl-	1644	94
Nitrogen-Containing Compounds			
3	Pentanenitrile, 4-methyl-	824	96
10	Hexanenitrile, 5-methyl-	928	90
19	Ethanone, 1-(2-pyridinyl)-	1024	96
Sulfur-Containing Compounds			
6	Ethanethioic acid, S-propyl ester	866	96
11	Disulfide, methyl propyl	929	93
13	Dimethyl trisulfide	948	94
20	Disulfide, 1-methylethyl propyl[4]	1063	91
26	Disulfide, dipropyl	1108	92
28	Dimethyl tetrasulphide	1187	93
33	Trisulfide, dipropyl	1323	95
Isothiocyanate			
8	Allyl Isothiocyanate	871	92
12	Isobutyl isothiocyanate [4]	944	90
14	1-Butene, 4-isothiocyanato-	972	91
Anisole			
27	Benzene, 1-ethenyl-4-methoxy-	1144	90

1) Names of compounds follow NIST Chemistry WebBook (https://webbook.nist.gov/chemistry/).

2) LRI is an abbreviation for Linear retention index.

3) SI% indicates similarity index with GCMSsolution (ver.4.54, Shimadzu Co., Ltd., Japan).

4) Identification was conducted by Mass spectrum only.

Table 2 mVOCs profiles identified in the chromatograms.

	No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Potato	**NC**																+													+										
	Pcc							+		*							+					+				+				+		+						+		
	Ep									+							*			+		+				+				+		+						+		
	Pmar									+							*					+	+	+						+		+						+		
	Xcc									*							+					+								+		+								
	Bgla																+																								
Cabbege	**NC**																																							
	Pcc					+		+						+					+			*																		
	Ep													*	*																									
	Pmar								+				+	*	+							+	+									+								
	Xcc					+								+								*						+												
Broccoli	**NC**			+							+			+															+											
	Pcc			*	+			+			*			+										+					+											
	Ep			*							*			+										*					+											
	Pmar	+	+	+	*						*			+		+						+	+						+		+				+					
	Xcc			*	+						*			+															+											
	Pvir			*							*			+								+	+						+											
Onion	**NC**																										*					+					+			
	Pcc						+			*		+					*	*				*						+					+		+		+	*	+		*
	Pmar																						+				+					+						+	+		+
	Bcc						+			+		+						+			+						+					+		+				+	+		+
	Bgla						+			*		+									+						+					+		+				*	+		*
Welsh onion	**NC**																					*					+					+	+					+	+		*
	Pcc						+			*		+										*	*				+					+	+	+			+	+	+	+	+	+
	Pmar																						+				*					+						+	+	+	+
	Bcc						+			*		+							+			+	*				+					+		+				+	+	+	+
	Bgla						*			*		+							*			+	+				+					+	+	*				*	+	+	*

+, identified peak with SI% > 80%; *, weak signal of specific MS was observed, though SI% < 80%

Figures

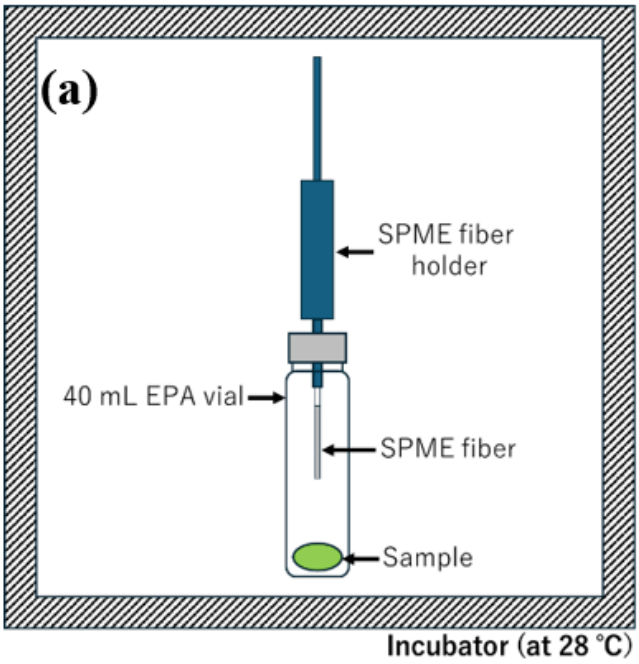
Fig. 1



Figure 1

A vegetable sample (potato) in a 40 ml EPA (United States Environmental Protection Agency) vials.

Fig. 2



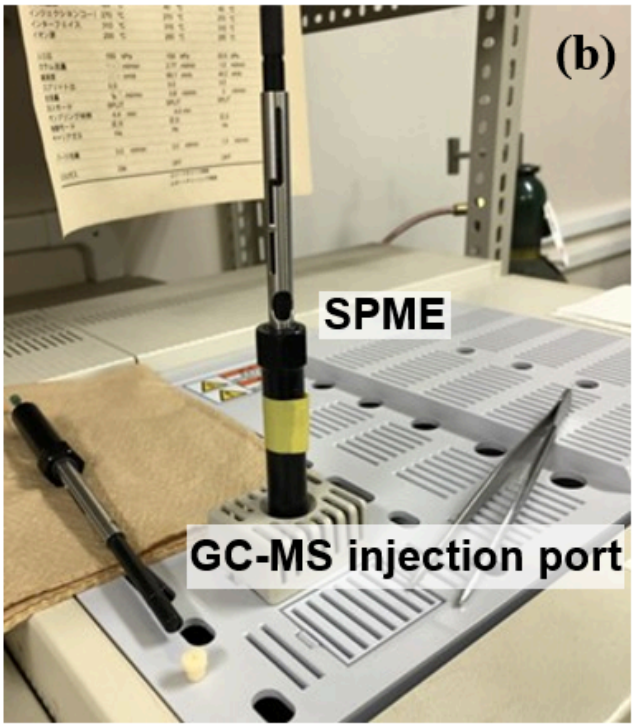


Figure 2

Analysis of mVOCs using gas chromatography-mass spectrometry (GC-MS). (a) Collection of mVOCs from vegetables by static-head space method with by solid phase micro extraction (SPME). (b) Injection of SPME fiber into the GC-MS injection port.

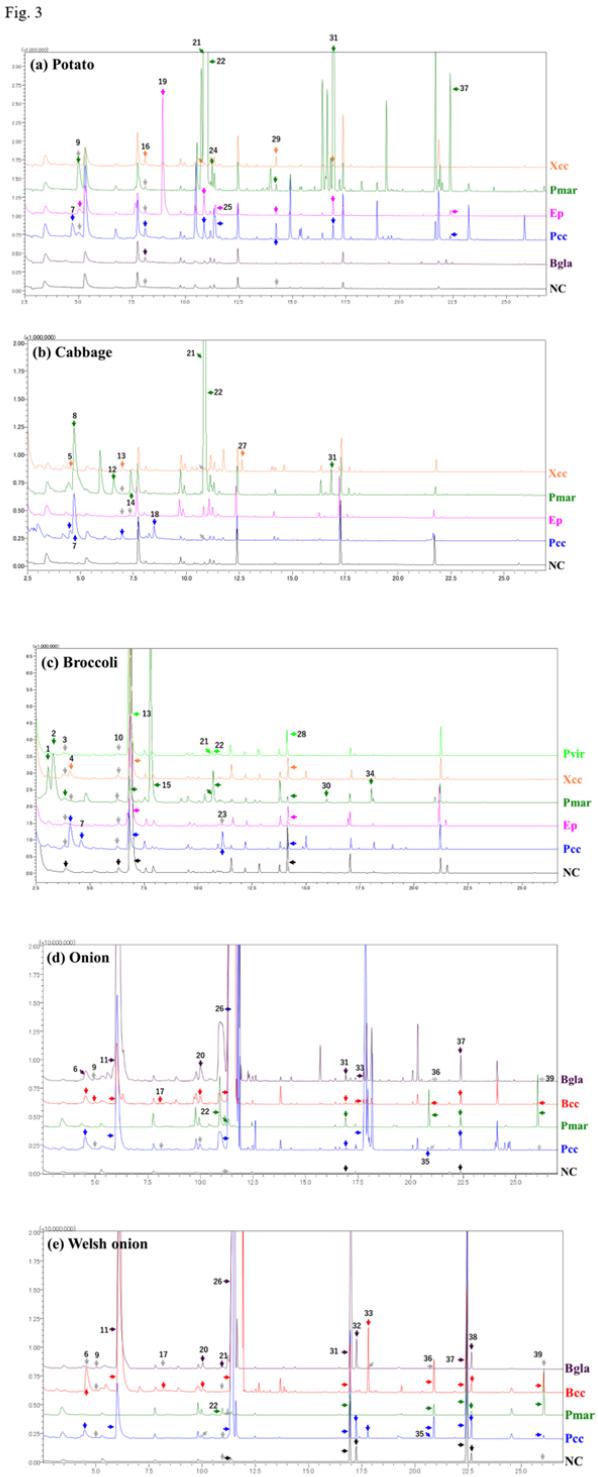


Figure 3

Total ion chromatograms of the mVOCs from vegetable samples. (a) Potato inoculated with Pcc (*Pectobacterium carotovorum* subsp. *carotovorum*), Ep (*Erwinia persicina*), Pmar (*Pseudomonas marginalis* pv. *marginalis*), Xcc (*Xanthomonas campestris* pv. *campestris*), Bgla (*Burkholderia gladioli*), and NC (negative control). (b) Cabbage inoculated with Pcc, Ep, Pmar, Xcc, and NC. (c) Broccoli inoculated with Pcc, Ep, Pmar, Pvir (*Pseudomonas*

viridiflava), Xcc, and NC. (d) Onion inoculated with Pcc, Pmar, Bcc (*Burkholderia cepacia*), Bgla, and NC. (e) Welsh onion inoculated with Pcc, Pmar, Bcc (*Burkholderia cepacia*), Bgla, and NC.