



Full Length Article

Exogenous Application of Signaling Compounds Enhances Rice Allelopathic Potential in Rhizosphere Soil

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Abstract

In this study, allelopathic induction in rhizosphere after exogenous application of signaling compounds methyl jasmonate and methyl salicylate was evaluated. Post applications of signaling compounds to rice seedlings imposed allelopathic affect on tester plant species barnyard grass (*Echinochloa cress-galli* L.) and lettuce (*Lactuca sativa* L.). Two rice cultivars with contrasting allelopathic abilities were evaluated through rhizosphere soil method, aqueous leaf and root leachates bioassays. Rhizosphere soil of high allelopathic rice cultivar (BR-41) reduced the shoot length by 35-38% and root length by 52-53% of lettuce seedlings after methyl jasmonate and methyl salicylate application, respectively, while lower allelopathic rice cultivar (Huanjingxian) wane down the lettuce shoot length (25 and 27%) and root length 31 and 36%, respectively. The aqueous leaf and root leachates of both rice cultivars also imposed inhibition on germination and seedling growth of barnyard grass after signaling compounds treatment. Transcriptome analyses of genes responsible for momilactone biosynthesis (*OsCyC1*) were also up regulated. The relative expression of *OsCyC1* was higher over basal levels present in control plant leaves. *OsPAL* is another key gene involved in phenolic compound biosynthesis and found up regulated after signaling compounds treatments. The maximum up regulation of *OsPAL* after methyl jasmonate and methyl salicylate application was 10 and 12 times higher at 12 h, respectively as compared to control plants. Exogenous application of signaling compounds can induce allelopathic potential for effective weed control in crop plants. © 2013 Friends Science Publishers

Keywords: Allelopathy; Root exudates; Methyl jasmonate; Methyl salicylate; Rhizosphere soil

Introduction

Methyl jasmonate and methyl salicylate are important signaling compounds and have pronounced affect on plant growth and development (Smith *et al.*, 2009; Gimenez-Ibanez and Solano, 2013). These signaling molecules mediate plant defense responses through induction of secondary metabolites in plants (Reymond and Farmer, 1998; Van Wees *et al.*, 2000; Smith *et al.*, 2009). The jasmonates and salicylates function as key signal molecules in plant defense (Kessler and Baldwin, 2002). These signal molecules act as elicitors for production of plant secondary metabolites (Chen *et al.*, 2006). The jasmonate and salicylate increase expression pattern of defense related genes (Thomma *et al.*, 1998) and regulate plant secondary metabolism (Zhao *et al.*, 2005). Jasmonate can stimulate

momilactone: a major phytoalexin and possible phytotoxic agent in rice (Nojiri *et al.*, 1996), which is involved in resistance in plant species against insect herbivores (Baldwin, 1998). Jasmonate, salicylate and their methyl esters are the naturally occurring regulators of higher plants and can induce endogenous level of secondary metabolites after exogenous application (Bi *et al.*, 2007).

Weeds are important constraints in agricultural production systems (Peltzer *et al.*, 2009; Bennett *et al.*, 2011). In recent years, agricultural yield has been increased but at the cost of our environment (Tilman *et al.*, 2002; Baumgartner *et al.*, 2005). Many reports emphasized on herbicide resistance in plants through activation of specialized enzymes (Macias *et al.*, 2004; Arias *et al.*, 2005; Owen and Zelaya, 2005; Funke *et al.*, 2006; Gressel, 2009; Busi *et al.*, 2011). Allelopathy has increasingly received

attention by scientists and has played important roles in plant biodiversity and sustainable agriculture (Chung *et al.*, 2006; Zeng *et al.*, 2008). Allelopathy provides an alternative for weed management (Macias *et al.*, 2004; Macias *et al.*, 2007). Allelopathy has been considered an environmental friendly approach for weed control in rice (*Oryza sativa* L.) production (Olofsdotter *et al.*, 2002). Plants can release allelopathic compounds into the environment through root exudation, leaching by dews and rains, volatilization, or decaying plant tissue (Rice, (1984). The rice allelopathy and weed control has been the focus of research (Dilday *et al.*, 1994; Olofsdotter *et al.*, 1999; Ebana *et al.*, 2001; Khanh *et al.*, 2007; Jensen *et al.*, 2008). A number of secondary metabolites were isolated and identified as allelochemicals in rice (Chou *et al.*, 1991; Inderjit 1996; Mattice *et al.*, 1998; Seal *et al.*, 2004a, b; Kato-Noguchi *et al.*, 2007). The momilactones has shown to be constitutively secreted from the roots of rice seedlings (Kato-Noguchi and Ino, 2003) as an allelopathic agent. The genetic markers associated with allelopathic activity in rice has been identified (Ebana *et al.*, 2001; Jensen *et al.*, 2008). There are several ways to induce rice allelopathic potential such as incorporating allelopathic character into desired cultivar and through induction of physiological processes that can impose allelopathic effect. Enhancing these traits in crop plants may also increase their resistance to insects and soil microorganisms. Improving the allelopathic ability of rice through genetic engineering provides an alternative for weed management but have had limited success and no rice cultivar released yet for commercial farming. The exogenous application of signaling molecules elevate allelopathic potential and researchers are working on these lines (Bi *et al.*, 2007; Kato-Noguchi, 2011; Mahmood, 2013).

Plants attain a range of mechanisms to combat invasion of other plants. These mechanisms include pre-existing physical and chemical barriers as well as inducible defense responses that become activated upon exogenous application of signaling compounds. Allelochemicals are secreted to the rhizosphere and suppress the growth of neighboring plants (Bais *et al.*, 2004) but still there is no evidence that methyl jasmonate and methyl salicylate can induce allelopathic potential strong enough to impose inhibition in soil condition. This study was conducted to establish whether allelopathic potential of rice can be induce in the rhizosphere. For this purpose, rhizosphere soil method and expression analysis of genes responsible for biosynthesis of allelochemicals after defense compounds treatment were used to evaluate allelopathic induction.

Materials and Methods

Plant Material

Two rice (*Oryza sativa* L.) cultivars Huajingxian and BR-41 with different known allelopathic potential were used. Rice cultivar BR-41 with known allelopathic potential (Kim *et*

al., 2005) was obtained from International Rice Research Institute, Los Banos, Philippines and Huajingxian, China, a low allelopathic cultivar (Bi *et al.*, 2007) was provided by Prof. Zhi-Qiang Chen at the South China Agricultural University. Barnyard grass (*Echinochloa crus-galli* L.) seeds were collected from the rice field of South China Agriculture University, Guangzhou, China, and lettuce seeds purchased from local vegetable market of Guangzhou. Methyl jasmonate and Methyl salicylate were purchased from Sigma (St. Louis, MO, USA). TRIzol reagent, AMV reverse transcriptase, Taq polymerase, and deoxynucleotide triphosphates were purchased from TaKaRa (Shuzo Co. Ltd., Shiga, Japan). MOPS and DEPC were bought from AMRESCO (Solon, OH, USA).

Growth Conditions

Rice seeds were surface-sterilized with 1% NaClO for 30 min, washed with distilled water several times and pre-germinated in petri-dishes for 3 days on moistened filter paper. All these and further manipulations were carried out under sterilized conditions. After three days, 20 germinated seeds were transplanted in each plastic pot (20×25 cm) filled with soil. These were raised in a growth chamber for forty days at 24–26°C with 150 μM m^{-2} sec^{-1} light and a photoperiod of 12-h light/12-h darkness.

The pots were watered and fertilized with Hoagland nutrient solution every alternate day. A 5 mL each of methyl jasmonate (0.05 mM) and methyl salicylate (5 mM) were applied by brushing on rice leaves and were grown further for ten days in the growth chamber for bioassay studies.

Bioassays

Rhizosphere soil: After methyl jasmonate and methyl salicylate application on rice leaves; plants were carefully removed from the pots without disturbing the soil. Plant roots were shaken softly to separate/collect the adhering soil from the surroundings of the root, called rhizosphere soil. Collected soils from different treatments were sieved in a 1 mm mesh to remove root hair and other organic debris as much as possible. This rhizosphere soil was put into agar (5%) and cooled at 42°C. Ten mL of prepared agar along with rhizosphere soil added into multi-dish. The five lettuce seeds were placed on the agar culture media and grown in dark condition to avoid light effect on germination (Mahmood *et al.*, 2013). The lettuce seeds were also sown in non-rice rhizosphere soil as control. Three replicates were maintained for each treatment and experiment was repeated four times. Root and shoot lengths of the lettuce seedlings were measured 3rd day after their growth.

Aqueous leachates: Aqueous extracts were prepared by extracting 10 g of treated rice leaves with 100 mL of distilled water for 24 h. Extracts were filtered through filter

paper and stored at 4°C until used. Barnyard grass (*Echinochloa crus-galli*) seeds were grown on the aqueous extract of rice leaves. Root and shoot lengths of the *E. crus-galli* seedlings were determined after 7 d. Three replicates were maintained for each treatment. Experiment was repeated three times.

RNA Isolation and Quantitative Polymerase Chain Reaction

Total RNA was isolated from rice leaves after signaling molecules treatments using Trizol reagent (Invitrogen, Carlsbad, CA, USA). For real time-PCR analysis, first-strand cDNAs were synthesized from DNaseI-treated total RNA using SuperscriptII reverse transcriptase (Invitrogen) according to the manufacturer's instructions. Real time PCR was performed in an optical 96-well plate with an ABI PRISM 7500 Real-time PCR System (Applied Biosystems, Foster City, CA, USA). Each reaction contained 10 µL 2× SYBR Green Master Mix Reagent (Applied Biosystems), 1.0 µL cDNA samples and 200 nM of gene-specific primer in a final volume of 20 µL. The thermal cycle was used as follows: 95°C for 3 min; 39 cycles of 94°C for 45 sec, 58°C for 30 sec, 72°C for 15 sec and 82°C for 10 min. The degenerate primer was used for amplification of putative genes. Actin gene was used as internal control with primers. The sequences of genes specific primer were presented below (Table 1). The relative expression levels were determined.

Statistical Analysis

SAS 8.0 (SAS Institute, Cary, North Carolina) package for windows was used for statistical analysis. The data were analyzed with a one-way analysis of variance with treatment differences among means tested using Tukey test at $P \leq 0.05$.

Results

Rhizosphere Soil

Exogenous applications of methyl jasmonate and methyl salicylate to rice shoot increased inhibitory effect on neighboring plants. Rhizosphere soil of rice plants of Huajingxian and BR-41 cultivars after exogenous application of signaling compounds inhibited the lettuce shoot length as compared to untreated rice plants. In case of BR-41, 35 and 38% inhibition of lettuce shoot was recorded, while even Huajingxian imposed 25 and 27% inhibitory effect on lettuce shoots length after treatment of signaling compounds (Table 2). The inhibitory effect on lettuce root length after signaling molecules application was very obvious. BR-41 caused 52 and 53% inhibition in lettuce root length as compared to untreated rice root adhering soil, while inhibitory effect of Huajingxian was 31 and 36%, respectively as compared to non-rhizosphere soil. After application of methyl jasmonate and methyl salicylate,

rhizosphere soil (Table 2). of BR-41 reduced the germination% of lettuce plants. From these results, it's inferred that signaling compounds can increase rice root exudates secretion into rhizosphere soil that impose inhibition on lettuce seedling growth.

Leaf Leachates

Aqueous leaf leachates of both the rice cultivars (high allelopathic and low allelopathic) inhibited barnyard seedling (*Echinochloa crus-galli* L.) growth after treatment of methyl jasmonate and methyl salicylate. Aqueous leaf leachates of BR-41 wane down the shoot (31% each), root lengths (49 and 56%), germination% (13 and 17), fresh weight (36 and 39%) and dry weight (36 and 40%) of barnyard grass as compared to control. Low allelopathic rice variety (Huajingxian) also caused inhibition to barnyard grass growth after exogenous application of signaling compounds. Huajingxian reduced the shoot (28 and 30%), root lengths (46 and 47%), germination (10% each), and (35% each) and dry weight (39% each) of barnyard grass as compared to control plants (Table 3).

Root Leachates

Aqueous root leachates of both rice cultivars also imposed inhibition on barnyard grass growth but inhibitory effects are less compared to aqueous leaf leachates. Aqueous root leachates of BR-41 reduced the shoot length (23% each), root length (40% each), germination (10%), fresh weight (36 and 38%) and dry weight (36 and 40%) of barnyard grass after methyl jasmonate and methyl salicylate treatment, respectively. Low allelopathic rice cultivar also caused reduction in barnyard grass growth after signaling compound exposure. Huajingxian root leachates wane down the shoot length (17 and 18%), root length (25 and 26%), germination (3 and 7), fresh (17 and 23%) and dry weight (25 and 32%), respectively.

Expression Analysis of *OsCYC1* and *OsPAL*

Signaling compounds can activate the genes responsible for momilactone biosynthesis and phenolic compound accumulation in rice leaves (Table 4). We found that expression pattern of *OsCYC1* and *OsPAL* was dramatically up regulated when analyzed through quantitative or real time polymerase chain reaction (QRT-PCR) after methyl jasmonate and methyl salicylate treatment. Exogenous application of methyl salicylate induce the relative expression pattern of *OsCyC1* as 4, 12, 3.5 and 2 fold higher after 6, 12, 24 and 48 h, respectively as compared to control plants (Fig. 1A). Methyl jasmonate application on rice leaves also activates *OsCYC1* in the same manner. The up regulation of *OsCYC1* was 2, 14, 10 and 6 times higher after 6, 12, 24 and 48 h, respectively over the basal levels present in control leaves (Fig. 1B). The *OsPAL* is a key gene involved in phenolic compounds biosynthesis. Exogenous application of Methyl salicylate

Table 1: Sequence of the genes specific primer used for Real-Time QRT-PCR

Gene	Accession Number	Specific Primer
<i>OsCYC1</i>	AB066270	F: 5'-gaggagatagaccagcaagtgga-3' R: 5'-tgagcagtaggcgacatagca-3'
<i>OsPAL</i>	X16099	F: 5-cacaagctgaagcaccacc-3 R: 5-gagttcacgtcctggttg-3
Actin	X15865	F: 5'-ctgacggagcgtggttac-3' R: 5'-ggaaggcgggaaggagac-3'

Table 2: Effects of rhizosphere soils of two rice cultivars on seed germination and seedling growth of lettuce after methyl jasmonate (MeJA) and methyl salicylate (MeSA) application

Observations	Huanjingxian			BR-41			Non rhizosphere soil
	Control	MeJA	MeSA	Control	MeJA	MeSA	
Shoot length (cm)	3.3±0.06ab	2.3±0.09c	2.3±0.09c	3.4±0.03a	2.0±0.04d	1.9±0.10d	3.1±0.07b
Root length (cm)	1.4±0.02ab	0.9±0.05c	0.8±0.05c	1.4±0.06a	0.6±0.02d	0.6±0.01d	1.3±0.04 b
Germination (%)	100±0.0a	100±0.0 a	100±0.0 a	100±0.0 a	85±5.77 b	95±3.33ab	100±0.0 a

Data are expressed as means ±SE values (n=3) followed by the same letter are not significantly different according to Tukey test (P< 0.05)

Table 3: Effects of aqueous leaf leachates of two rice cultivars (Huanjingxian and BR-41) exposed to methyl jasmonate (MeJA) and methyl salicylate (MeSA) on seed germination and seedling growth of barnyard grass (*Echinochloa crus-galli* L.)

Observations	Huanjingxian			BR-41			Control (water)
	Control	MeJA	MeSA	Control	MeJA	MeSA	
Shoot length (cm)	6.2±0.14ab	4.8±0.23c	4.7±0.14c	5.8±0.18b	4.6±0.21c	4.6±0.20c	6.6±0.05a
Root length (cm)	3.8±0.09b	2.6±0.15c	2.6±0.14c	3.3±0.13b	2.5±0.25c	2.3±0.12c	4.9±0.32a
Germination %	97±3.33 ab	90±5.77abc	90±3.33abc	93±3.33abc	87±3.33bc	83±3.33 c	100±0.0a
Fresh weight (g)	0.39±0.01b	0.30±0.01c	0.30±0.01c	0.35±0.02b	0.30±0.01c	0.29±0.01c	0.47±0.02a
Dry weight (g)	0.04±0.004ab	0.03±0.001cd	0.03±0.001cd	0.04±0.003bc	0.03±0.005cd	0.03±0.002d	0.05±0.002a

Data are expressed as means ±SE values (n=3) followed by the same letter are not significantly different according to Tukey test (P< 0.05)

Table 4: Effects of aqueous root leachates of two rice cultivars (Huanjingxian and BR-41) exposed to methyl jasmonate (MeJA) and methyl salicylate (MeSA) on seed germination and seedling growth of barnyard grass (*Echinochloa crus-galli* L.)

Observations	Huanjingxian			BR-41			Control (water)
	Control	MeJA	MeSA	Control	MeJA	MeSA	
Shoot length (cm)	6.1±0.10b	5.5±0.28c	5.5±0.18c	5.9±0.038bc	5.2±0.15d	5.1±0.17d	6.7±0.05a
Root length (cm)	4.0±0.03b	3.6±0.12c	3.5±0.18c	3.4±0.13c	2.9±0.11d	2.8±0.18d	4.8±0.22a
Germination (%)	100±0.00a	97±3.33a	93±3.33a	100±0.00a	90±5.77a	90±5.77a	100±0.00a
Fresh weight (g)	0.42±0.01b	0.38±0.01c	0.36±0.02c	0.35±0.01c	0.30±0.02d	0.29±0.01d	0.46±0.01a
Dry weight (g)	0.05±0.002 a	0.04±0.001 b	0.03±0.001 c	0.04±0.003b	0.03±0.003 c	0.03±0.002 c	0.05±0.001a

Data are expressed as means ±SE values (n=3) followed by the same letter are not significantly different according to Tukey test (P< 0.05)

activate the expression of *OsPAL* as 4, 10, 5 and 3 fold higher after 6, 12, 24 and 48 h, respectively over the basal levels present in control leaves (Fig. 2A). After Methyl jasmonate application corresponding gene activation was 7, 12, 5 and 4 times higher at 6, 12, 24 and 48 h, respectively as compared to control rice plant leaves (Fig. 2B).

Discussion

Plants are subjected to various biotic and abiotic stresses and adapt changing climate through inducing internal mechanisms (Atkinson and Urwin, 2012). Plant chemical defense against herbivores and pathogens are inducible and regulated by both the jasmonate and salicylate signaling pathways (Thaler *et al.*, 2002). This study found that rice

phytotoxic effect on barnyard grass and lettuce seedling could be induced through methyl jasmonate and methyl salicylate. The phytotoxicity of the root exudates of rice at higher plant densities increased after treatment with methyl jasmonate and methyl salicylate at natural soil conditions evaluated through rhizosphere soil method. Aqueous extracts of both leaves and roots of methyl jasmonate and methyl salicylate treated Huanjingxian and BR-41 rice cultivars showed enhanced inhibitory effects on barnyard grass root growth. Exogenous addition of jasmonate increases the resistance of wild plants to insects in the field (Baldwin, 1998). Many studies have shown that signal compounds can induce plant defense mechanism against insect herbivores and microbial pathogens but lack of information available to demonstrate that signaling pathways are involved in allelopathy. A paper has been

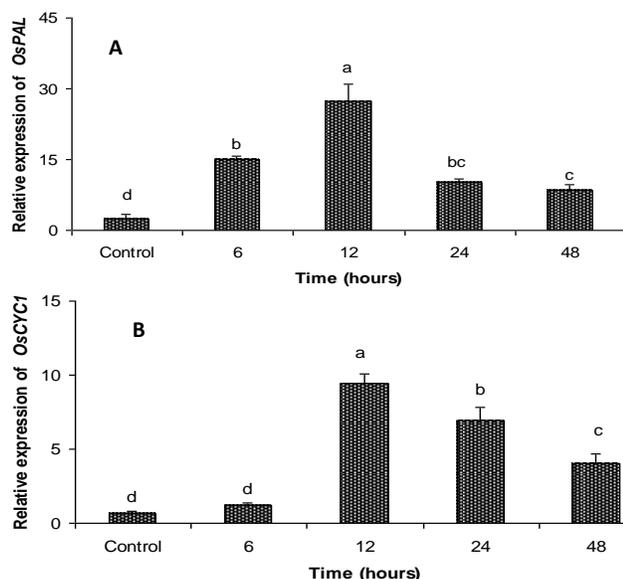


Fig. 1: Relative expression of gene transcriptome of *OsPAL* (A) and *OsCYC1* (B) of rice cultivar BR-41 at 4 leaf stage after exogenous application of methyl jasmonate. Data are expressed as means \pm SE values (n=3) followed by the same letter are not significantly different according to Tukey test ($P < 0.05$)

published by Bi *et al.* (2007) demonstrated that signaling compounds can induce rice allelopathic potential but still no evidence that emphasize on rice allelopathy in soil conditions.

This study suggests that signaling compounds up-regulate gene transcription of *OsPAL* and resulting in increased biosynthetic activities and accumulation of phenolic acids, which likely lead to enhanced phytotoxicity. We found that methyl jasmonate and methyl salicylate treated rice plants showed up-regulation of *OsCyCl*, which is a key gene for momilactone biosynthesis. The momilactone is key compounds for allelopathy of rice (Kato-Noguchi *et al.*, 2007). Exogenous application of signaling compounds up-regulate gene transcription of *OsCyCl*, resulting in increases biosynthetic activities and production of momilactone, which likely lead to enhanced allelopathic potential. The findings are ecologically significant in a sense that jasmonate and salicylate signaling pathways may control the production and release of phytotoxins (Dixon *et al.*, 2002). Thus, plants may respond to competition or stress by activating physiological mechanisms to release chemicals that interfere with a neighbor's growth (Martin *et al.*, 2003).

In crux, signaling compounds can enhance synthesis and accumulation of secondary metabolites in rice rhizosphere that resulted in rice phytotoxicity and its allelopathic potential (Metlen *et al.*, 2009). We are reporting for the first time, exposure to signaling compounds to one

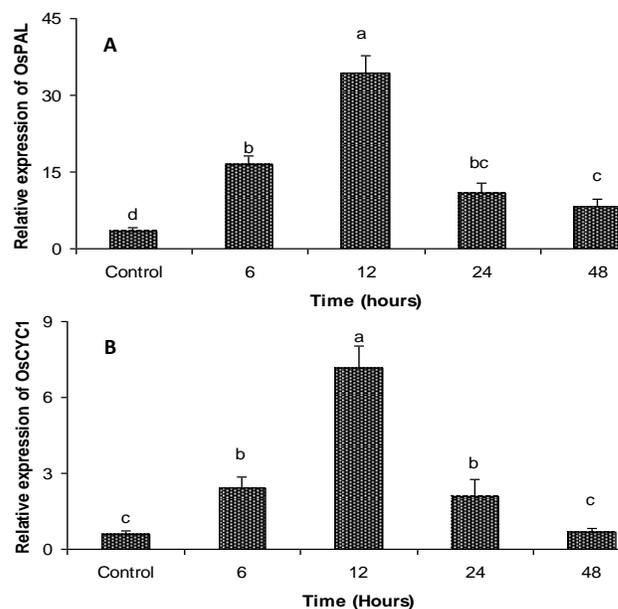


Fig. 2: Relative expression of gene transcriptome of *OsPAL* (A) and *OsCYC1* (B) after exogenous application of methyl salicylate to BR-41 rice cultivar at 4-leaf stage. Data are expressed as means \pm SE values (n=3) followed by the same letter are not significantly different according to Tukey test ($P < 0.05$)

plant species that causes inhibition on the growth of neighboring plants in natural soil conditions, although at higher plant density. Plant roots recognize and respond to the identities of their neighbors and changes in root ecology on exogenous application of methyl jasmonate and methyl salicylate may affect root neighbors.

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