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Biological Activities of Rice Allelochemicals Momilactone A and B

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Abstract

Momilactone A and B had been demonstrated to play critical roles in rice allelopathy by the findings of physiological and genetical approaches. Rice plants secrete momilactones into the rhizosphere over their entire life cycle at phytotoxic levels, and momilactones are able to account for the majority of the observed rice allelopathy. However, allelopathic activities of momilactones were determined on only a few test plant species. Therefore, this study was to determine the allelopathic activities of momilactones against nine test plant species including weed species, and four rice cultivars.

Momilactone A and B inhibited Arabidopsis, alfalfa, lettuce, cress, timothy, barnyard grass, *E. colonum*, crabgrass and ryegrass at concentrations greater than 3 and 0.3 μM, respectively. The inhibition on those test plants was concentration dependent. On the other hand, effectiveness of momilactone A and B on rice cultivars, Koshihikari, Nipponbare, Norin 8 and Sasanishiki was very weak. Those rice cultivars were only inhibited by momilactone A and B at concentrations greater than 300 and 100 μM, respectively. Momilactone A and B may have potential as templates for the development of new plant control substances because of their selective inhibitory activities on weed plant species. More importantly, momilactone A and B as allelochemicals in rice may provide a molecular marker for breeding and/or engineering efforts directed at increasing allelopathic activity of this critical staple food crop.

Keywords: Allelochemical; Momilactone; Growth inhibitor; *Oryza sativa;* Rice allelopathy

Introduction

Many plants were found to secrete a wide range of compounds into the rhizosphere and to change the chemical and physical properties of the rhizosphere soil, which affect the community of microbial, fungi and plants [1-4]. Through the secretion of compounds such as allelochemicals, plants inhibit the germination and growth of neighboring plants to compete more effectively for the resources [3,5,6].

The negative impacts of commercial herbicide use on the environment make it desirable to diversify weed management options [7-9]. Many investigations have been attempted to exploit allelopathy of plants for weed control purposes in a variety of agricultural settings [10-12]. Rice has also been extensively studied with respect to its allelopathy as part of a strategy for sustainable weed management, such as breeding allelopathic rice strains [13-15].

A large field screening programs and laboratory experiments in many countries have proved that rice is allelopathic and releases allelochemical(s) into its rhizosphere [16-24]. A number of compounds, such as phenolic acids, fatty acids, phenylalkanoic acids, hydroxamic acids, terpenes and indoles, have been identified as potential rice allelochemicals [25,26]. However, the studies demonstrated that the diterpenoid compounds, momilactone A and B are the most important rice allelochemicals, with momilactone B playing a particularly critical role [27-29].

Rice plants secrete momilactones from their roots into the rhizosphere over their entire life cycle at phytotoxic levels, and momilactones are able to account for the majority of the observed rice allelopathy [30-32]. In addition, genetic studies have shown that selective removal of only the momilactones from the complex mixture found in rice root exudates significantly reduces allelopathy, demonstrating that these serve as allelochemicals, the importance of which is reflected in the presence of a dedicated momilactone biosynthetic gene cluster in the rice genome [33,34]. However, allelopathic activities of momilactones were determined on only a few test plant species such as lettuce and barnyard grass [25,32]. Therefore, in the present study, the allelopathic activities of momilactone A and B were determined nine test plant species including weed plants, and toxicities of momilactone A and B on four rice cultivars were also determined.

Materials and Methods

Plant materials

Cress (*Lepidum sativum* L.), lettuce (*Lactuca sativa* L.), alfalfa (*Medicago sativa* L.) were chosen as test plants for bioassay due to their known seedling growth behavior. Weed species, ryegrass (*Lolium multiflorum* Lam), timothy (*Phleum pratense* L.), barnyard grass (*Echinochloa crus-galli* (L) Beauv), *Echinochloa colonum* L. Link, and crabgrass (*Digitaria sanguinalis* L.) were also chosen for bioassay. Typical model plant, *Arabidopsis thaliana* L. ecotype Columbia and four rice (*Oryza sativa* L.) cultivars, Koshihikari, Nipponbare, Norin 8 and Sasanishiki were chosen for bioassay. Seeds of cress, lettuce and alfalfa were purchased from Takii Co. Ltd. and seeds of timothy, barnyard grass, *E. colonum* and crabgrass were purchased from Herbiseed (London UK). Arabidopsis were grown and its seeds were harvested.

Momilactone A and B

Momilactone A and B were isolated from husks of rice (cv. Koshihikari) as described by Kato-Noguchi et al. [35,36]. Husks (1 kg) of rice were extracted with 4 L methanol for three days. After filtration using filter paper (No. 2; Toyo ltd, Tokyo) filtrate was concentrated at 40°C in vacuo to produce an aqueous extract. The aqueous extract was

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adjusted to pH 7.0 with 1 M phosphate buffer and the extract was then partitioned three times against an equal volume of ethyl acetate. The ethyl acetate phase was evaporated and separated with columns of silica gel and Sephadex LH-20. Momilactone A and B were finally purified by HPLC and identified by ^{1}H-NMR spectra.

Bioassay of momilactone A and B

Momilatone A and B were dissolved in 0.2 mL methanol, added to two sheets of filter paper (No. 2) in a 5.5-cm Petri dish. Methanol was subsequently evaporated and the filter paper in the Petri dishes was moistened with 3 mL of 1 mM MES buffer. The final concentrations of momilactone A and B were 0.01, 0.03, 0.1, 0.3, 1, 3, 10, 30, 100, 300, 1000, 3000 and 10000 μM. Seeds of cress, lettuce, alfalfa, ryegrass, timothy, barnyard grass, E. colonum, crabgrass, Arabidopsis and rice cultivars (Koshihikari, Nipponbare, Norin 8 and Sasanishiki) were surface sterilized in a 2% (w/v) solution of sodium hypochlorite for 15 min, rinsed four times in distilled water and germinated in the darkness at 25°C for 16-72 h.

Then, 10 germinated seeds of each test plant were individually placed on the filter paper in Petri dishes. The length of roots and shoots of these seedlings was measured after 48 h of incubation in the darkness at 25°C. For control treatments, methanol was added to the filter paper in the Petri dish and evaporated. Control germinated seeds of each test plants were then placed on the filter paper moistened with 3 mL of 1 mM MES buffer as described above. Percentage inhibition was determined by the formula: [(control plant length-plant length incubated with momilactone A or B)/control plant length]×100. These were three replicates per treatment and the experiment was repeated six times.

Results and Discussion

Inhibitory activities of momilactone A and B on nine plant species

Momilactone A inhibited the growth of roots and shoots of ryegrass at concentrations greater than 10 μM (Figure 1). The inhibition was increased with increased concentration of momilactone A. When inhibition of ryegrass roots and shoots were plotted against the logarithm of momilactone A concentrations as described by Streibig [37], significant logistic functions (sigmoid) were obtained. The equation of the functions of momilactone A was $Y=[(-0.313-84.479)/\{1+(X/68.673)^{30.046}\}]+84.479$; ($r^2=0.995$ and $Y=[(-0.552-77.290)/\{1+(X/73.372)^{0.958}\}]+77.290$; ($r^2=0.998$) for ryegrass roots and shoots, respectively. Y in the equations indicates the inhibition (%) and X indicates the concentration (μM) of momilactone A as shown in Figure 1.

Momilactone B inhibited the growth of roots and shoots of ryegrass at concentrations greater than 1 μM (Figure 2). The inhibitory activity

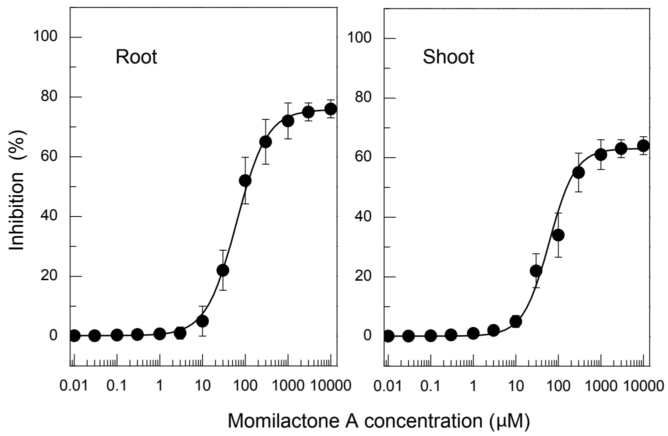

Figure 1: Effect of Momilactone A on the root and shoot growth of ryegrass. Means ± SE from 6 independent experiments with 30 plants for each determination are shown.

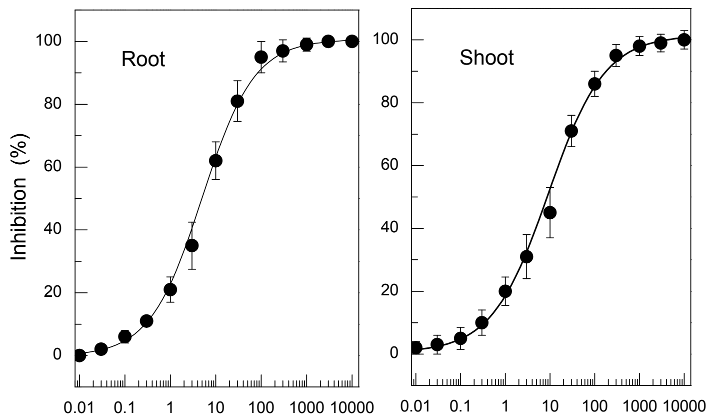

Figure 2: Effect of Momilactone B on the root and shoot growth of ryegrass. Means ± SE from 6 independent experiments with 30 plants for each determination are shown.

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was also dependent on momilactone B concentration. The equation of the significant logistic functions of momilactone B was $Y=[(1.638-98.472)/\{1+(X/6.886)^{0.077}\}+98.472]$; ($r^2=0.995$) and $Y=[(0.934-98.733)/\{1+(X/6.423)^{0.821}\}+98.733]$; ($r^2=0.996$) for the roots and shoots, respectively. The concentrations required for 50% growth inhibition (defined as I_{50}) for roots and shoots of ryegrass were calculated from the equations of the logistic functions (Table 1). Comparing those values, inhibitory activity of momilactone B on ryegrass root and shoot growth, respectively, was 13.3- and 21.2-fold greater than that of momilactone A.

Inhibitory activity of momilactone A and B on Arabidopsis, alfalfa, lettuce, cress, timothy, barnyard grass, *E. colonum*, and crabgrass were also determined at concentrations of 0.01, 0.03, 0.1, 0.3, 1, 3, 10, 30, 100, 300, 1000, 3000 and 10000 μM. Momilactone A and B, respectively, inhibited the growth of these plant roots and shoots at concentrations greater than 3-30 μM and 0.3-10 μM, respectively. The inhibition on those test plants of momilactone A and B was concentration dependent and the significant logistic functions were obtained for all test plant species. I_{50} values were then determined by the equations of the logistic functions as described above (Table 1). Comparing I_{50} values, the inhibitory activity of momilactone B on root and shoot growth of those test plant species was 5.6- to 22.2-fold greater than that of momilactone A.

I_{50} values of momilactone A on monocotyledonous plants (timothy, barnyard grass, *E. colonum* and crabgrass) were 66.7 to 98.5 μM and 138 to 275 μM for roots and shoots, respectively, and I_{50} values of momilactone B on monocotyledonous plants were 5.6 to 9.5 μM and 6.3 to 12.4 μM for roots and shoots, respectively (Table 1). On the other hand, I_{50} values of momilactone A on dicotyledonous plants (Arabidopsis, cress, lettuce and alfalfa) were 204 to 479 μM and 86.2 - 395 μM for roots and shoots, respectively, and I_{50} values of momilactone B on dicotyledonous plants were 9.8 to 67.3 μM and 12.4 to 82.4 μM for roots and shoots, respectively. Therefore, the sensitivities of monocotyledonous plant species to momilactone A and B were greater than those of dicotyledonous plant species except for Arabidopsis. Sensitivity of Arabidopsis was similar to that of monocotyledonous plants.

In addition, it was reported that momilactone A and B inhibited the growth of *Amaranthus lividus* and *Poa annua* at concentrations greater than 20 ppm (ca. 60 μM) and 4 ppm (ca. 12 μM), respectively [38]. The growth inhibitory activities of momilactome B are also greater than those of momilactone A under other bioassay systems [25,32,39-42].

Inhibitory activities of momilactone A and B on rice

Momilactone A and B inhibited the growth of all plant species including the weed plants at μM level (Figures 1 and 2 and Table 1). Rice plants produce momilactone A and B and secret momilactone A and B into the rhizosphere [31,32,34]. Thus, the growth inhibitory activities of momilactone A and B against rice plants themselves were determined at concentrations of 0.01, 0.03, 0.1, 0.3, 1, 3, 10, 30, 100, 300, 1000, 3000 and 10000 μM. Effectiveness of momilactone A and B on rice cultivars, Koshihikari, Nipponbare, Norin 8 and Sasanishiki was weak. Momilactone A and B only inhibited root and shoot growth of all rice cultivars at concentrations greater than 100 and 300 μM, respectively.

I_{50} values of momilactone A and B on rice root and shoot were not obtained because of their weak inhibitory activities. Thus, the concentrations required for 25% growth inhibition (defined as I_{25}) for roots and shoots of rice were calculated from the equations of the logistic functions (Table 2). Comparing I_{25} values, the inhibitory activities of momilactone B on the rice root and shoot growth, respectively, were 3.1- to 4.1-fold and 2.4- to 3.7-fold greater than those of momilactone A, which was consistent with results obtained with other plant species (Table 1).

I_{25} values of Arabidopsis, alfalfa, lettuce, cress, timothy, barnyard grass, *E. colonum*, crabgrass and ryegrass were 10.2 to 88.7 μM and 2.1 to 41.6 μM for momilactone A and momilactone B, respectively

	Momilactone A		Momilactone B		Ratio (Momilactone A/Momilactone B)	
	Root	Shoot	Root	Shoot	Root	Shoot
Arabidopsis	204 ± 12	86.2 ± 7.1	9.8 ± 1.1	12.4 ± 1.1	20.8	7.0
Alfalfa	379 ± 19	315 ± 29	67.8 ± 5.3	82.4 ± 6.7	5.6	3.8
Lettuce	472 ± 37	395 ± 31	54.3 ± 4.5	77.9 ± 6.7	8.7	5.1
Cress	476 ± 32	337 ± 27	35.4 ± 3.1	40.5 ± 4.3	13.4	8.3
Timothy	76.5 ± 6.3	157 ± 12	5.6 ± 0.4	7.9 ± 0.8	13.7	19.9
Barnyard grass	91.2 ± 7.2	145 ± 11	6.7 ± 0.4	6.3 ± 0.4	13.7	23.0
E. colonum	66.7 ± 5.4	238 ± 21	7.2 ± 0.5	11.6 ± 0.8	9.3	20.5
Crabgrass	98.5 ± 7.3	275 ± 19	9.5 ± 0.6	12.4 ± 1.1	10.3	22.2
Ryegrass	91.9 ± 8.3	138 ± 12	6.9 ± 0.4	6.5 ± 0.3	13.3	21.2

Table 1: I_{50} values (μM) of momilactone A and B on root and shoot growth of test plants and the ratio of I_{50} values of momilactone A and B. The values were determined by the logistic functions as described in the text. Means ± SE from six independent experiments with three Petri dishes for each experiment are shown.

	Momilactone A		Momilactone B		Ratio ((Momilactone A/Momilactone B)	
Rice cultivar	Root	Shoot	Root	Shoot	Root	Shoot
Koshihikari	843 ± 76	967 ± 84	214 ± 18	278 ± 23	3.9	3.4
Nipponbare	956 ± 87	976 ± 92	314 ± 26	401 ± 34	3.1	2.4
Norin 8	805 ± 75	924 ± 85	195 ± 21	249 ± 19	4.1	3.7
Sasanishiki	911 ± 91	974 ± 76	245 ± 19	301 ± 23	3.7	3.2

Table 2: I_{25} values (μM) of momilactone A and B on root and shoot growth of rice plants and the ratio of I_{25} values of momilactone A and B. The values were determined by the logistic functions as described in the text. Means ± SE from six independent experiments with three Petri dishes for each experiment are shown.

	Momilactone A		Momilactone B	
	Root	Shoot	Root	Shoot
Arabidopsis	54.5 ± 4.7	24.5 ± 1.7	4.5 ± 0.6	4.7 ± 0.2
Alfalfa	85.8 ± 6.5	78.5 ± 5.3	34.5 ± 2.4	39.6 ± 2.7
Lettuce	88.7 ± 7.2	71.4 ± 4.8	32.7 ± 3.1	41.6 ± 3.1
Cress	82.5 ± 6.3	75.6 ± 6.4	31.5 ± 1.8	35.5 ± 3.7
Timothy	10.2 ± 0.9	13.5 ± 1.3	3.2 ± 0.2	3.5 ± 0.3
Barnyard grass	12.5 ± 1.1	16.3 ± 1.1	2.6 ± 0.2	2.5 ± 0.2
E. colonum	14.2 ± 1.2	25.3 ± 2.1	3.5 ± 0.2	3.2 ± 0.2
Crabgrass	41.5 ± 3.6	43.5 ± 3.7	3.2 ± 0.3	3.9 ± 0.2
Ryegrass	35.6 ± 2.9	34.3 ± 2.5	2.1 ± 0.1	1.6 ± 0.1

Table 3: I_{25} values (μM) of momilactone A and B on root and shoot growth of test plants. The values were determined by the logistic functions as described in the text. Means ± SE from six independent experiments with three Petri dishes for each experiment and are shown.

(Table 3). Comparing I_{25} values, the effectiveness of momilactone A and B on the root and shoot growth of rice cultivars was much less than that of weed plant species, barnyard grass, *E. colonum*, crabgrass and ryegrass. Barnyard grass is the most significant biological constrain to rice production [43].

The effectiveness of momilactone A and B on the growth of those rice cultivars was much less than that on the growth of barnyard grass. In addition, no visible damage to rice cultivars by momilactone A and B was observed at levels that are cytotoxic to these other plant species. These results suggest that the toxicities of momilactone A and B to rice cultivars may be much less than those to other plant species. The basis for rice resistance is currently unknown, but presumably involves either efflux (e.g. via the same transport mechanism responsible for momilactone secretion), insensitivity of the molecular target, and/or degradation.

Conclusion

Rice allelochemicals momilactone A and B inhibited Arabidopsis, alfalfa, lettuce, cress, timothy, barnyard grass, *E. colonum*, crabgrass and ryegrass by concentration dependently (Figures 1 and 2 and Table 1). However, the ability of momilactones A and B to suppress the growth of rice was by far less than their effects on other plant species (Table 2). Allelopathic substances have potential as either herbicides or templates for new synthetic herbicide classes [6,7,10,12,44,45].

Natural compounds are considered to be more environmentally benign than most synthetic herbicides [12]. In many cases, the natural compounds are also highly active at a molecular target site [45]. Momilactone A and B may have potential as a template for the development of new plant control substances because their selective inhibitory activities for weed plant species. More importantly, identification of momilactone A and B as allelochemicals in rice provides a molecular marker for breeding and/or engineering efforts directed at increasing allelopathic activity of this critical staple food crop.

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