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Allelochemicals Released from Rice Plants

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ABSTRACT

Rice has been extensively studied with respect to its allelopathy as part of a strategy for sustainable weed management. Rice plants possibly release allelochemicals into the neighboring environment or the rhizosphere because they inhibit the growth of several plant species when rice and these plants are grown together. A large number of compounds, such as phenolic acids, fatty acids, indoles and terpenes have been identified in rice root exudates and decomposing rice residues as putative allelochemicals which possess growth inhibitory activity against neighboring plant species. Thus, these compounds may play an important role in defense mechanism of rice in the rhizosphere for competition with invading root systems of neighboring plants. This paper summarizes the compounds released from living rice plants and decomposing rice residues, and discusses their possible involvement in rice allelopathy.

Keywords: allelopathy, growth inhibitor, momilactone B, *Oryza sativa*, phenolic acid, phytotoxity, root exudates

CONTENTS

INTRODUCTION

Allelopathy is the direct influence of an organic chemical released from one living plant on the growth and development of other plants. Allelochemicals are organic chemicals involved in allelopathy (Rice 1984; Putnam and Tang 1986; Inderjit 1996).

Rice has been extensively studied with respect to its allelopathy as part of a strategy for sustainable weed management, such as breeding allelopathic rice strains and searching for rice allelochemicals (Olofsdotter 2001, 2002a; Takeuchi *et al.* 2001). A large number of rice varieties were found to inhibit the growth of several plant species when grown together under field and/or laboratory conditions (Dilday *et al.* 1998; Kim *et al.* 1999; Olofsdotter *et al.* 1999; Azmi *et al.* 2000). These findings suggest that living rice may produce and release allelochemical(s) into the neighboring environment, thus encouraging the exploration of allelochemicals in rice.

A number of secondary metabolites, phenolic acids, phenylalkanoic acids, hydroxamic acids, fatty acids, terpenes and indoles, were identified in extracts of rice plants (Rimando and Duke 2003). These compounds are ubiquitous in plants and some of them have a growth inhibitory activity against several plant species, including weed species. It is not clear, however, whether these compounds are released from living rice plants into the neighboring environment, and act as allelochemicals in natural ecosystems. In addition, it was found that there was no significant correlation between the level of growth inhibitory substances in plants and their level in root exudates (Wu *et al.* 2001).

To date, in the trials searching for putative allelochemicals released from living rice plants, dozens of compounds were found and identified in rice root exudates and decomposing rice residues. The compounds released from living rice plants and decomposing rice residues are summarized and their possible involvement in rice allelopathy is discussed.

DOES LIVING RICE RELEASE ALLELOPATHIC SUBSTANCES?

The first observation of allelopathy in rice was made in field examinations in Arkansas, U.S.A. in which about 191 of 5,000 rice accessions inhibited the growth of *Heteranthera limosa* (Dilday *et al.* 1989). This finding led to a large field screening program. More than 16,000 rice accessions from 99 countries in the USDA-ARS germplasm collection have been screened. Of these, 412 accessions inhibited the growth of *H. limosa* and 145 accessions inhibited the growth of *Ammannia coccinea* (Dilday *et al.* 1994, 1998). In Egypt, 1,000 rice varieties were screened for suppressive ability against *Echinochloa crus-galli* and *Cyperus difformis* under field conditions, and inhibitory activity was found in more than 40 of them (Hassan *et al.* 1998). Similar attempts have been conducted in some other countries, and many rice varieties were found to inhibit the growth of several plant species (Kim and Shin 1998; Olofsdotter *et al.* 1999; Pheng *et al.* 1999). It is obscure, however, whether this inhibition was caused by only allelopathic effects be-

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Invited Review

cause competitive interference and allelopathy cannot be separated under field conditions (Fuerst and Putnam 1983; Leather and Einhellig 1998).

Plant-to-plant interference is a complex combination of competitive interference for resources such as light, nutrients and water, and allelopathic interactions (Qasem and Hill 1989; Einhellig 1996). Considering the allelopathic potential of plants, it is essential to distinguish between the effects of competitive interference and allelopathy (Fuerst and Putnam 1983; Leather and Einhellig 1986; Inderjit and Olofsdotter 1998). Thus, bioassays in allelopathy research should be designed to eliminate the effects of competitive interference from their experimental systems. Many scientists have also paid attention to test solution characteristics for bioassays in allelopathy research because the growth of roots and shoots of several plants as well as germination are inhibited by extreme pH and osmotic potential in test solutions (Wardle *et al.* 1992; Haugland and Brandsaeter 1996; Hu and Jones 1997).

Well-designed bioassays under controlled environments can evaluate the allelopathic potential of plants (Leather and Einhellig 1986; Inderjit and Olofsdotter 1998). A laboratory whole-plant bioassay for allelopathic rice screening, called "relay-seedling assay", was developed at the International Rice Research Institute in the Philippines (Navarez and Olofsdotter *et al.* 1996). This bioassay may eliminate the effects of competitive interference for resources between rice and test plants from the experimental system, and may evaluate the allelopathic potential of rice. By using this bioassay, several rice varieties were found to possess strong growth inhibitory activity. In addition, the 111 rice varieties were tested for their growth inhibitory activity under laboratory and field conditions, but the results were inconsistent (Olofsdotter *et al.* 1999).

Screenings for allelopathic rice have also been undertaken in several other laboratories. These studies show that there is a marked difference among rice varieties in growth inhibitory activity and that about 3-4% of tested rice varieties have strong allelopathic potential (Fujii 1992; Hassan *et al.* 1998; Kim *et al.* 1999; Olofsdotter *et al.* 1999; Azmi *et al.* 2000). This suggests that some living rice varieties may release allelochemical(s) into their neighboring environment.

The allelopathic potential of rice seedlings of eight cultivars was determined at an early developmental stage in Petri dishes under controlled laboratory conditions (Kato-Noguchi and Ino 2001). Three plants, alfalfa (*Medicago sativa*), cress (*Lepidium sativum*) and lettuce (*Lactuca sativa*) were chosen for the bioassay as test plants because of their known germination behaviors. According to the test solution of Weidenhamer *et al.* (1987), phosphate buffer (pH 6.0) was chosen as the test solution, which did not affect the germination and growth of cress, lettuce, alfalfa or rice, and did not cause any significant pH changes during the bioassay. In addition, no effect of osmotic potential of the test solutions in all dishes was detected on the germination and growth of these plant species.

The trial indicated that all rice cultivars tested inhibited the growth of roots, shoot and fresh weights of these test plants. However, the effectiveness of cv. 'Koshihikari' on growth inhibition was greatest among these rice cultivars and more than 60% inhibition was recorded by cv. 'Koshihikari' in all bioassays. Test plants could germinate and grow with the rice seedlings without competition for nutrients and water, because no nutrients were added in the bioassay and water was supplied regularly (Kato-Noguchi and Ino 2001). Light is also unnecessary in the developmental stages of these seedlings, since seedlings mostly withdraw nutrients from the reserve of their seeds during early developmental stages (Fuerst and Putnam 1983). Thus, during early development, rice seedlings inhibited the growth of the test plants. The inhibitory effect may not be due to competitive interference, suggesting that rice seedlings may release allelochemicals into the neighboring environment.

ALLELOPATHIC POTENTIAL OF CRUDE EXTRACTS OF RICE PLANTS

Aqueous extracts of some rice plants were found to inhibit the germination and growth of *Avena ludovicina*, *Convolvulus arvensis*, *Heteranthera limosa*, *Phalaris minor*, *Monochoria vaginalis*, cabbage (*Brassica oleracea*), wheat (*Triticum aestivum*), oats (*Avena sativa*), berseem (*Trifolium alexandrinum*), lentil (*Lens culinaris*), lettuce and rice under laboratory conditions (Chou *et al.* 1991; Tamak *et al.* 1994a; 1994b; Kawaguchi *et al.* 1997; Das and Goswami 2001; Ebana *et al.* 2001). Aqueous methanol extracts of rice plants were also found to inhibit the germination and growth of lettuce and *Echinochloa crus-galli* (Ahn and Chung 2000; Chung *et al.* 2001; Mattice *et al.* 2001; Kato-Noguchi 2002; Chung *et al.* 2002).

A number of secondary metabolites, such as phenolic acids, phenylalkanoic acids, hydroxamic acids, fatty acids, terpenes, and indoles, were identified in extracts of rice plants (Rimando and Duke 2003). Even though most plant tissues contain potential allelochemicals, only compounds released from the plants into environments enable the germination and growth of neighboring plant species to be inhibited and act as allelochemicals in natural ecosystems (Putnam and Tang 1986). Therefore, it was postulated that, for allelopathy research, compounds in root exudates are more biological meaningful than compounds in plant tissues (Perez and Ormeno-Nunez 1991; Neimeyer and Perez 1995). In addition, Wu *et al.* (2001) found that there was no significant correlation between the level of growth inhibitory substances in plants and their levels in root exudates.

ALLELOPATHIC SUBSTANCES IN DECOMPOSING RICE RESIDUES

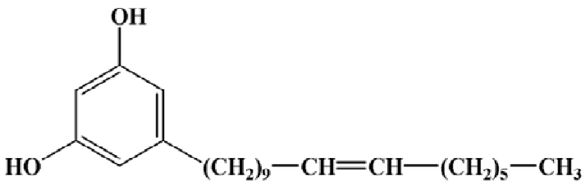
It is well known that the crop residues left in soil are sometimes harmful to plant growth. Plant residues in soil can release phytotoxic substances during decomposition. Chou and Lin (1976) observed a decrease in plant productivity of the second rice crop in a paddy field containing residues from the first rice crop. They found that aqueous extracts of decomposing rice residues in soil inhibited the growth of mung bean (*Vigna radiata*) and lettuce as well as rice. Aqueous extracts of rice residues were also found to suppress the growth of *Phalaris minor*, *Echinochloa crus-galli* and lettuce (Khan *et al.* 2001; Jung *et al.* 2004).

Several phenolic acids, such as 2-hydroxyphenylacetic acid (3), 4-hydroxybenzoic acid (11), vanillic acid (16), *p*-coumaric acid (23) and ferulic acid (25) were found in aqueous extracts of decomposing rice residues (Chou and Lin 1976) and in soil from paddy fields which rice was grown (Chou and Chiou 1979).

Kuwatsuka and Shindo (1973) isolated 13 different phenolic acids in decomposition of rice straw; benzoic acid (10), 4-hydroxybenzoic acid (11), protocatechuic acid (13), gallic acid (14), vanillic acid (16), syringic acid (17), salicylic acid (18), gentisic acid (19), β-resorcylic acid (20), *p*-coumaric acid (23), caffeic acid (24), ferulic acid (25) and sinapinic acid (26). They found that *p*-coumaric acid (23) was released in the greatest amount from decomposing rice straw. However, Tanaka *et al*. (1990) doubted the involvement of phenolic acid in rice allelopathy, as the levels of phenolic acids found in rice soil are not sufficient to cause phytotoxic effects. In support of this view, phenolic acids are usually present in rice soils at concentrations below 5 mg kg^{-1} soil, which is below the bioactive threshold causing the allelopathic effects (Olofsdotter *et al.* 2002b).

ALLELPATHIC SUBSTANCES IN RICE ROOT EXUDATES

Several phenolic acids and fatty acids were found in water obtained from soils in which allelopathic or non-allelopathic rice plants were incubated for 48 h (Mattice *et al.* 1998). Concentrations of 4-hydroxybenzaldehyde (9), 4-



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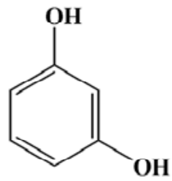

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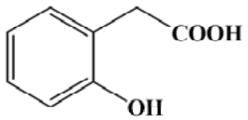

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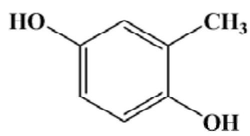

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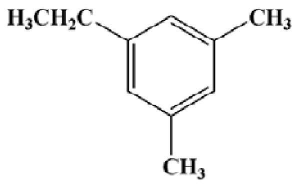

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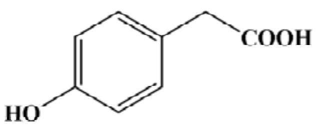

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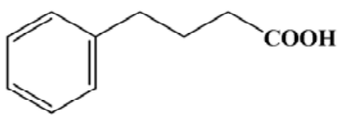

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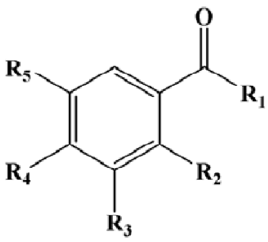
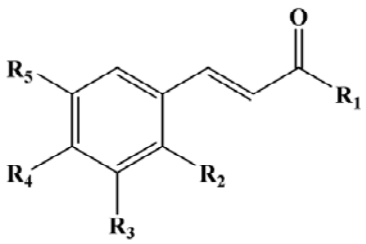




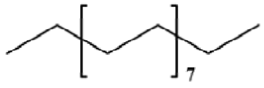
	R_1	R_2	R_3	R_4	R_5		R_1	R_2	R_3	R_4	R_5
8	H	H	H	H	CH_2CH_3	**18**	OH	OH	H	H	H
9	H	H	H	OH	H	**19**	OH	OH	H	H	OH
10	OH	H	H	H	H	**20**	OH	OH	H	OH	H
11	OH	H	H	OH	H	**21**	H	H	H	H	H
12	OH	H	OH	H	H	**22**	OH	H	H	H	H
13	OH	H	OH	OH	H	**23**	OH	H	H	OH	H
14	OH	H	OH	OH	OH	**24**	OH	H	OH	OH	H
15	OH	H	OH	OCH_3	H	**25**	OH	H	OCH_3	OH	H
16	OH	H	OCH_3	OH	H	**26**	OH	H	OCH_3	OH	OCH_3
17	OH	H	OCH_3	OH	OCH_3						

1, 5-(12-heptadecenyl)-resorcinol; **2**, resorcinol; **3**, 2-hydroxyphenylacetic acid; **4**, 2-methyl-1,4-benzenediol; **5**, 1-ethyl-3,5-dimethylbenzene; **6**, 4-hydroxy-phenylacetic acid; **7**, 4-phenylbutyric acid; **8**, 4-ethylbenzaldehyde; **9**, 4-hydroxybenzaldehyde; **10**, benzoic acid; **11**, 4-hydroxybenzoic acid; **12**, 3-hydroxybenzoic acid; **13**, protocatechuic acid; **14**; gallic acid; **15**, 3-hydroxy-4-methoxybenzoic acid; **16**, vanillic acid; **17**, syringic acid; **18**, salicylic acid; **19**, gentisic acid; **20**, β-resorcylic acid; **21**, cinnamic aldehyde; **22**, cinnamic acid; **23**, *p*-coumaric acid; **24**, caffeic acid; **25**, ferulic acid; **26**, sinapinic acid.

hydroxybenzoic acid (11), 3-hydroxybenzoic acid (12), *p*-coumaric acid (23) and caffeic acid (24) were greater in water obtained from soils containing allelopathic rice plants than water obtained from soils containing non-allelopathic rice plants. Mattice *et al.* (1998) also identified compounds contained in these soils, and found that concentrations of 4-hydroxybenzaldehyde (9), 4-hydroxybenzoic acid (11), 3-hydroxy-4-methoxybenzoic acid (15), valeric acid (30), tetradecanoic acid (31) and stearic acid (32) were greater in soils of allelopathic rice than soils of non-allelopathic rice plants. Based on these experiments, it was suggested that allelopathy of rice against weeds was correlated with the amount of phenolic acids released by living rice roots (Mattice *et al.* 1998). Phenolic acids are shown to be phytotoxic against various plants at concentrations greater than about 1 mM (Hartley and Whitehead 1985; Dalton 1999). However, Mattice *et al.* (1998) did not provide the exact values of phenolic acid concentrations in the water and soils containing rice plants. Thus, it is impossible to evaluate whether phenolic acids were responsible for the allelopathy of rice.

Kim and Kim (2000) identified several compounds in the acidic fraction isolated from root exudates of allelopathic rice cv. Kouketsumochi. These compounds were 2-methyl-1,4-benzenediol (4), 1-ethyl-3,5-dimethylbenzene (5), 4-ethylbenzaldehyde (8), cinnamic aldehyde (21), octadecane (27), 3-epicosene (28), 1-eicosanol (29), 9,12-octadecadienoic acid (33), 7-hexadecenoic acid methyl ester (34), 12-octadecenoic acid methyl ester (35). 12-methyl-tridecanoic acid methyl ester (36), *cis*-1-butyl-2-methylcyclopropane (37), dehydroabietic acid (43) and cholest-5-en-3(β)-ol (45). They considered that 2-methyl-1,4-benzenediol (4), 4-ethylbenzaldehyde (8), cinnamic aldehyde (21) and cholest-5-en-3(β)-ol (45) were candidates for allelochemicals of rice plants because inhibitory activities of these compounds are relatively high in comparison to the other compounds found. However, the concentrations of these compounds were not provided and inhibitory activities of these compounds were reported to be not high enough to cause allelopathic effects (Olofsdotter *et al.* 2002; Seal *et al.* 2004b).

Fifteen compounds were identified and quantified in the root exudates of four alleloapthic and five non-allelopathic rice cultivars (Seal *et al.* 2004a). The concentrations of 4-



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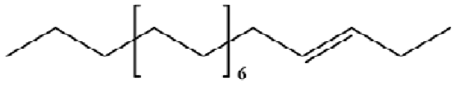

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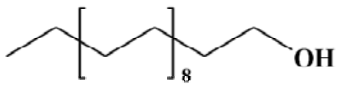

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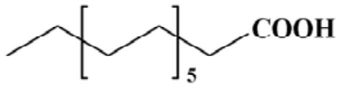

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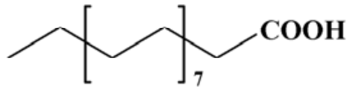

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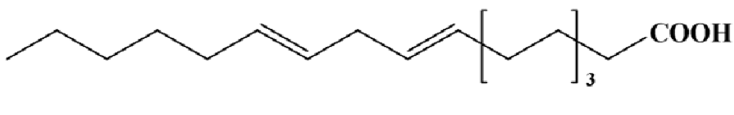

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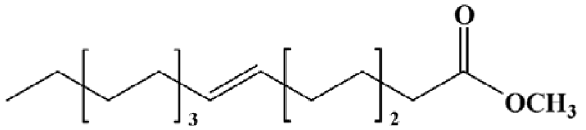

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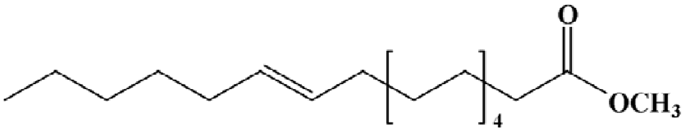

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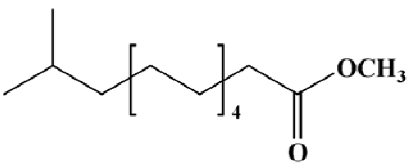

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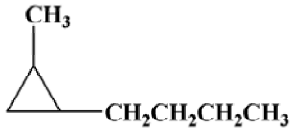

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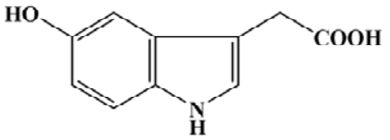
27, octadecane; **28**, 3-epicosene; **29**, 1-eicosanol; **30**, valeric acid; **31**, tetra-decanoic acid; **32**, stearic acid; **33**, 9,12-octadecadienoic acid; **34**, 7-hexadecenoic acid methyl ester; **35**, 12-octadecenoic acid methyl ester, **36**, 2-methyl-tridecanoic acid methyl ester; **37**, *cis*-1-butyl-2-methylcyclopropane.

hydroxybenzoic acid (11), caffeic acid (24) and ferulic acid (25) were greater in the exudates of allelopathic rice cultivars than those of non-allelopathic rice cultivars, while concentration of abietic acid (42) was greater in those of non-allelopathic rice cultivars than those of allelopathic rice cultivars. The other 11 compounds, resorcinol (2), 2-hydroxy-phenylacetic acid (3), 4-hydroxyphenylacetic acid (6), 4-phenylbutyric acid (7), cinnamic acid (22), vanillic acid (16), syringic acid (17), salicylic acid (18), *p*-coumaric acid (23), 5-hydroxyindole-3-acetic acid (38) and indole-5-carboxylic acid (39) did not differ in the concentrations between alleloapthic and non-alleloapthic rice cultivars (Seal *et al.* 2004a). 5-(12-Heptadecenyl)-resorcinol (1) was also found in rice root exudates (Bouillant *et al.* 1994).

About 5,000 rice seedlings, cv. Koshihikari, were hydroponically grown for 14 days in order to screen for any allelochemicals in rice root exudates. Keeping track of the biological activity, the culture solution was purified by several chromatographic fractionations and finally 2.1 mg of putative compound causing the inhibitory effect of the rice seedlings was isolated (Kato-Noguchi *et al.* 2002; Kato-Noguchi and Ino 2003a). The chemical structure of the inhibitor was determined from high-resolution MS, and ^{1}H- and ^{13}C-NMR spectral data as momilactone B (44). Momilactone B is quite active at submillimolar concentrations (Takahashi *et al.* 1976; Kato *et al.* 1977; Lee *et al.* 1999b), indicating that it may account for allelopathic effects of some rice cultivars. Momilactone B was later found in root exudes of other allelopathic rice cultivars, PI312777, with 5,7,4'-trihydroxy-3',5'-dimethoxyflavone (40) and 3-isopropyl-5-acetoxycyclohexene-2-one-1 (41) (Kong *et al.* 2004).

VOLATILE COMPOUNDS FROM RICE CALLUS

It was found that the growth of soybean callus was inhibited by rice callus when both calluses were incubated together in a flask (Yang and Futsuhara 1991). The experimental system was designed to prevent substance diffusion through culture medium. Thus, only volatile compounds could affect the growth of soybean callus. Involvement of ethylene in growth inhibition was ruled out, but further analysis of



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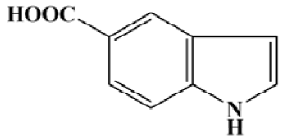

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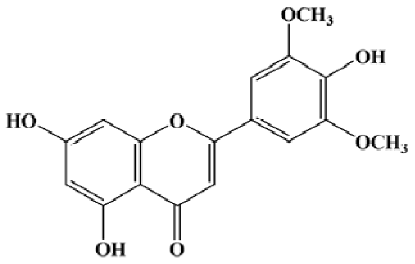

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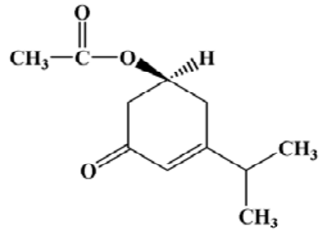

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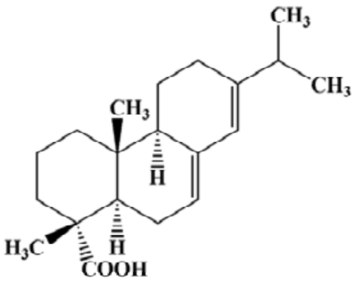

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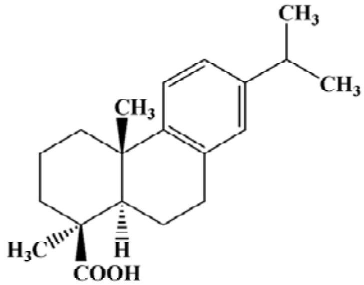

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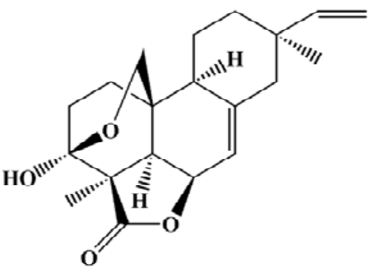

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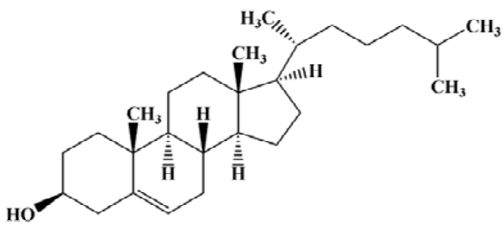

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38, 5-hydroxyindole-3-acetic acid; 39, indole-5-carboxylic acid; **40**, 5,7,4'-trihydroxy-3',5'-dimethoxyflavone; **41**, 3-isopropyl-5-acetoxycyclohexene- 2-one-1; **42**, abietic acid; **43**, dehydro-abietic acid; **44**, momilactone B; **45**, cholest-5-en-3(β)-ol.

the volatiles was not carried out.

PHENOLIC ACIDS

Phenolic acids are often mentioned as putative allelochemicals and the most commonly investigated compounds among potential allelochemicals since they have been found in a wide range of soils (Hartley and Whitehead 1985; Inderjit 1996; Dalton 1999). Hsu *et al.* (1989) evaluated the inhibitory activities of phenolic acids against germination of lettuce and alfalfa. 4-hydroxybenzoic acid (11) and salicylic acid (18) were the most active inhibiting germination at a concentration greater than 0.5-1.5 mM.

Olofsdotter *et al.* (2002) evaluated whether phenolic acids are responsible for rice allelopathy. They found that allelopathic rice cultivars did not release a significantly greater amount of phenolic acids than non-allelopathic cultivars. The maximum release rate of phenolic acid from rice plants was approximately 10 μg $plant^{-1}$ day^{-1}. Therefore, at a conventional plant density (100 rice plants m^{-2}), the release rate of phenolic acids would be approximately 1 mg m^{-2} day^{-1}. Considering the inhibitory activity of phenolic acids, it was concluded that, even if all phenolic acids were as phytotoxic as 4-hydroxybenzoic acid (11), the release level of phenolic acids from rice is not sufficient to cause growth inhibition of neighboring plants (Olofsdotter *et al.* 2002).

Five major phenolic acids in rice root exudates, 4-hydroxybenzoic acid (11), vanillic acid (16), syringic acid (17), *p*-coumaric acid (23) and caffeic acid (24), were mixed and their biological activities were determined against *Sagittaria monotevidensis* (Seal *et al.* 2004b). The concentration required for 50% growth inhibition (I_{50}) of the mixture of these five phenolic acids was 502 μM. The concentrations of these phenolic acids detected in rice roots exudates were by far less than 500 μM (Seal *et al.* 2004b). The inhibitory activity of a mixture of all 15 compounds identified in rice roots exudates, resorcinol (2), 2-hydroxyphenylacetic acid (3), 4-hydroxyphenylacetic acid (6), 4-phenylbutyric acid (7), 4-hydroxybenzoic acid (11), vanillic acid (16), syringic acid (17), salicylic acid (18), cinnamic acid (22), *p*-coumaric acid (23), caffeic acid (24), ferulic acid (25), 5-hydroxyindole-3-acetic acid (38) and indole-5-carboxylic acid (39) and abietic acid (42), was also determined and I_{50} of the mixture was found to be 569 μM (Seal *et al.* 2004a, 2004b). In addition, it was clarified that synergistic action of phenolic acids on growth inhibition did not work well (Seal *et al.* 2004b). These studies indicate that any compounds found in rice root exudates including phe-

Table 1 Inhibitory activities of momilactone B and major phenolic acids found in rice root exudates.

	Barnyard grass germination	Barnyard grass root growth	Lettuce germination	*Amaranthus lividus* germination
Momilactone B		50% (0.2 mM) *		50% (0.05 mM)
Caffeic acid	82% (1 mM)		50% (3.9 mM)	
p-Coumaric acid	92% (1 mM)		50% (4.3 mM)	
Ferulic acid	92% (1 mM)		50% (3.6 mM)	
Gallic acid	9% (1 mM)		50% (5.9 mM)	
4-Hydroxybenzoic acid	94% (1 mM)		50% (1.5 mM)	
Resorcylic acid	5% (1 mM)		50% (4.2 mM)	
Salicylic acid	50% (1 mM)		50% (1.4 mM)	
Syringic acid	74% (1 mM)			
Vanillic acid	73% (1 mM)		50% (2.4 mM)	
Reference	Chung *et al.* 2002	Kong *et al.* 2004	Olofsdotter *et al.* 2002	Lee *et al.* 1999b

Concentration required for indicated inhibition.
*estimated from the data of the reference.

nolic acids are not responsible for the allelopathy of rice.

All information available suggests that phenolic acid concentrations in rice root exudates were much lower than the required threshold of these phytotoxic levels, and phenolic acids seem not to act as rice allelochemicals.

MOMILACTONE B

Momilactone B (44) was originally isolated from rice husks together with momilactone A (Kato *et al.* 1973; Takahashi *et al.* 1976) and also found in rice leaves and straw (Cartwright *et al.* 1977, 1981; Kodama *et al.* 1988; Lee *et al.* 1999a). Thereafter, the function of momilactone A as a phytoalexin was extensively studied and several lines of evidence indicated that it has an important role in rice defense system against pathogens (Nojiri *et al.* 1996; Araki and Kurahashi 1999; Takahashi *et al.* 1999; Tamogami and Kodama 2000; Agrawal *et al.* 2002). Although the growth inhibitory activity of momilactone B was much greater than that of momilactone A (Takahashi *et al.* 1976; Kato *et al.* 1977), the function of momilactone B is obscure.

The inhibitory activity of momilactone B against the germination and growth of several plant species was reported. A 5 μM solution of momilactone B inhibited the germination of *Amaranthus lividus* by 50%, while a 50 μM solution inhibited root and shoot growth of *Digitaria sanguinalis* and seed germination of *Poa annua* by more than 50% (Lee *et al.* 1999b). The compound also inhibited the root and hypocotyl growth of cress seedlings at concentrations greater than 3 μM. The inhibition increased with increasing concentrations of momilactone B. The concentrations required for 30% inhibition were 12 and 16 μM on cress roots and hypocotyls, respectively, and for 50% inhibition on cress roots and hypocotyls were 36 and 41 μM, respectively (Kato-Noguchi *et al.* 2002; Kato-Noguchi and Ino 2003a). Judging from its inhibitory activity, momilactone B was considered to be a candidate for a rice allelochemical (**Table 1**; Rimando and Duke 2003).

Rice plants were hydroponically grown for 130 days and the release level of momilactone B from plants into the medium was determined (Kato-Noguchi and Ino 2003b). Rice plants released momilactone B throughout its life cycle and the release rate increased with plant growth until flowering initiation. Its release rate on the day of flowering started at 2.1 μg $plant^{-1}$ day^{-1} and on average a single rice plant released about 100 μg of momilactone B into the medium over its life cycle (Kato-Noguchi and Ino 2003b). At a conventional plant density (100 rice plants m^{-2}), momilactone B would be released at approximately 10 mg m^{-2}. Thus, accumulation of momilactone B may occur under field conditions sufficiently to inhibit germination and growth of neighboring plants.

The release level of momilactone B from rice plants and the effectiveness of momilactone B on the growth inhibition suggest that momilactone B may act as an allelopathic agent for inhibiting neighboring plant growth. Thus, momilactone B may play an important role in rice allelopathy.

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JAPANESE ABSTRACT

アレロパシーを利用した環境と調和した循環型農業の開発のため、イネのアレロパシーに関する多くの研究が世界中で行われてきた。その結果、イネ植物を幾つかの別種植物と共存させると、それらの植物の成長を抑制することが明らかになった。アレロパシー物質は植物の成長を抑制することから、イネは、アレロパシー物質を生産し、イネの周辺や根圏に分泌することで、周りに進入してくる他の植物の成長を抑制し、それらの植物との栄養塩類等をめぐる生存競争を有利にしている可能性がある。また、イネの根の分泌液中から、フェノール、脂肪酸、インドール、テルペノイド類等の多くの化合物が発見されており、これらの化合物の幾つかは成長抑制活性を有し、イネのアレロパシーに関与している可能性がある。このような、イネのアレロパシーに関する研究は、イネの生理学・化学生態学を明らかにするために重要である。本総説では、イネが放出している化合物と、それらの化合物がアレロパシー物質としてどの程度機能しているかを討論した。