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Effects of potato-onion intercropping on root morphology of tomato through volatile organic compounds

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ABSTRACT

Facilitative interactions occur between the plants in intercropping systems, however, the underlying allelopathy mechanisms are poorly understood. We determined the effects of potato-onion (*Allium cepa var. agrogatum* Don.) intercrop on root morphology of tomato (*Lycopersicon esculenum* L.) through volatile organic compounds (VOCs). There were four treatments as (i) Tomato/tomato without VOCs interaction (-TT), (ii) Tomato/tomato with VOCs interaction (+TT, control), (iii) Potato-onion/tomato without VOCs interaction (-OT) and (iv) Potato-onion/tomato with VOCs interaction +(OT) in glasshouses. As compared to tomato, VOCs from potato-onion significantly increased the number of root tips total length but decreased the root diameter of tomato, however significantly the increase the tomato root length (0-0.5 mm mean diameter). These results indicated that the tomato root morphology has influenced by aboveground secreted VOCs from neighboring plants in potato-onion intercropping system.

Key words: *Allium cepa var. agrogatum*, *Lycopersicon esculenum*, plant interaction, potato-onion, root morphology, tomato, VOCs

INTRODUCTION

Intercropping is cheap synergistic to growth and reduces the use of chemicals and pesticides (20,48). The intercropping in more than 79 % studies reduces the disease severity caused by bacteria, fungi and viruses as than monocropping (4). Therefore, intercropping seems to be a promising strategy to overcome the soil borne diseases, improve plant growth, development and increase the productivity (6,21,29,43).

Volatile organic compounds (VOCs) are very important in mediating the intra and interspecific interactions among all organisms in the ecosystem (28,33,36). There studies on plant VOCs has gained great attention in last decade (13,15,17,35). VOCs from plants mediates the multiple co-occurring interactions, making them a medium for plant communication (5,9). They can affect the neighboring plants through allelopathy (10,19) and plants can sense/feel the VOCs released by neighboring plants to activate their own defense response and improve their competitive abilities (2). VOCs can influence the

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expression of genes involved in various growth regulating hormones (auxins and cytokinins) thereby affecting the belowground traits (8,31). Silva (36) found that VOCs from fresh and dry leaves of *Heterothalamus psiadioides* Less and *Baccharis patens* Baker shrubs had allelopathic effects on the root elongation of lettuce and onion, respectively. These studies provide evidence of VOCs-mediated governance of neighbor plant growth. However, most of these studies were conducted under laboratory conditions, and the concentrations of VOCs were not always enough to affect the neighboring plants under natural field conditions (3). Therefore, it is not clear, whether the reported VOCs effects would occur in neighboring plants under natural field conditions.

The growth and morphological characteristics of plant roots are the result of their interactions with environment. Root length is the most important parameter to describe the root capacity for absorbance of water and nutrients from soil (12,14,25,39). Fine roots play a vital role in root system, as they show high physiological activity during nutrients and water uptake (30,34,43). Research has revealed that intercropping could change the neighbour plant root morphology and helps the root growth (40), however, precise mechanism of how VOCs from neighbour plant influence the root architecture is still unknown.

Tomato (*Solanum lycopersicum* L.), is commonly continuously mono-cropped in greenhouse. The continuous monocropping of single species results in sickness reducing the crop yield and quality (49). However, numerous studies have reported that diversified cropping systems promote the plant growth, which are important in sustainable agriculture (22). Previous studies have found that potato-onion (*Allium cepa var. agrogatum* Don.) intercropping can improves the root metabolism, overall plant biomass, growth and production of tomato (11,44). However, how VOCs from potato-onion influenced the tomato root architecture during intercropping is still unknown. Since the interaction (i.e. competition) between experimental plants and other plants could affect the nature and secretion rate of VOCs to cause error, in the study we developed a well-controlled experimental structure and elucidated the effects of potato-onion VOCs on root morphology of tomato in greenhouse. The reverse types of interactions. Tomato/tomato with and without VOCs interaction, and Potato-onion/tomato with and without VOCs interaction.

MATERIALS AND METHODS

The experiment was conducted from April to July 2019 in greenhouse, Horticultural Station, Northeast Agricultural University, Harbin, China (45°41' N, 126°37' E). The soil type was sandy loam, [NH_4^+-N 15.25 mg·kg^{-1}; NO_3^-N 193.17 mg·kg^{-1}; available P 453.26 mg·kg^{-1}; available K 227.64 mg·kg^{-1}; organic matter 35.84 g·kg^{-1}; pH 7.46 (1:2.5, *w/v*); EC 0.411mS·cm^{-1} (1:2.5, *w/v*).] The tomato variety 'Dongnong 708' was provided by the Tomato Breeding Centre our University. The potato-onion variety 'Suihua', a native variety with allelopathy potential, was provided by Vegetable Physiological Ecology Laboratory (Harbin, China). To avoid the effects of damage-related VOCs, only visibly undamaged plants were used.

Tomato cv. ‘Dongnong708’ seeds were treated with hot water (55 ºC) and germinated in plastic basket using a gauze (Fig. 1). Briefly, seeds were placed inside layers of wet gauze and basket was placed with wet gauze in dark at 28 ℃. Tomato seedling with two cotyledons was planted in pots (8 × 8 cm) containing 100 g soil. After 34 days (4- true leaves stage) the plants were transplanted in bigger pots (18 cm dia × 22 cm depth) contained 4 kg soil, for further growth. The seedlings were maintained in the phytotron (12/12 h light/dark cycle, 30/17 ºC day/night temperature). The potato-onion cv. Suihua was stored at 4 ℃ before planting.

Figure 1. Tomato seeds treated with hot water (55 ºC) and germinated in basket with wet gauze in dark at 28 ºC.

Steam distillation

Fresh potato-onion leaves were collected 23 d after sowing, washed with water to remove dirt, chopped, dried in the shade and extracted by steam distillation for 5 h. The distilled oil was extracted thrice with analytically pure ethyl acetate. It was dehydrated overnight to remove the moisture by adding anhydrous sodium sulfate and concentrated in rotary evaporator at 25 °C. The volatile solution was filtered with 0.22 µm filter membrane to remove ethyl acetate and to obtain the original volatiles (46). The determination of VOC was then done by GC-MS.

GC-MS Conditions

Five ml volatiles were dried with nitrogen and dissolved in 1 ml of acetonitrile. The solution was filtered with 0.22 μm filter paper. The volatiles were chemically analysed in GC-MS system (Tqs8000, Thermo Inc., USA). The injection volume was 1 µL. The GC-MS conditions were initial temperature 50 ºC for 5 min, temperature increased up to 240 ºC for 12 min, used column was HP-5 MS capillary column (60 m × 0.25 mm× 0.25 μm), injection port 250 ºC, ion source 200 ℃, helium carrier gas, flow rate (1.5 mL/min), EI mode (70 eV), and mass scan range of 35~355AMU. The unknown compounds were identified by computer retrieval using NIST98 mass spectral database.

Exposure of plants to VOCs and pot experiment

Exposure to VOCs from another plant was done in a cage called 'Two-Chamber Cage Structure' (Fig 2) designed by Ninkovic (30). The two-chamber cage, consisted of clear glass and separated into two parts as inducing chamber (IC) and responding chamber (RC) (each chamber was 60 cm long, 30 cm wide and 50 cm high). There were two types of separations: (a) Complete separation without VOCs interaction and (b) Incomplete separation with VOCs interaction. In "b" separation, IC and RC chambers were connected by a 5 cm diameter hole in the middle glass. Air was entered into IC chamber and then it passed through connecting hole to RC chamber.

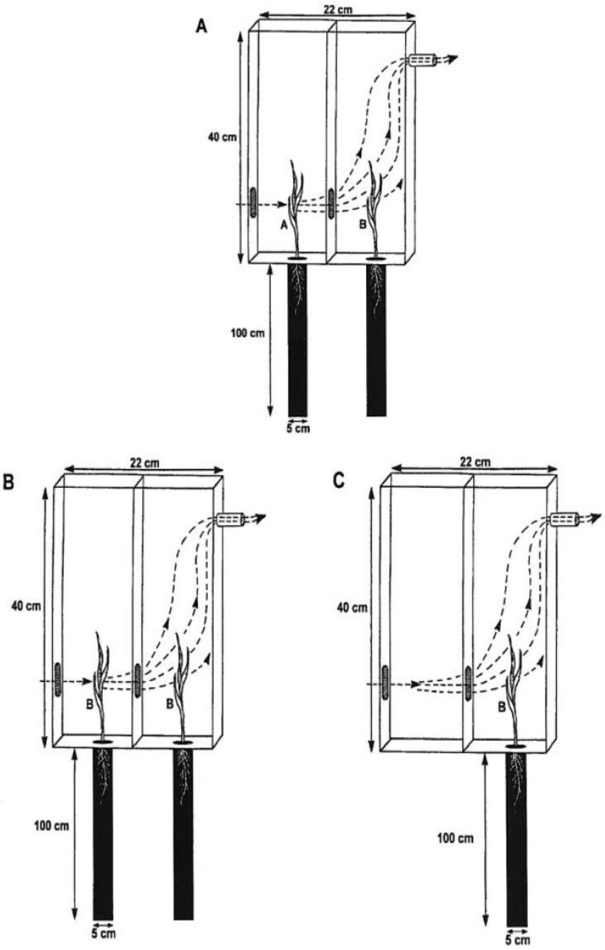

Figure 2. Twin-Chamber Cages System used to study the effects of volatiles of one plant on another plant. (A) The Recipient plant B was exposed to volatiles emitted from Donor plant A. (B) Plant B was exposed to volatiles from the same cultivar. (C) Control (Plant B was not exposed to plant volatiles). Source: Ninkovic (30).

There were 4- experimental treatments: (i) Tomato/tomato without VOCs interaction (-TT), (ii) Tomato/tomato with VOCs interaction (+TT) (as control), (iii) Potato-onion/tomato without VOCs interaction (-OT), and (iv) Potato-onion/tomato with VOCs interaction (+OT). In (i) and (ii) treatments, one tomato seedling was planted per chamber, i.e. 2 seedlings in both chambers (i.e. IC and RC) of cage. While in (iii) and (iv) treatments, one tomato seedling was planted only in RC chamber of the cage and 5-potato-onion sprouted bulbs (approximately growth: 23.5 cm dia and 15 cm height) were planted into IC chamber (I) on June 20, 2018.

The experiment was set in randomized block design with three replicates and conducted in cages. The position of glass cages was changed every 4-days to provide equal environmental conditions. Tap water was applied to maintain soil moisture (55-60% of soil water holding capacity). No pesticides or fertilizer was used and weeds were manually removed.

Measurement of tomato root morphology

The tomato root samples were collected carefully 20 d after planting by soaking roots in distilled water for 30 min, to ensure that roots were not damaged physically till all analysis were completed. Before scanning the roots, were arranged by tweezers to prevent their overlapping. The roots were scanned with Wan-sheng plant image scanner (LA-S2400). Thereafter, root samples were used for morphological parameters [mean diameter (cm), root length ($cm \cdot strain^{-1}$), root volume ($cm^3 \cdot strain^{-1}$) and total surface area ($cm^2 \cdot strain^{-1}$)]. These measurements were made at different root positions i.e. 0-0.5 mm, 0.5-2 mm, 2-3 mm, 3-5 mm and more than 5 mm. In addition, numbers of root tips were counted for root vigour parameter.

Data Analysis

The compilation of the test raw data was done using Microsoft Excel (Office 2016) software. The means of different treatments were compared based on Tukey's Honestly Significant Difference (HSD) test at 0.05 probability level in IBM SPSS Statistics 19 software. Figures of analyzed data were prepared using Ms Excel.

RESULTS AND DISCUSSION

Tomato root morphology in potato-onion intercrop system

Tomato seedlings from +OT treatment significantly increased the root length and number of root tips as compared to all other treatments, while -OT treatment had the minimum root length ($P < 0.05$) (Fig 3). The root average diameter was higher in +TT and -OT treatments, while lowest in +OT treatment ($P < 0.05$). The +OT treatment increased the root length and root tip number by 17.1 % and 38.8 % respectively, but decreased the root Diameter by 24.3 % than control (+TT). However, the tomato root volume and root surface area in +OT were 6.2 % and 12.3 % less than +TT, respectively (Fig 2). Compared with +TT, the number of root tips in -TT and -OT increased by 7.2 % and 12.0 % respectively. Contrarily, the root length, root surface area, root volume and root diameter were decreased.

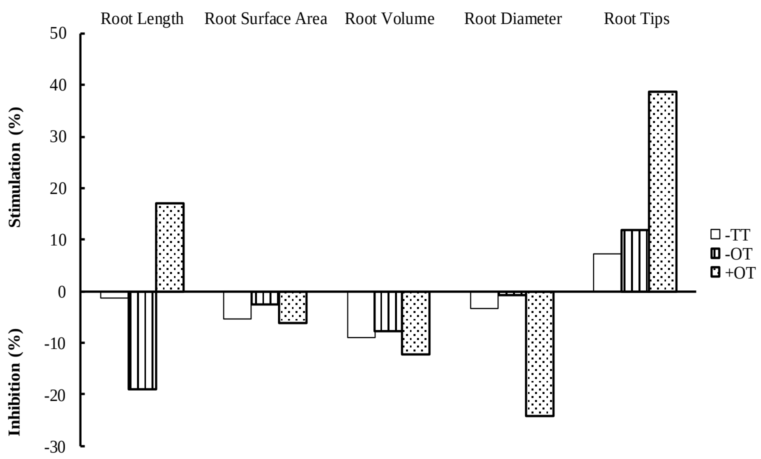

Figure 3. Effects of VOCs from potato-onion on the tomato total root length, surface area, volume, average diameter and number of tips.

Plant VOCs affects the root morphology of neighbour plant, promotes/inhibits the root growth and influences the overall plant growth and development (8). For example, Zhang *et al*. (44) reported that maize (*Zea mays* L.) intercropped with faba-bean (*Vicia faba* L.) had longer roots length and greater shoot biomass than maize monocropping. Studies have also indicated that the increased plant root length and number of tips facilitated the absorption of water resources and nutrients from the soil (12,25,41). Hong *et al.* (18) found that many plants with longer roots had higher total N uptake, as well as the root length and uptake of nutrients were positively correlated. Similarly, wheat root responses to low N availability were mainly through increased root elongation (23). These findings indicate that plant volatiles can change root morphology of neighbour plant, promotes root growth and improves the plant living situation (8). Previously, we have observed that potato-onion intercropping with tomato promotes tomato plant growth and changes its root structure through belowground interactions (11). However, the influence of aboveground VOCs from potato-onion on root morphology of tomato remained unclear. Here, we observed that VOCs from potato-onion increased the total length and number of tips while decreased the diameter of tomato roots (Fig 1). Although, VOCs from potato-onion decreased the tomato root total surface area, root volume and root diameter (Fig 2), but increased the root length. Brooker (7) reported that root length or increased root surface area provided the access to more underground resources. We found that VOCs from potato-onion promoted the tomato root elongation, increased the number of tips and root diameter, which could help tomato in facilitating nutrients absorption.

Tomato roots morphology

In +OT treatment, tomato fine roots (d ≤ 0.5mm) were 73.5 % of the total root length (Fig. 4). The diameters of different treatments for tomato root length mainly ranged from 0.00-0.50 mm and 0.50-2 mm. With the increase in root diameter, the total

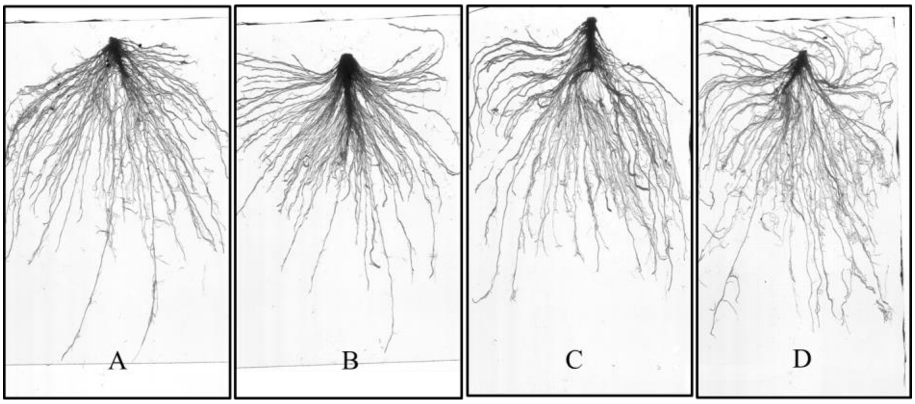

Figure 4. Effect of VOCs from potato-onion on root morphology of tomato. (A): tomato/tomato without VOCs interaction (-TT). (B): tomato/tomato with VOCs interaction (+TT). (C): potato-onion/tomato without VOCs interaction (-OT). (D): potato-onion/tomato with VOCs interaction (+OT).

root length significantly decreased ($P < 0.05$). The tomato root length of +TT, -TT and -OT were 34.8 %, 37.6 % and 34.0 % less than +OT at 0.00-0.50 mm, respectively ($P < 0.05$) (Table 1). The tomato root surface of +TT, -TT and -OT were 20.0 %, 22.4 % and 23.3 % less than +OT at 0.00-0.50 mm, respectively ($P < 0.05$) (Table 1).

These results indicated that in potato-onion/tomato, the VOCs significantly increased the proportion of roots to root diameter ≤ 0.5 mm. Tomato root mostly promoted the root elongation by increasing the number of fine roots (d ≤ 0.5 mm). As compared to potato-onion volatiles, tomato VOCs had no influence on tomato root morphology in different diameter classes. Fine roots are essential for the uptake of water and nutrients by plants, which increases the absorption and utilization of nutrients and improves the overall plant health (47). It is evident that root diameter plays significant role in mycorrhizal colonization, nutrients uptake and nutrients transportation (27,42). Besides, the fine roots absorb the nutrients from a larger soil volume per unit root surface than coarse roots (45). Ma *et al*. (26) tested four plants with contrasting root morphology (maize, wheat, lentil and lupine) to explore the effects on enzyme activity. They found that the enzyme activity was 2 to 8-folds higher in thin roots (wheat) as compared to thick roots (maize).

Identification and quantification of the chemical components

The VOCs from potato-onion, obtained using laboratory hydrodistillation, were characterized by GC-MS. There were 16 main chemical components in the oils of potato-onion leaves, which were mainly organosulfur compound along with few fatty acid derivatives (Table 2). The VOCs were dominated by organosulfur compound, including 4-methyl-1.2-dithiazole-3-thione (4.96 %), 2-ethyl-3-methyltetrahydrothiazole (1.39 %), 3,5-diethyltrithiane (0.98 %), and Dipropyl disulfide (0.87 %). The most abundant chemical in fatty acid derivatives was dibutyl phthalate (0.47 %).

Table 1. Effects of VOCs from potato-onion on tomato root morphology at different diameters of roots

Root diameter (mm)	Root Parameters	-TT	+TT(Control)	-OT	+OT
(0.000mm≤d<0.500mm)	Root length (cm)	496.509 ± 78.428 b	506.841 ± 46.310 b	509.858 ± 56.173 b	683.062 ± 58.773 a
	Root surface area (cm^2)	39.742 ± 6.388 ab	40.987 ± 5.209 ab	39.285 ± 9.427 b	51.220 ± 2.781 a
	Root volume (cm^3)	0.307 ± 0.051 a	0.316 ± 0.048 a	0.295 ± 0.068 a	0.374 ± 0.013 a
(0.500mm≤d<2.000mm)	Root length (cm)	223.115 ± 37.151 a	218.612 ± 50.495 a	225.403 ± 65.486 a	212.215 ± 18.986 a
	Root surface area (cm^2)	57.772 ± 9.558 a	56.196 ± 11.932 a	60.544 ± 17.597 a	54.055 ± 5.774 a
	Root volume (cm^3)	1.373 ± 0.237 a	1.339 ± 0.257 a	1.498 ± 0.423 a	1.268 ± 0.161 a
(2.000mm≤d<3.000mm)	Root length (cm)	10.187 ± 2.064 a	10.074 ± 3.063 a	13.039 ± 2.009 a	9.061 ± 2.263 a
	Root surface area (cm^2)	8.357 ± 3.197 a	7.673 ± 2.479 a	10.020 ± 1.478 a	6.885 ± 1.686 a
	Root volume (cm^3)	0.472 ± 0.117 a	0.470 ± 0.161 a	0.621 ± 0.101 a	0.422 ± 0.089 a
(3.000mm≤d<5.000mm)	Root length (cm)	8.676 ± 0.319 ab	9.812 ± 1.503 a	10.459 ± 0.699 a	5.555 ± 1.578 b
	Root surface area (cm^2)	10.229 ± 0.451 ab	11.601 ± 1.801 a	12.490 ± 1.037 a	6.827 ± 1.961 b
	Root volume (cm^3)	0.983 ± 0.053 ab	1.116 ± 0.180 ab	1.208 ± 0.126 a	0.681 ± 0.197 b
(d ≥5.000mm)	Root length (cm)	21.936 ± 2.159 a	25.445 ± 4.178 a	21.556 ± 3.406 a	19.766 ± 2.364 a
	Root surface area (cm^2)	78.526 ± 4.782 a	88.263 ± 12.267 a	77.238 ± 6.143 a	73.847 ± 8.477 a
	Root volume (cm^3)	24.057 ± 0.711 a	26.365 ± 3.070 a	23.845 ± 1.568 a	23.609 ± 1.489 a

-TT : Tomato/tomato without VOCs interaction, +TT : Tomato/tomato with VOCs interaction, -OT : Potato-onion/tomato without VOCs interaction, +OT : Potato-onion/tomato with VOCs interaction

Different methods of collecting and separating the volatiles from potato-onion have been used and identified different components, and most of them were mainly sulfur compounds (38,39). Similarly, this study also found that the chemical components from potato-onion mainly contained organosulfur compound (diallyl disulfide, diallyl sulfide and dipropyl trisulfide), which is consistent with our previous results. In addition, we observed that the total root length and fine root length of tomato from +OT treatment were significantly higher than those of +TT treatment. Cheng *et al*. (8) demonstrated that lower concentrations (0.01-0.62 mM) of diallyl disulfide (DADS) from garlic (*Allium sativum* L.) volatiles significantly promoted the root growth of tomato seedlings. In addition, the phenols, terpenoids, esters and dibutyl phthalate in volatile compounds also affects the growth and development of recipient plants (1,17,24,32). Therefore, we speculate that some organosulfur compound in the volatiles from potato-onion, such as diallyl disulfide and diallyl sulfide, might play an important role in the growth of tomato root system.

Table 2. The abundance of VOCs emitted from potato-onion

Compounds	Molecular formula	Retention time (min)	Similarity (%)	Relative content (%)
2,4-dimethylthiophene	C_6H_8S	3.40	84.99	0.47
2-methyl-2-hexyl mercaptan	$C_7H_{16}S$	7.91	73.79	0.76
2-ethyl-3-methyltetrahydrothiazole	$C_7H_{14}S$	8.79	81.05	1.39
Dipropyl disulfide	$C_6H_{14}S_2$	11.26	89.43	0.87
1,2,4,5-tetrahydro-3,6-dithione	$C_2H_4N_4S_2$	11.64	40.58	0.67
2-mercapto-dimethyl-dihydrothiophene	$C_6H_{10}S_2$	14.05	82.40	0.48
Benzothiazole	C_7H_5NS	16.38	68.01	0.52
3-(methylthio)propylamine	$C_4H_{11}NS$	18.57	42.78	0.45
3,5-diethyltrithiane	$C_6H_{12}S_3$	21.06	72.76	0.61
Diallyl disulfide	$C_6H_{10}S_2$	21.44	58.62	0.41
Propyl propyl thiosulfonate	$C_6H_{12}S_3$	23.94	69.09	0.98
Diallyl sulfide	$C_6H_{10}S$	25.12	80.15	1.94
4-methyl 1.2-dithiazole-3-thione	$C_4H_{11}NS$	26.78	51.56	4.96
Octasiloxane	$C_{16}H_{50}O_7Si_8$	28.78	13.91	0.36
2(3H)-benzofuran	$C_{11}H_8O_2$	29.20	32.22	0.19
Dibutyl phthalate	$C_{16}H_{22}O_4$	41.40	91.65	0.47

There are variabilities in different plant VOCs, and plants express their identity by releasing VOCs. Tomato VOCs mainly contains cis-3-hexenal, hexa-nal, 3-methylbutanal and trans-2-hexenal (40), while VOCs of Allium plant are dominated by allyl polysulfides (16). This study has identified the organosulfur compounds (diallyl disulfide, diallyl sulfide and dipropyl trisulfide), and Dibutyl phthalate as the main volatile components from potato-onion. However, this study did not influence the volatile components, therefore more research is needed in future on composition of VOCs and their particular effects on neighboring plant belowground/aboveground traits to explore more of allelopathic effects of *Allium* spp.

CONCLUSIONS

The tomato seedlings from +OT treatment increased the total length of roots and diameter range: 0-0.5 mm), and the average root diameter decreased. These results were supported by our previous studies where we found that tomato intercropped with potato-onion increased the root growth and root metabolism. Our results also indicated that as compared to potato-onion VOCs, tomato VOCs had no affects on tomato root morphology. The main VOCs from potato-onion were organosulfur compounds (diallyl disulfide, diallyl sulfide and dipropyl trisulfide) and Dibutyl phthalate. However, the role of specific volatiles component from potato-onion on the tomato root needs further study.

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