

## Effect of insect herbivory on the volatile profile of tomato cultivars

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**Abstract** An attempt was made in this study to investigate the distribution of volatile organic compounds in the aerial parts of tomato and also pre and post damage of leaves by the herbivore *Spodoptera litura* (Fab.), by capturing metabolite profiles to explore the metabolomics of the insect-plant interaction. The profile displayed an array of volatile compounds with terpenes being the major components (78%). While tomato flowers released maximum quantity (65% of total volatiles), more types of volatiles were recorded from leaves (25 types). The Principal component analysis indicated that Caryophyllene, Eugenol, Phellandrene and Sabinene as the major contributors that lead to variation in quantum and spectrum of Volatile organic compounds in tomato. The study gave an insight into the short term responses of plant signaling and a micro-ecological change that takes place in plants after herbivory. Deciphering such early response knowledge of plants would help in developing first line defense against crop damages.

**Key words:** Volatile organic compounds, terpenes, tomato, *Spodoptera litura*

### Introduction

Plant-Insect interactions are complex in nature, with a large number of volatile organic compounds (VOC's) channelized in communication networks. The VOC's emanating from different plant parts have multiple and functional interaction at tissue, leaf surface, ecosystem and atmospheric levels. These organic compounds are characterized by volatility, aroma, flavor and toxicity and are involved in defense, plant-to-plant communication and pollinator attraction (Pichersky and Gershenzon, 2002). The VOC's can be either constitutive (synthesized in plants continuously) or inducible (synthesized and released only after damage). A specific group of VOC's called herbivore induced plant volatiles (HIPVs) are emitted from the plant after the herbivore inflicts damage and play different roles as stated above.

The HIPVs play a significant role in plant-arthropods interactions (Arimura *et al.*, 2005). They act either directly by deterring oviposition by pest insects (Kessler and Baldwin, 2001), or indirectly, by attracting natural enemies of herbivores (Dicke and Sabelis, 1988). This has been demonstrated in lima bean (Takabayashi and Dicke, 1996), maize (Turlings *et al.*, 1998), cotton (Loughrin *et al.*, 1995); and Brussel sprouts (Geervliet *et al.*, 1996). The HIPVs differ in the quantity released per unit of plant biomass and also in the composition of volatile blend. The composition differs from species to species of plants and within species, even at cultivar levels. It also depends on the inducing herbivores (Colette *et al.*, 2007) and the plants environment.

Tomato (*Lycopersicon esculentum* Mill.), a solanaceous plant, releases a diverse blend of volatiles from its stem, leaves, flowers and berry, throughout its life time (Chris *et al.*, 2007).

These volatile compounds belong to different classes of volatiles and suggested to have unique role in the plant defense against insect herbivores. However, specific roles of each compound are being understood and established. In this study, an attempt was made to analyze and estimate the VOCs from both un-induced (stem, leaves, flowers and berry) and herbivore induced (leaves) tomato plants raised organically. It is an effort to know the ecological relevance of individual compounds of the complex HIPV mixture in tomato and further to advocate the techniques of genetic engineering of terpenoid metabolism to generate transgenic plants that constitutively emit these volatiles and attract crop defenders to tomato.

### Material and methods

The studies were conducted during 2008 using tomato plants raised in the green house. The tomato seedlings of three ruling cultivars (All Rounder, Lakshmi and Shaktiman) were raised in coco-peat based substrate in multicavity trays and was transferred to earthen pots containing 2:1:1 ratio of red soil, sand and vermicompost. The plants were organically maintained in the green house (average temperature 28° C/20° C (day/night) till fruiting and different plant parts were used for volatiles extraction.

Third instar larvae of *S. litura* were starved for 12 hours and released to feed on the experimental plants @ 2 larvae per plants. The larvae were allowed to feed on leaves until they inflicted damage of 5mm<sup>2</sup> /per larva and then removed. After the 4 and 6 hrs of undisturbed incubation period, the leaf samples were harvested for volatile extraction.

Volatiles were extracted from plant samples using 60 ml of Dichloromethane (HPLC grade) through simultaneous

distillation process (Fragoulis *et al.*, 2002) using Likens-Nickerson's apparatus. Twenty grams of plant tissue (leaf, stem, flower and berries separately) was taken in 120 ml of Milli-Q water. The extraction was performed for a period of 4 hr with continuous ice-cold water circulation in condensers. Extract was concentrated to 4 ml using a Buchi rotavapour system at water bath temperature of  $25\pm 1^\circ\text{C}$  and vacuum pressure of 500 mbar. The concentrated samples were analyzed by Gas Chromatography-Mass Spectrometer system (Shimadzu QPS 2010). Samples were injected in 1  $\mu\text{l}$  aliquot with in split injector (1:4) held at  $250^\circ\text{C}$ . Following injection, performed with a transfer line temperature of  $280^\circ\text{C}$ , ion source temperature of  $200^\circ\text{C}$ , ionization energy of 70 eV with a scan range of 50 to 400 atomic mass units. All standard chemicals of ~99% pure GC grade (R)-(-)- $\alpha$ -Phellandrene [Fluka], p-Cymene [Fluka], (-)-Carvone [Fluka], (R)-(+)-Limonene [Fluka], (-)-trans-Caryophyllene [Fluka], Methyl Jasmonate [Sigma Aldrich], Eugenol [Aldrich], Hexadecanoic acid [Fluka], 1-Octanol [Spectrochem] and Methyl Salicylate [Acros] obtained commercially, were used in GC-MS analysis for the quantification of the volatiles of plant samples. The VOCs were identified on the basis of retention time and mass spectral comparison with standard volatile compounds. The similarity searches were performed in National Institute of Standards and Technology and Wiley Libraries. The amount of each volatiles was calculated, based on linear calibration curve (log amount v log abundance) obtained by subjecting serially diluted solutions of standard synthetic compounds and internal standard to GC-MS analysis. Carl Pearson-Principle Component Analysis was performed for 14 volatiles which include monoterpenes, sesquiterpenes and few other volatiles to have an idea of volatiles that would contribute more towards the variation among the cultivars.

## Results and discussion

The spectrum of volatile compounds detected from different parts of tomato, across cultivars is tabulated in table 1. Similarly the profile obtained after 4 and 6 hours of insect herbivory is presented in table 2.

The VOCs from aerial parts of tomato plant by GC-MS revealed a spectrum of terpenes, benzenoids, alcohols and fatty acid derivatives. The different ranges of volatile compounds were identified in plant parts like stem, leaves, flowers and berry (Table 1). The total quantity of volatiles secreted by flowers, across classes of compounds and tomato cultivars was considerably high (65.76% of total volatiles) followed by leaves (24.75%) and berries (5.54%). The spectrum of volatiles detected was wide in leaves (25 compounds) compared to flower (17), stem (14) and berries (9). While terpenes were prominent in flowers, benzenoids and fatty acid derivatives were the major in the leaves and berries, respectively. Terpenes constituted the major portion of the VOCs. Among them, the monoterpenes

were more abundant and diverse. While sabinene, limonene and terpinene were prominent among monoterpenes, linalool is conspicuous by being a VOC in all plant parts. In sesquiterpenes only caryophyllene and  $\alpha$ -caryophyllene were in detectable quantities in flowers and leaves. The volatile blend also comprised of few benzenoids, fatty acid derivatives, alcohols and others. Eugenol, Methyl salicylate (benzenoids) and Hexadecanoic acid (fatty acid derivatives) were specific among them.

The metabolite composition was different between cultivars also. The quantum and types of volatiles released was more in Shaktiman hybrid of tomato compared to All Rounder and Lakshmi suggesting that the volatile blend can vary even at the cultivar level. The polypagous herbivore insect *S. litura* was made to damage tomato leaves and the HIPVs were analyzed. The total volatiles increased after 4 hrs while it tended towards the initial level after 6 hrs of herbivore induction (Fig 1). The trend remained same for many volatiles except for benzenoids where in the quantity decreased after 4 hrs and shoot-up later.

The correlation matrix analysis showed that 0 hr treatment is more correlated to 6 hr induction treatment than to 4 hr (Table 3). The values further indicate that control and 6 hr are less variant in state, than 4 hr where a change in volatiles emission has occurred, driving it towards un-correlation among the treatments. The relationship here thus suggests that the quantum as well as distribution of volatiles in tomato probably vary considerably immediately after the herbivore damage, but become normal by 6 hours of post damage. However, the situation may be really different as there could be continuous herbivore damage and continuous release of volatiles making the situation complex. Principal Component Analysis (PCA) done on mean values of 14 volatiles showed that two principal components (F1 and F2) account for a total of 87.77 per cent variance across treatments. It also conclusively indicated that the four volatiles (Fig. 2) viz., Caryophyllene (Cary), Eugenol (Eug), Phellandrene (Phel) and Sabinene (Sab) were major contributors among treatments that lead to variation in quantum and spectrum of VOCs in tomato.

The monoterpenes and sesquiterpenes because of their low-molecular-weight, lipophilic nature and high vapor pressures at ordinary temperatures, can convey signals over long distances in crop environment. In our study sabinene, caryophyllene, phellandrene and eugenol were present in relatively higher amounts in both un-induced and induced conditions of leaf samples substantiating their previously identified roles in attracting some of the pest species such as lepidopterans (Batista-Pereira *et al.*, 2006). Earlier studies have also suggested that certain volatiles emitted by corn and cotton (*i.e.*, nerolidol and caryophyllene) could detrimentally and directly target the herbivores (Ted *et al.*, 1995).

Table 1. Volatile profile from different parts of tomato plants under normal condition

VOC's	Stem				Flower				Berry				Leaves			
	A	L	S	Avr	A	L	S	Avr	A	L	S	Avr	A	L	S	Avr
Monoterpenes																
α-Pinene	0.087	0	0	0.029	2.682	0.207	0.759	1.216	0	0	0	0.000	0.251	0	0.055	0.102
Myrcene	0.042	0.039	0	0.027	0.464	0.106	0.191	0.254	0	0	0	0.000	0.107	0.051	0.066	0.075
Cymene	0	0	0	0.000	0	0	0.653	0.218	0	0	0	0.000	0	0	0	0.000
Terpinene	0	0.096	0.076	0.057	1.552	2.358	6.964	3.625	0	0	0	0.000	0	0.196	0.399	0.198
Limonene	0.144	0.051	0.051	0.082	5.676	0.998	1.924	2.866	0	0	0	0.000	0.529	0.102	0.137	0.256
Phellandrene	0.071	0	0	0.024	0.521	0.197	0.115	0.278	0	0	0	0.000	0.108	0.043	0.045	0.065
Sabinene	0.938	0.14	0.179	0.419	5.847	7.674	22.349	11.957	0	0	0	0.000	0	0.596	1.048	0.548
Ocimene	0	0	0	0.000	0	0	0.086	0.029	0	0	0	0.000	0	0	0	0.000
α-Terpinolene	0	0	0	0.000	0.179	0	0.657	0.279	0	0	0	0.000	0	0.122	0.399	0.174
Linalool	0.213	0	0	0.071	1.769	0.229	0.429	0.809	0.261	0.043	0.045	0.116	0.885	0	0.552	0.479
Terpineol	0	0	0	0.000	0.377	0	0.362	0.246	0.041	0.014	0.038	0.031	0.304	0	0.155	0.153
Diterpene																
Phytol	0	0	0	0.000	0	0	0	0	0	0	0	0.000	0	0.504	0.428	0.311
Sesquiterpenes																
Caryophyllene	0	0	0	0.000	1.932	0.868	1.911	1.570	0	0	0	0.000	0.629	1.104	2.913	1.549
α-Caryophyllene	0	0	0	0.000	0	0.162	0.601	0.254	0	0	0	0.000	0.272	0.275	0.79	0.446
Total terpenes	1.495	0.326	0.306	0.709	20.999	12.799	37.001	23.600	0.302	0.057	0.083	0.147	3.085	2.993	6.987	4.355
Benzenoids																
Methyl salicylate	1.251	0.117	0.219	0.529	1.041	0.47	0.364	0.625	0.051	0.026	0.03	0.036	0.137	0.139	0.104	0.127
Eugenol	0	0	0	0.000	0	0	0	0.000	0	0	0	0.000	8.292	2.005	2.083	4.127
Phenyl ethyl	0	0	0	0.000	0	0	0	0.000	0.076	0	0	0.025	0.184	0	0	0.061
Sub total	1.251	0.117	0.219	0.529	1.041	0.47	0.364	0.625	0.127	0.026	0.03	0.061	8.613	2.144	2.187	4.315
Fatty acid derivatives																
Hexadecanoic acid	0	0.253	0.182	0.145	0	0	0	0.000	2.791	0	2.051	1.614	0.199	0.217	0.439	0.285
Octanoic acid	0	0	0	0.000	0	0	0	0.000	0	0	0	0.000	0	0	0.059	0.020
Decanoic acid	0	0	0	0.000	0	0	0	0.000	0.046	0.018	0	0.021	0	0	0	0.000
Sub total	0	0.253	0.182	0.145	0	0	0	0.000	2.837	0.018	2.051	1.635	0.199	0.217	0.498	0.305
Alcohols																
4-Heptanol	0	0.016	0	0.005	0	0	0	0.000	0	0	0	0.000	0	0.037	0	0.012
1-Nonanol	0	0.033	0	0.011	0	0	0	0.000	0	0	0	0.000	0	0	0	0.000
4-Octanol	0	0	0	0.000	0	0	0.124	0.041	0	0	0.01	0.003	0	0	0.039	0.013
4-Dodecanol	0	0.03	0	0.010	0	0	0	0.000	0	0	0	0.000	0	0	0	0.000
3-Hexen-1-ol	0	0	0	0.000	0	0	0	0.000	0.116	0.235	0.119	0.157	0	0	0.056	0.019
Sub total	0	0.079	0	0.026	0	0	0.124	0.041	0.116	0.235	0.129	0.160	0	0.037	0.095	0.044
Others																
1-Octyne	0	0	0	0.000	0	0	0	0.000	0	0	0	0.000	0	0.202	0	0.067
Cyclohexane, bromo	0	0.081	0	0.027	0	0.219	0	0.073	0	0	0	0.000	0	0.11	0	0.037
Hexylene glycol	0	0.084	0	0.028	0	0.065	0	0.022	0	0	0	0.000	0	0.066	0	0.022
2-Undecanone	0	0	0	0.000	0	0	0	0.000	0	0.143	0	0.048	0	0.066	0	0.022
Sub total	0	0.165	0	0.055	0	0.284	0	0.095	0	0.143	0	0.048	0	0.444	0	0.148
Total	2.746	0.94	0.707	1.464	22.04	13.553	37.489	24.361	3.382	0.479	2.293	2.051	11.897	5.835	9.767	9.166

Data are expressed as mean (N = 3) in ppm quantities, All Rounder (A), Lakshmi (L) and Shaktiman(S), 0 = not detected, Avr = Average.

Table 2. Volatile profile from leaves of tomato upon herbivore induction

Volatile profile	Leaves (Un-Induced)				Leaves (Induced- Post 4 Hours)				Leaves (Induced- Post 6 Hours)			
	A	L	S	Avr	A	L	S	Avr	A	L	S	Avr
<b>Monoterpenes</b>												
á-Pinene	0.251	0	0.055	0.102	0.256	0	0	0.085	0	0	0	0.000
Myrcene	0.107	0.051	0.066	0.075	0.354	0.051	0.042	0.149	0	0.052	0.054	0.035
Cymene	0	0	0	0.000	0	0	0	0.000	0	0	0	0.000
Terpinene	0	0.196	0.399	0.198	0.151	0.155	0	0.102	1.656	0.179	0	0.612
Limonene	0.529	0.102	0.137	0.256	1.123	0.08	0.091	0.431	0.258	0.121	0.09	0.156
Phellandrene	0.108	0.043	0.045	0.065	5.542	0.127	0.044	1.904	6.442	0.118	0.045	2.202
Sabinene	0	0.596	1.048	0.548	0	0.411	0.587	0.333	0	0.401	0.594	0.332
Ocimene	0	0	0	0.000	0	0	0	0.000	0	0	0	0.000
á-Terpinolene	0	0.122	0.399	0.174	0	0	0	0.000	0.098	0	0	0.033
Linalool	0.885	0	0.552	0.479	0.313	0	0.146	0.153	0.375	0	0.143	0.173
Terpineol	0.304	0	0.155	0.153	0.051	0	0	0.017	0	0	0	0.000
<b>Diterpene</b>												
Phytol	0	0.504	0.428	0.311	0	0.361	0.246	0.202	0	0.329	0.09	0.140
<b>Sesquiterpenes</b>												
Caryophyllene	0.629	1.104	2.913	1.549	5.895	0.609	0.814	2.439	0.632	0.744	0.828	0.735
á-Caryophyllene	0.272	0.275	0.79	0.446	1.375	0.161	0.198	0.578	0.328	0.186	0.217	0.244
Sub total	3.085	2.993	6.987	4.355	15.06	1.955	2.168	6.394	9.789	2.13	2.061	4.660
<b>Benzenoids</b>												
Methyl salicylate	0.137	0.139	0.104	0.127	0.253	0.122	0	0.125	0.366	0.11	0.093	0.190
Eugenol	8.292	2.005	2.083	4.127	3.982	0.508	3.138	2.543	8.335	2.635	1.494	4.155
Phenyl ethyl alcohol	0.184	0	0	0.061	0	0	0	0.000	0.171	0	0	0.057
Sub total	8.613	2.144	2.187	4.315	4.235	0.63	3.138	2.668	8.872	2.745	1.587	4.401
<b>Fatty acid derivatives</b>												
Hexadecanoic acid	0.199	0.217	0.439	0.285	3.045	0.272	0.302	1.206	1.157	0.217	0.171	0.515
Octanoic acid	0	0	0.059	0.020	0	0	0	0.000	0	0	0	0.000
Decanoic acid	0	0	0	0.000	0.076	0	0	0.025	0	0	0	0.000
Sub total	0.199	0.217	0.498	0.305	3.121	0.272	0.302	1.232	1.157	0.217	0.171	0.515
<b>Alcohols</b>												
4-Heptanol	0	0.037	0	0.012	0	0	0	0.000	0	0	0	0.000
1-Nonanol	0	0	0	0.000	0	0	0	0.000	0	0	0	0.000
4-Octanol	0	0	0.039	0.013	0	0	0	0.000	0	0	0	0.000
4-Dodecanol	0	0	0	0.000	0	0	0	0.000	0	0	0	0.000
3-Hexen-1-ol	0	0	0.056	0.019	0.431	0	0	0.144	0	0	0	0.000
Sub total	0	0.037	0.095	0.044	0.431	0	0	0.144	0	0	0	0.000
<b>Others</b>												
1-Octyne	0	0.202	0	0.067	0	0	0	0.000	0	0	0	0.000
Cyclohexane, bromo	0	0.11	0	0.037	0	0	0	0.000	0	0	0	0.000
Hexylene glycol	0	0.066	0	0.022	0	0	0	0.000	0	0	0	0.000
2-Undecanone	0	0.066	0	0.022	0	0	0	0.000	0	0	0	0.000
Sub total	0	0.444	0	0.148	0	0	0	0.000	0	0	0	0.000
Total	11.897	5.835	9.767	9.166	22.847	2.857	5.608	10.437	19.818	5.092	3.819	9.576

Data are expressed as mean (N = 3) in ppm quantities, (A)All Rounder, (L) Lakshmi (S) Shaktiman, 0 - not detected, Avr -Average.

Larvae of the lepidopteron *S. frugiperda* use volatile terpenes released by the host plants upon wounding to locate them (Jonathan and Natalia., 2007). Their emissions from the plants, along with other major volatile components, serve as attractive odoriferous call for predators and parasitoids of herbivores. Enhanced emission of linalool (nerolidol) through genetic engineering and the significance preference of the predatory mites to the volatiles emitted by transgenic plants have been demonstrated in *Arabidopsis* (Iris *et al.*, 2005). Any such effort to incorporate the mechanism of linalool over expression in crops like tomato and other vegetables could benefit the crops to overcome the damage by few dreaded insect pests. It would help the plants in calling the natural enemies of these pests upon herbivory or damage.

There is an intricate genetic network regulating the plant defense mechanisms overlapping the window of reproductive events in a plant system. These volatile blends emitted from different plant parts points to distinct signaling cascades in plant herbivore resistance. Hence, naturally occurring perfect

blend and amounts of plant volatiles provide umpteen possibilities of generating pest resistant crops. A better understanding of the physiological and biochemical mechanisms behind this phenomena, as well as ecological studies on similar more naturally evolved systems, may help to fully grasp the significance of the chemical signals emitted by plants in response to herbivory.

The secondary metabolite or volatile organic compounds in tomato can assume significance in IPM either as pest deterrents or as chemical cues to attract natural enemies of the pests. Though still to be researched and established, a mechanism to ascertain and control their release from the plants will have long term impact on the plant protection strategies of pesticide abused crops like tomato. This study would be an initial step towards generating eco-friendly strategies in pest management based on plant chemical ecology.

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Table 3. Correlation matrix of relationships pre and post herbivory by *Spodoptera* on tomato plants

Sl.No.Variables	A-0	A-4	A-6	L-0	L-4	L-6	S-0	S-4	S-6
1 A-0	1	0.385	0.751*	0.84*	0.438	0.966*	0.522	0.957*	0.839*
2 A-4	0.385	1	0.665*	0.525	0.547*	0.466	0.655*	0.456	0.531
3 A-6	0.751*	0.665 *	1	0.585*	0.301	0.713*	0.32	0.705*	0.591*
4 L-0	0.84*	0.525	0.585*	1	0.834*	0.937*	0.858*	0.95*	0.969*
5 L-4	0.438	0.547*	0.301	0.834*	1	0.637*	0.89*	0.663*	0.796*
6 L-6	0.966*	0.466	0.713*	0.937*	0.637*	1	0.686*	0.991*	0.934*
7 S-0	0.522	0.655*	0.32	0.858*	0.89*	0.686*	1	0.701*	0.859*
8 S-4	0.957*	0.456	0.705*	0.95*	0.663*	0.991*	0.701*	1	0.949*
9 S-6	0.839*	0.531	0.591*	0.969*	0.796*	0.934*	0.859*	0.949*	1

\* Values are significantly different from 0 with a significance level  $\alpha=0.05$  (A) All Rounder, (L) Lakshmi (S) Shaktiman 0, 4, 6 indicate hours post herbivory

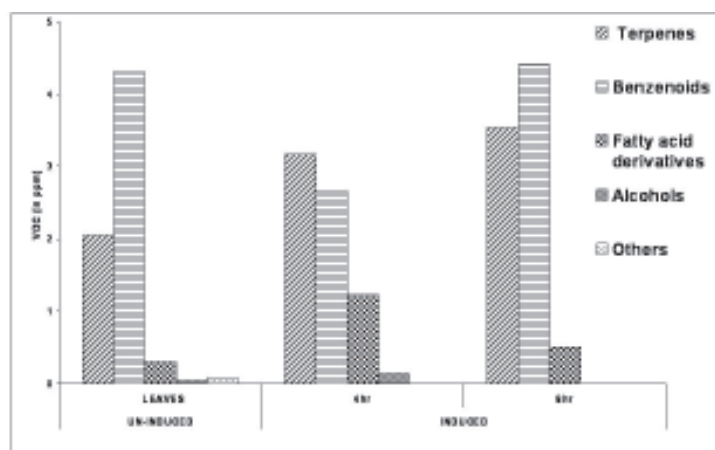


Fig 1. Comparative account of different volatile compounds from tomato leaves pre and post herbivory by *Spodoptera litura*

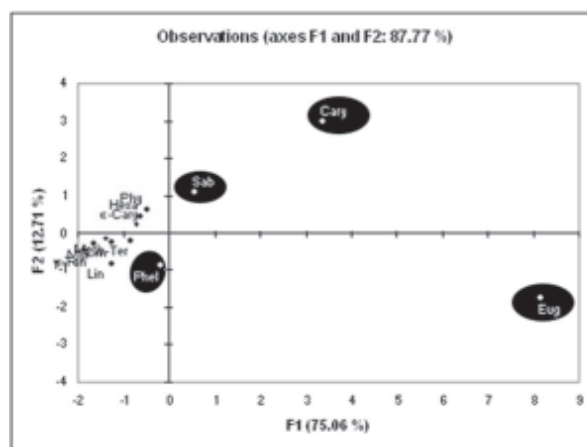


Fig 2. Volatile compounds deciding the variation among tomato cultivars and treatments



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