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Full Length Research Paper

Allelopathy of root exudates from different resistant eggplants to *Verticillium dahliae* and the identification of allelochemicals

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Three eggplant cultivars were inoculated with *Verticillium dahliae* Kleb. to assess their resistance to Verticillium wilt. Solanum tor was resistant, "Liyuanziqie" was tolerant, and "Xi'anlvqie" susceptible. The disease incidence and disease index of Verticillium wilt and the amount of *V. dahliae* in rhizospheric soil, variation of microbial composition, the allelopathy of root exudates to mycelium growth of *V. dahliae* and the chemical substances of root exudates from eggplant cultivars with different resistance to Verticillium wilt were investigated in this experiment. The results showed that the root exudates of resistant type could not only affect the growth and development of *V. dahliae*, but also influence *V. dahliae* indirectly through regulating soil microbial community composition. This may be one of the reasons for the increase of disease resistance. However, the susceptible type exhibited an opposite trend. It was inferred that the resistant type contained some particular components, such as acohd, amide, pyranoid, fluorene, while the susceptible one comprised more types of components, that is, ketone, phenol, ester and phenolic acid.

Key words: Allelopathy, allelochemical, root exudates, eggplant, *Verticillium dahliae*, Verticillium wilt, microbial composition.

INTRODUCTION

Verticillium wilt is one of the most destructive deceases of eggplant in China, which is caused by *Verticillium dahliae* Kleb. The recent researches showed that *V. dahliae* invaded eggplant through the roots, then secreted toxin to affect the growth of eggplant or blocked the vascular bundle with the growth of mycelium. Indirectly, because of the large population of *V. dahliae*, the delicate balance of microbial population and ecological distribution of the rhizospheric microorganisms was destroyed (Zhou et al., 2010). Recently, allelopathy, the phenomenon that one plant (including microorganisms) can influence another, was found to be one of the important factors of pest and disease control (Yang and Gao, 2009; Liu et al., 2009).

Allelopathy works through releasing allelochemical to the environment. While the root exudates can act on the rhizospheric microorganism directly and then, affect the soil-borne diseases directly or indirectly (Han et al., 2006a). Studies in recent years showed that the root exudates from resistant cultivars or species usually inhibited the spore germination, mycelium growth and biomass, while the susceptible one played a role in the promotion (Yuan et al., 2002; Han et al., 2006b; Wu et al., 2010). Pan and Wu, 2007, Pan and Yao, 2008, suggested that because of the differences of the types and quantities of amino acid of the root exudates, different resistant cucumbers cultivars improved the growth or development of the fungi from rhizospheric soil and the promoting effect of susceptible cultivars were greater. It was believed that the root exudates from rootstocks and grafted eggplants inhibited the spore germination and mycelium growth of *V. dahliae* (Lian and Wang, 2009; Zhou et al., 2001, 2010). Liu (2008) tested the root exudates of eggplant grafted onto a tomato rootstock to find that the mycelium growth of *V. dahliae* was inhibited by the root exudates of grafted eggplants. In contrast, the root exudates of nongrafted eggplants enhanced the growth. And the result of gas chromatography-mass

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spectrometry analysis showed that this phenomenon should be caused by the differences of compositions in the root exudates.

Previous studies about root exudates and their effects to Verticillium wilt of eggplant almost focus on the effect of grafting (Wang et al., 2005; Lian and Wang, 2009; Liu and Zhou, 2009). While the root exudates from different resistant eggplant cultivars have not been researched, in this study, three different resistant types (resistant, tolerant, susceptible) eggplant were chosen to test their resistance to Verticillium wilt in field, the variation of microorganism and *V. dahliae* in rhizospheric soil, the allelopathy of root exudates to *V. dahliae* and their chemical substances. After comprehensive analysis of the relation of root exudates and resistance, this study tried to find out the biochemistry basis for the resistance to Verticillium wilt and provide allelopathic foundation for the development of resistant varieties.

MATERIALS AND METHODS

Plant material

Three different resistant eggplant cultivars were selected through the assessment of disease resistance of 22 main varieties eggplants to *V. dahliae*. Solanum tor was resistant types, “Liyuanziqie” was tolerant and “Xi’anlvqie” was susceptible.

Experimental design

The plant materials were planted in a plastic greenhouse of the Vegetable Crops Experimental Station at Shenyang Agricultural University during February to October, 2009. The eggplants were cultured by conventional breeding methods. When the seedlings reached the two leaves growth stage, half of them were transplanted into plastic pots (13× 13 cm) containing sterilized nursery substrates for root exudates collecting. The others were transplanted into the same containers with soil, peat and horse manure (3:2:1) for soil analysis. The eggplants were grown under general management. Each treatment had fifteen plants and was repeated twice.

Pathogen

V. dahliae isolated from pathogenic eggplant was identified by the Mycology Laboratory of College of Plant Protection, Shenyang Agricultural University. After 14 days growing at 27°C, on PDA culture medium, the colonies were put into sterile distilled water in 250 ml triangular flask for a night, with shaking. The filter liquid was adjusted to 1×10^7spores/ml with sterile distilled water, using hemocytometer.

Disease assessment

Each plant was inoculated 10 ml of the *V. dahliae* spore suspension at the 4 leaves growth stage. Plants injected with water were taken as the control for each cultivar. The disease was assessed on leaf symptoms by a wilt index 0 to 4, according to Xiao and Lin (1995). Disease incidence and disease index were evaluated every 5 days since the first appearance of the typical wilt, using the following calculations:

Disease incidence (%) = (Number of Infected Plants/Total Number of Plants) × 100%

Disease Severity Index =∑ (Rating number× number of plants with the rating)/ (Total number of plants × highest rating) ×100

Classification method of resistance type: Resistant type (R), DI≤15; moderate resistant type (MR), 15<DI≤30; tolerant type (T), 30<DI≤50; moderate susceptible (MS), 50<DI≤70; susceptible type (S), DI>70. The colonies of *V. dahliae* were isolated and analyzed using the selective medium researched by Jia and Yang (2005).

Microbial composition in rhizosphere

The soil suspension was adopted to analyze the microbial composition in rhizosphere. The Martin’s medium, beef extract peptone medium and Gause’s synthetic No. 1 medium modified were used to isolate and culture fungi, bacterium and actinomyces (Xu and Zheng, 1986). The dilution method of plate counting was used to count the numbers. Each concentration was inoculated three plates, which were three replications. All these plates were incubated at 27°C in darkness and counted according to the growth process in time.

Collection and bioassay of root exudates

The root exudates of eggplant cultivars were collected 14 days after inoculation, using the root soaking method (Wang et al., 2005). Ten plants were taken to collect root exudates for each cultivar (without inoculation) and cultured 10 h under continuous aeration. The solution was filtered and concentrated to each milliliter from 0.5 m^2 actively absorbing root areas, using the rotary evaporator under 40°C. The mycelia growth rate method was used to assay the effect of root exudates on *V. dahliae.* One milliliter root exudates was put into a plate and mixed with sterilized PDA medium (cooled to 45°C and added 0.3 ml 1% streptomycin per 100 ml). Medium mixed with one milliliter sterile distilled water was taken as control. Four plates were prepared for each treatment. After cooling completely, one *V. dahliae* agar disk in 0.6 cm diameter was put on the medium and incubated at 27°C in darkness. After 3 days incubation, the colony diameters were measured twice a plate for five days continuously. The growth of mycelia was expressed in RI (allelopathic index) value, which was defined by Williamson and Richardson (1988) as:

If T≥C, then RI = 1-C/T

If T<C, then RI = T/C-1

Where, C is the colony diameter of the control; T is the treatment. When RI>0, it indicates stimulation; if RI<0 indicates inhibition. The intensity of allelopathic effect was expressed in RI value. The RI data were processed using DPS software.

Identification of root exudates

The root exudates after concentrating were extracted with an equal volume of ether in a separate funnel for three times. The supernatants of each sample were compounded and filtered through anhydrous sodium sulfate and concentrated to the quondam concentration. The extracts were analyzed by gas chromatography-mass spectrometry (GC-MS) (6890GC/5973MSD; Agilent Co., Santa Clara, CA), using an HP-5MS capillary column (30 m × 0.32 mm, 0.25 μm film). The detail experiment methods were the same as Liu and Zhou (2009). Ether was taken as blank control to reduce the experimental error. Relative percentages of the compounds were obtained by peak area normalization method and elucidated on the standard mass spectral data.

Table 1. Resistance of different eggplant cultivars to Verticillium wilt.

Cultivar	17 day		22 day		27 day		32 day		Resistant type
	Incidence (%)	Disease index	Incidence (%)	Disease index	Incidence (%)	Disease index	Incidence (%)	Disease index	
L	10.0	10.0	50.0	23.8	60.0	41.3	80.0	71.7	S
Z	5.0	2.5	25.0	6.3	44.7	23.5	60.0	43.3	T
S.tor	0.0	0.0	0.0	0.0	4.4	4.4	8.7	6.7	R

S, Susceptible; T, tolerant; R, resistant; L, Liyuanziqie; Z, Xi'anlvqie; S.tor, Solanum tor

RESULTS

Resistance to Verticillium wilt

The outbreak of Verticillium wilt of "Liyuanziqie" was the earliest and its disease incidence and disease index were significantly higher than others (Table 1). According to the disease index 32 days after inoculation, Solanum tor was the resistant types, "Liyuanziqie" was tolerant and "Xi'anlvqie" was susceptible.

The amount of variation of the microsclerotia of *V. dahliae* was coincident with the incidence of Verticillium wilt and resistance of eggplant cultivars (Figure 1). The number of *V. dahliae* in the soil "Liyuanziqie" grown was increasing significantly during whole time while the Solanum tor had not increased so rapidly, especially in the first 14 days.

Variation of soil microorganism

The soil microorganisms were obviously influenced by the cultivar and inoculation. The population of the main microorganism of the inoculated cultivars increased from the 7 days to the 14 days and then decreased (Table 2). But compared with the control without inoculation, the numbers were reduced gradually because of the lessening of bacterium, and the change rate showed L>Z>S.tor. The quantity of fungi increased during the whole test, moreover, the increase and change rates appeared as L>Z>S.tor. The change rates of total main microorganism, bacterium actinomyces and fungi were different significantly. The B/F and A/F were S.tor>Z>L and the differences were great or remarkable.

Allelopathy to *V. dahliae*

The allelopathical effect varied with the cultivars and days after incubating (Table 3). During the investigation, the susceptible type (L) always stimulated the mycelium growth of *V. dahliae* while Z and S. tor showed inhibitory action, the effect of Z decreased (86.30%) in just 5 days, but S.tor inhibited the mycelium growth persistently.

Identification of chemicals

The chemicals of root exudates from different resistant eggplants contained hydrocarbon, ketone, ester, phenol, phenolic acid, aldehyde, alcohol, quinones and others (Table 4). These components and contents are related to the cultivars and inoculation. The amounts and varieties of ketone, ester and phenol of susceptible type (L) after inoculation, were larger than others. While the contents of ketone, ester and phenol of resistant type (S. tor) were much lower than that without inoculation, phenolic acid was only found in the root exudates from the susceptible type (L) after inoculation. Only in root exudates of tolerant type, alcohol was identified. The chemicals, dibutyl phthalate, 1,2-benzenedicarboxyli acid, bis(2-methyl-propyl) ester, 2,4-bis(1,1-dimethylethyl) phenol and 2,5-cyclohexadiene-1,4-dione, 2,6-bis(1,1-dimethylethyl) were the main components of all treatments. The contents of phenol and quinones increased in resistant cultivar, but decreased in tolerant and susceptible types, after inoculation. Pyran, amine and fluorine were specific substances of resistant cultivar (S.tor) with or without inoculation.

DISCUSSION

In this study, we found that the numbers of *V. dahliae* increased continuously, which corresponded with the incidence of Verticillium wilt in field. But the growth ratio of resistant cultivar was much lower than tolerant and susceptible types. The reasons for that were two-fold: firstly, as the result of the antibacterial experiment showed, the root exudates from resistant and tolerant cultivars inhibited the mycelium growth, but the suscep-tible one accelerated it. Secondly, resistant cultivars could adjust the number and composition of microbial community to keep the ratio of B/F, A/F higher than others. The result of GC-MS provided a biochemical basis for the mentioned phenomenon: the resistant type contained some special substances, such as amine, pyran and fluorene; while phenolic acids were only found in the root exudates from susceptible type. The kinds and

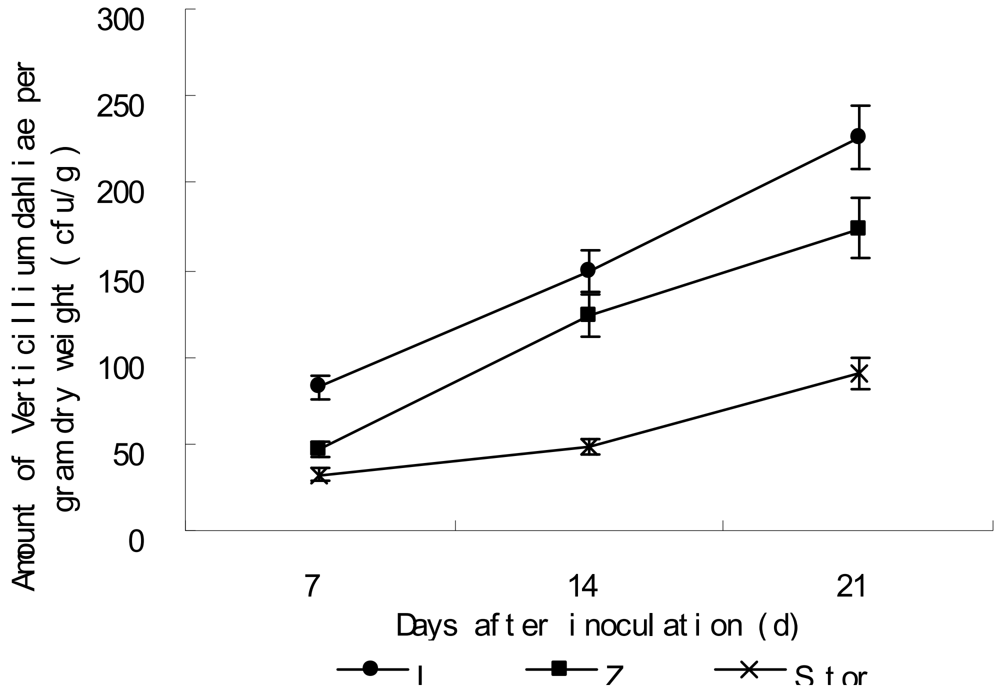

Figure 1. The amount variation of *V. dahliae* in soil of different resistant eggplants.

Table 2. Variation of main microorganism in the rhizosphere soil of different resistant eggplants after inoculation.

Day after inoculation (day)	Cultivar	Total of main microorganism /(10^5cfu·g^{-1}DM)		Bacterium (B) /(10^5cfu·g^{-1}DM)		Actinomyces (A) /(10^5cfu·g^{-1}DM)		Fungi (F) /(10^5cfu·g^{-1}DM)		B/F	A/F
		Number	Change rate (%)	Number	Change rate (%)	Number	Change rate (%)	Number	Change rate (%)		
7	L	12654.27	-21.60^{cC}	12375.10	-21.92^{cC}	264.83	-6.87^{aA}	14.34	74.78^{aA}	862.98^{cC}	18.47^{cC}
	Z	15547.66	-12.72^{bB}	15253.40	-12.97^{bB}	282.41	1.27^{bB}	11.85	47.58^{bB}	1287.21^{bB}	23.83^{bB}
	S.tor	23742.29	-4.26^{aA}	23340.21	-4.60^{aA}	391.76	20.89^{cC}	10.32	14.44^{cC}	2261.65^{aA}	37.96^{aA}
14	L	14300.05	-19.92^{cC}	14024.68	-19.76^{cC}	259.24	-29.70^{aA}	16.13	48.37^{aA}	1290.22^{cC}	23.85^{bB}
	Z	18874.17	-17.17^{bB}	18614.89	-17.41^{bB}	246.20	3.95^{bB}	13.08	29.88^{bB}	1848.55^{bB}	24.45^{bB}
	S.tor	28998.03	-7.48^{aA}	28600.02	-7.94^{aA}	387.22	45.11^{cC}	10.79	9.91^{cC}	2915.39^{aA}	39.47^{aA}
21	L	9364.62	-37.78^{cC}	9095.21	-38.11^{cC}	255.21	-25.69^{aA}	14.20	28.82^{aA}	640.51^{cC}	17.97^{cC}
	Z	15552.15	-18.56^{bB}	15281.17	-18.92^{bB}	259.78	8.45^{bB}	11.20	23.34^{bB}	1363.17^{bB}	23.17^{bB}
	S.tor	23855.82	-10.20^{aA}	23404.54	-10.81^{aA}	438.42	40.02^{cC}	12.86	6.45^{cC}	1819.95^{aA}	34.09^{aA}

Change rate is compared with the control without inoculation for each cultivar. Different small and capital letters within each column show significant differences at the levels of 0.05 and 0.01, respectively, Han et al., 2006b.

Table 3. Effect of root exudates from different resistant eggplants on mycelium growth of *V. dahliae.*

Root exudate	RI (Resistant index) value				
	4 day	5 day	6 day	7 day	8 day
L	0.0613^{aA}	0.1369^{aA}	0.0653^{aA}	0.0676^{aA}	0.0636^{aA}
Z	-0.3510^{bB}	-0.2010^{bB}	-0.1060^{bB}	-0.1003^{bB}	-0.0481^{bB}
S.tor	-0.6513^{cC}	-0.6842^{cC}	-0.6373^{cC}	-0.6487^{cC}	-0.5693^{cC}

Table 4. Relative contents of main chemical substances of the root exudates from different resistant eggplants.

Name of the chemical	Relative content (%)					
	Without inoculation			Inoculation		
	S.tor	Z	L	S.tor	Z	L
Hydrocarbon	53.17	63.16	40.01	61.66	46.64	36.44
1-Dodecene	1.48	-	-	0.63	-	-
Dodecane	1.76	-	2.24	2.72	-	1.61
Octadecane	-	4.20	0.61	-	-	-
Tetradecane	-	3.17	1.65	-	1.18	1.64
2,6,10-trimethyltetradecane	-	3.26	-	-	1.98	-
Hexadecane, 7,9-dimethyl-	2.53	5.49	5.89	-	--	-
Hexadecane	0.73	6.86	0.56	-	-	1.73
Pentadecane, 2-methyl-	0.92	-	-	-	-	-
Hexadecane, 2,6,10,14-tetramethyl-	-	-	0.79	0.88	3.84	0.63
(1R)-(+)-Trans-Pinane	-	-	0.56	-	-	-
Hexadecane, 2-methyl-	0.76	-	3.60	0.72	0.87	1.07
Octadecane, 3-methyl-	3.03	-	-	-	3.06	
2,6,10,14-Tetramethylpentadecane		-	0.65	-	-	1.03
Dodecane, 2,6,11-trimethyl-	-	-	-	1.25	-	-
Ketone	4.12	0.00	1.21	2.71	1.75	14.07
2-Acetylcyclopentanone	-	-	-	1.1	-	-
2-Methyl-4-decanone	-	-	-	-	1.16	-
4-Methyl-5-nonanone	-	-	-	-	-	0.64
4-Dodecanone	-	-	-	-	-	0.75
6-Dodecanone	-	-	-	0.66	-	1.11
5,8-Tridecadione	-	-	-	0.95	-	3.08
Benzofuran, ,3-dihydro-2-methyl-7-phenyl	2.98	-	-	-	-	-
2,6-bis(1,1-dimethylethyl)-4-ethylidene-5-cyclohexadien-1-one	-	-	-	-	-	10.36
Ester	4.76	5.15	3.62	3.88	4.53	5.46
Hexadecanoic acid, 2-hydroxy-,methyl ester	-	-	0.90	-	0.46	0.67
Ethanol,2-(dodecyloxy)-	-	5.15	-	-	-	-
Butetamate	1.93	-	-	0.65	-	-
1,2-Benzenedicarboxyli acid, bis(2-methylpropyl)ester	0.93	-	1.38	1.27	2.30	2.45
Dibutyl phthalate	1.90	-	1.34	1.96	1.77	2.34
Phenol	22.14	24.60	27.90	19.60	26.50	31.10
phenol,2,4-Bis(1,1-dimethylethyl)	22.14	24.60	27.90	19.60	26.50	31.10
Phenolic acid	0.00	0.00	0.00	0.00	0.00	1.24
3,5-Di-tert-butylbenzoic acid	-	-	-	-	-	0.49
2,4,6-Triisopropylbenzoic acid		-	-	-	-	0.75
Aldehyde	0.71	0.00	0.61	0.00	2.43	0.56
Tetradecanal	-	-	-	-	1.57	-
3,5-di-tert-Butyl-4-hydroxybenzaldehyd	0.71	-	0.61	-	0.86	0.56
Alcohol	0.00	0.00	0.00	0.00	2.58	0.00
Phytol	-	-	-	-	0.73	-
1-octano，2-butyl-	-	-	-	-	1.85	-
Quinones	1.46	1.92	0.48	0.84	1.74	0.95
2,5-Cyclohexadiene-1,4-dione,2,6-bis(1,1-dimethylethyl)	1.46	1.92	0.48	0.84	1.74	0.95
Others	13.64	5.17	26.17	11.31	13.83	10.18
Dodecane,1,1'-oxybis-	-	-	-	-	0.49	-
2(3H)-Furanone, dihydro-5-pentyl-	-	-	-	1.21	-	-
6,7-dimethoxy-2,2-dimethyl-2h-1-benzopyra;	-	-	-	3.75	-	-
Benzamide, N-decyl-	1.51	-	-	-	-	-
9H-Fluorene, 9-butyl-9-methyl-	1.48	-	-	-	-	-

amounts of ketones, ester and phenol in the root exudates from inoculated susceptible cultivar were richer than other treatments. It was inferred that the type and quantity of allelochemical in root exudates were one of the factors for differences of eggplant resistance to *V. dahliae*.

The root exudates played important roles in the occurrence and development of plant diseases, especially soil sickness. On the one hand, the exudates or some parts of them affected the growth and development of pathogen directly (Li et al., 2009; Wu et al., 2006, 2010). Wang (2010) detected the effects of root exudates of cucumber on population of *Fusarium oxysporum* f.sp. *cucumerinum* (Foc) in soil, using real-time PCR, found that root exudates from resistant cultivar shortened the survival period of Foc, but that from susceptible one prolonged its survival. In our study, the root exudates from resistant and tolerant cultivars inhibited the growth of *V. dahliae*, but the susceptible one promoted it and the effect of root exudates weakened gradually. In field, the amount of the microsclerotia of *V. dahliae* increased of all treatment, but the growth rate of susceptible type was significantly higher than others. This consisted with the outbreak of Verticillium wilt in field. That is to say, the root exudates played an important role in the occurrences of Verticillium wilt and other soil sickness.

On the other hand, the root exudation serves as an important carbon and energy source for microorganisms contained in the rhizosphere (Cheng et al., 1996; Quian et al., 1997; Yin et al., 2008, 2009; Pan and Yao, 2008). The similar conclusion was got in this study: the competition between microorganisms, caused by the infliction of *V. dahliae* spore suspension, destroyed the balance of soil microbial community structure in the rhizosphere. The size of bacterium was the smallest, but total amounts were the biggest and development stage was the shortest, so their species and quantities changed quickly with the treatment. Comparing with the controls without inoculation, the population of actinomyces of all cultivars increased, except the susceptible type. After inoculation, fungus of all cultivars grew and propagated fast and the growth rate appeared as L>Z>S.tor. All these caused to the ratios of B/F and A/F increased with the enhancing of resistance. The root exudation of resistant cultivar might be one reasons of promoting the soil in rhizosphere turned into fungi type from bacterium type to control the severity of soil sickness.

Previous studies showed that some allelochemicals of root exudates affected the growth and development of plants and microflora including organisms, in order to control soil-borne pathogens (Hu et al., 2007; Liu et al., 2009a, b; Waller et al., 1986; Ye, 2004; Zhang and Gao, 2000). This study discovered that the derivatives of methyl benzoic acid were only detected from the inoculated susceptible cultivar, at the same time, the types and amounts of ketone, ester and phenol of it were richer than others. That could partly explain the high rates of Verticillium wilt in field. The special compound (6,7-dimethoxy-2,2-dimethyl-2h-1-benzopyra), which only existed in the resistant type after inoculation, was confirmed to be allelochemical, which showed great allelopathic and synergistic effect (Kong et al., 1998, 2002). The compounds 1,2-benzenedicarboxyli acid, bis(2-methylpropyl) ester and dibutyl phthalate, which were contained in every treatments, were verified to be allelochemical (Geng et al., 2009; Ren et al., 2004). Some studies confirmed that butylated hydroxytoluene and 2,6-bis(1-methylethyl)-phenol, 2,6-bis (1,1-dimethylethyl)- phenol had allelopathic effect (Zhou, 2007; Wang et al., 2007). Whether the similar substances, 2,5-Cyclohexadiene-1,4-dione,2,6-bis(1,1-dimethylet-hyl) and 2,4-Bis(1,1-dimethylethyl)- phenol are allelochemical, deserves to be confirmed by further study. Meanwhile, further examination and validation are needed to find out the main allelochemicals and the interacting rule and mechanism among them.

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