Antifeedant and Insecticidal Effects of Mandelic Acid on the Brown Planthopper *Nilaparvata lugens* Stål

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To study the effects of mandelic acid (MA) on the brown planthopper (BPH), *Nilaparvata lugens*, the survival rate and behaviour of BPH fed on an artificial diet with different dosages of MA was observed. The survival rate of BPH decreased with the increase of the MA concentration and feeding time. In contrast to the control, the survival rate of BPH 72 h after feeding decreased significantly. Electrical penetration graph (EPG) data indicated that MA absorbed by the rice plant from Kimura B solution significantly affected the feeding behaviour of BPH. At the concentrations of 0.1, 0.5, and 1.0 mg/ml, duration of the phloem ingestion of BPH decreased from 115.34 min (control) to 30.41, 7.63, and 0.36 min, respectively. Periods of xylem ingestion of MA-treated BPH were significantly shorter than those of the control (50.44 min). Moreover, BPH spent more time walking around or being at rest on MA-treated rice plants, as well as in stylet activities. The GST (glutathione *S*-transferase) activity of BPH increased with the increasing MA concentration, while the GPX (glutathione peroxidases) activity did not change significantly. The results indicate that MA has an antifeedant and insecticidal effect on BPH.

Key words: Mandelic Acid, *Nilaparvata lugens*, Antifeedant Effect, Insecticidal Activity

Introduction

The brown planthopper (BPH), *Nilaparvata lugens* Stål, is one of the most important insect pests of rice (*Oryza sativa* L.) crops in Asia and causes severe damage to rice plants (Gorman *et al*., 2008). It damages crops by ingesting nutrients specifically from the rice phloem using its piercing mouthparts (stylet), leading to stunted growth of the plants, and it is a vector of grassy stunt and ragged stunt viruses, respectively (Hibino, 1996; Hao *et al*., 2008). In the recent 20 years, the BPH has frequently caused widespread destruction of rice crops and heavy yield reductions in most of the rice cultivation areas (Shi *et al*., 2003; Park *et al*., 2007).

Currently, the methods available for protecting plant crops against insect infestation heavily depend on applying chemical insecticides or developing resistant rice varieties. Considering both the costs and the environment, exploitation of host resistance is the best method for controlling BPH outbreaks (Renganayaki *et al*., 2001). The resistant cultivars of rice contain a wide array of defense compounds that could affect the growth and development of BPH (Karban and Chen, 2007). In order to breed rice crops with high yields and resistance to insect pests, many studies have focused on the resistance mechanism of rice varieties to BPH (Noda *et al*., 2008; Du *et al*., 2009; Liu *et al*., 2010; Xue *et al*., 2010).

For the biochemical basis of resistance, soluble silicic acid (Yoshihara *et al*., 1979), oxalic acid (Yoshihara *et al*., 1980), tricin (Caballero *et al*., 1986; Ling *et al*., 2007), and apigenin-*C*-glycosides (Grayer *et al*., 1993), isolated from the leaf sheath of rice, have been identified as potent sucking inhibitors. Oxalic acid was found to enhance the activities of defence enzymes and defence-related compounds in rice plants (Jayaraj *et al*., 2010). Diterpenes, sesquiterpenes, and other secondary metabolites are considered to be responsible for the antifeedant and insecticidal activities in several plants (Villegas *et al*., 2009).

Mandelic acid (MA, 2-hydroxy-2-phenylacetic acid) is a natural product occurring in some plants, and is a useful precursor to various drugs. It has a long history of being used in the medical community as an antibacterial agent, particularly in the treatment of urinary tract infections

(Putten, 1979). MA has been used as an oral antibiotic, as well as an alternative to glycolic acid in skin care products (Taylor, 1999). MA has also been supposed to be involved in the resistance of rice crops against BPH infestation, for the fact that there were more MA and its derivatives in the resistant rice varieties than in the susceptible ones (P.-y. Hao, personal communication). However, details of the effects of MA on BPH and the action mechanism are still largely unknown.

The aim of the present study was to explore the effects of MA on BPH and to attempt to elucidate the mechanism involved in the rice resistance to BPH. We first examined the survival rate of BPH treated with MA added to the artificial diet, then studied the feeding behaviour of BPH on the susceptible rice variety Taichung Native 1 (TN1) treated with MA, using the electrical penetration graph (EPG) technique. Finally, the effects of MA on the activity of some detoxification enzymes, such as glutathione *S*-transferase (GST) and glutathione peroxidases (GPX), of BPH were determined.

Material and Methods

Insect and plant

Unless otherwise mentioned, BPH and rice plants were macropterous female insects and the susceptible rice variety TN1, respectively. BPH were reared on TN1 continuously at (26 ± 2) °C, (70 ± 8)% relative humidity, and a 16 h:8 h light/dark photoperiod for more than 2 years. Rice seeds were sown in soil, and seedlings were maintained in a greenhouse until the 3-leaf-stage prior to the experiments. All experiments were carried out in Zhejiang Provincial Key Laboratory of Biometrology and Inspection & Quarantine Technique, China Jiliang University, Hangzhou, China.

Effect of MA on BPH survival rate

To estimate the effect of MA on BPH as a function of its dose, a series of artificial diets (consisting of 5% sucrose) with different concentrations of MA (0.5, 1.0, 2.0, 4.0 mg/ml) was prepared, by dissolving crystalline (*R*)-(–)-mandelic acid (Sangon Inc., Shanghai, China). Then, 15 ml artificial diet were pipetted into a test tube (13 cm × 1.5 cm), where it was absorbed by a piece of filter paper (10 cm × 3 cm) mounted on the inside of the tube. A cotton plug at the bottom of the tube held the artificial diet and kept the filter paper wet, so that the BPH could feed continuously. Afterwards, 12 BPH individuals of 4th to 5th instar nymph stage were introduced in each tube, and maintained at (26 ± 2) °C, (70 ± 8)% relative humidity, and a 16 h:8 h light/dark photoperiod. In this way, BPH ingested MA with the artificial diet. Survival rates of BPH were scored after treatment for 6 h, 12 h, 24 h, 48 h, and 72 h, respectively. Raw bioassay data was analysed by probit analysis using the computer program SPSS 15.0, Kruskal-Wallis one-way ANOVA ranking, and Duncan's multiple range test ($P < 0.05$).

HPLC analysis

Preparation of samples: Three-week-old rice plants were selected and divided into two groups. One group was firstly treated with 1.0 mg/ml MA by culturing the rice plant in Kimura B solution (Yoshida *et al.*, 1976) with MA for 24 h, and then transferred to Kimura B solution without MA for 24 h. The other group was continuously treated with Kimura B solution without MA for 48 h as control. The rice plants sampled from the two groups were rinsed with methanol five times, ground in methanol (1 ml/g fresh plant), sonicated for 30 min, and the homogenate filtered through a 0.45-μm membrane. The filtered extract was used for HPLC analysis. The MA standard solution was prepared in methanol (1.0 mg/ml).

HPLC conditions: The HPLC analysis was performed using a Varian ProStar 240 HPLC system (Palo Alto, USA) and a Shimadzu (Kyoto, Japan) Shim-pack VP-ODS C18 column (4.6 × 150 mm) with water/acetonitrile gradient elution (from 5% to 45% acetonitrile including 0.1% trifluoroacetic acid). The column temperature was adjusted to 25 °C, the injection volume was 10 μl, the flow rate was 1.0 ml/min, and the absorption of the eluate was measured at 254 nm. The total run time per injected sample was 40 min. Each sample was analysed in triplicate. All chemicals and reagents were of analytical grade unless otherwise stated.

EPG recording

The EPG recording of BPH on rice was carried out using a Giga-4 DC EPG amplifier (Wageningen University, The Netherlands). One end of a gold wire (20 μm in diameter and 5 cm in length) was attached to the dorsal thorax of BPH with water-soluble silver conductive glue, and the

other end of the wire was connected to the amplifier through the EPG probe (Seo *et al.*, 2009). The wired BPH was then placed on the rice leaf sheath previously treated with MA as described above.

The BPH probing behaviour on treated and control rice plants was recorded simultaneously for 8 h. All EPG tests were conducted at (26 ± 2) °C, (60 ± 5)% relative humidity under continuous light conditions. The experiment was repeated 13 times.

Electrical signals and their correlation with BPH behaviour were identified based on the categories described by Seo *et al.* (2009). The EPG data was analysed using the PROBE 3.4 software (Wageningen University, The Netherlands).

Enzyme assay

BPH were treated with MA as mentioned above, except that the concentration of MA was adjusted to 0.1, 0.5, and 1.0 mg/ml. After treatment for 96 h, BPH were sampled for the following enzyme assay.

For glutathione *S*-transferase (GST) and glutathione peroxidases (GPX) analyses, ten BPH individuals were homogenized in 1.0 ml of ice-cold sodium phosphate buffer (20 mM, pH 7.0) with a tissue grinder. The crude homogenate was centrifuged at 10,000 × *g* for 10 min, at 4 °C. The supernatant was removed for determination of enzyme activities. Each treatment was repeated 9 times.

The GST activity was assayed by the method modified by Cheng *et al.* (2007), using a GST assay kit (Jiancheng Inc., Nanjing, China). Briefly, the reaction mixture consisting of 1 μM CDNB (1-chloro-2,4-dinitrobenzene), 1 μM GSH (glutathione), 1 ml ethanol, and 0.1 ml crude enzyme was prepared in a final volume of 2.4 ml with phosphate buffer (20 mM, pH 7.0). The supernatant of the reaction mixture (2 ml), reagent III (2 ml) and reagent IV (0.5 ml) were mixed. After 15 min, the absorbance was measured at 412 nm and 25 °C in a UV-1600 spectrophotometer (MAPADA Inc., Shanghai, China).

The GPX activity was measured by a spectrophotometric method according to Drotar *et al.* (1985), using a GSH assay kit (Jiancheng), as follows. The reaction mixture (2.5 ml) contained GSH (0.2 μmol), reagent I (0.1 ml), reagent II (2 ml), and the crude enzyme (0.2 ml). After 10 min, the supernatant liquid of the reaction mixture (1 ml), reagent III (1 ml), reagent IV (0.25 ml), and reagent V (0.05 ml) were mixed and allowed to stand for 15 min. The absorbance was measured at 412 nm and 25 °C. The non-enzymatic reaction without crude enzyme served as control. All tests were repeated 9 times.

Results and Discussion

Effect of MA on BPH survival rate

The BPH ingested MA with the artificial diet. The survival rate of BPH decreased with increasing MA concentration and feeding time (Table I). In contrast to the control (64.42%), the survival rate of BPH at 72 h decreased significantly to 40.59%, 27.00%, and 18.17%, at concentrations of 1.0, 2.0, and 4.0 mg/ml, respectively.

No significant difference in the BPH was observed among the treatments in the first 24 h except for the group receiving 4.0 mg/ml MA. At 48 h, the survival rate of BPH treated with 2.0 mg/ml MA was 60.25%, while it was 80.08% in the control. Therefore, MA affected the viability of BPH in a dose-dependent way.

Table I. Survival rate (%) of brown planthopper fed on artificial diet with different dosages of MA added.

MA [mg/ml]	Survival rate (%) of BPH at different feeding times				
	6 h	12 h	24 h	48 h	72 h
0.0	100.00 ± 0.00 a	98.58 ± 1.42 a	89.42 ± 2.75 a	80.08 ± 28.25 a	64.42 ± 4.92 a
0.5	100.00 ± 0.00 a	98.58 ± 1.42 a	86.58 ± 6.00 a	73.08 ± 5.50 ab	62.92 ± 7.00 a
1.0	100.00 ± 0.00 a	98.92 ± 1.08 a	87.42 ± 4.83 a	72.50 ± 8.83 ab	40.59 ± 9.42 b
2.0	98.58 ± 1.42 ab	98.58 ± 1.42 a	83.75 ± 4.75 ab	60.25 ± 4.33 b	27.00 ± 7.58 bc
4.0	94.25 ± 3.67 b	87.00 ± 1.42 a	63.33 ± 12.08 b	41.33 ± 7.75 c	18.17 ± 6.25 c

Values (means ± SE) followed by the same letter within a column are not significantly different; Duncan's multiple range test ($P < 0.05$); Kruskal-Wallis one-way ANOVA by ranks.

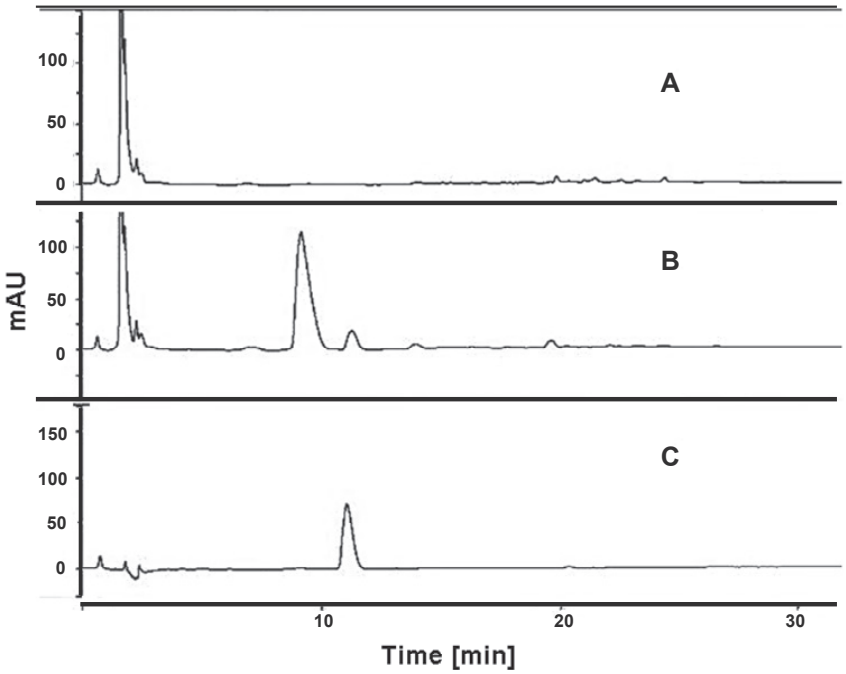

Fig. 1. HPLC of extract from (A) control, (B) MA-treated rice plant, and (C) MA standard.

Detection of MA by HPLC

Absorption of MA by rice seedlings fed with MA was investigated by HPLC. The HPLC profile of the MA-treated plants clearly showed two additional peaks (Fig. 1B) compared to the control (Fig. 1A), one was considered to be MA, because its retention time (12.65 min) was the same as that of the reference standard MA (Fig. 1C), the other was supposed to be a product derived from MA (Fig. 1B). These results suggested that MA was absorbed by the rice plants, and it was now possible to examine the effect of MA on the feeding behaviour of BPH with MA-treated plants.

Observation of the BPH feeding behaviour by EPG

The EPG technique is useful for the observation of the real-time feeding behaviour of a piercing-sucking insect on different plants, with variations in the composition of phloem sap or other cell layers (Dinant and Lemoine, 2010). In this study, EPG waveforms of BPH were identified according to Seo *et al.* (2009) with some modifications, and were assigned to the following 7 groups: np, non-penetration of stylets; N1, penetration initiation; N2, salivation and stylet movement; N3, mechanical puncture near the phloem region; N4 and N5, ingesting activities in the phloem (N4) and xylem (N5), respectively. Furthermore, N4 was divided into 2 subgroups: N4-a stands for secreting water-soluble components to avoid the response of the rice defense system, and N4-b for phloem sap ingestion (Fig. 2).

In an 8-h recording period, there were significant differences in some waveforms between BPH fed on plants treated with 1.0 mg/ml MA and the control (Table II). The average duration of N4 and N5 waveforms in the MA-treated BPH group was much shorter than that in the control. BPH fed on MA-treated rice spent 3.05 min ingesting from the xylem, which was significantly shorter than that in the control (50.44 min). Meanwhile, they spent more time walking around or being at rest (np), as well as in stylet pathway activities (Fig. 2C, Table II).

Compared with the control, fewer BPH on plants treated with 1.0 mg/ml MA performed N4 in an 8-h period, which meant that they ingested little phloem sap. At concentrations of 0.1, 0.5, and 1.0 mg/ml MA, the phloem ingestion time

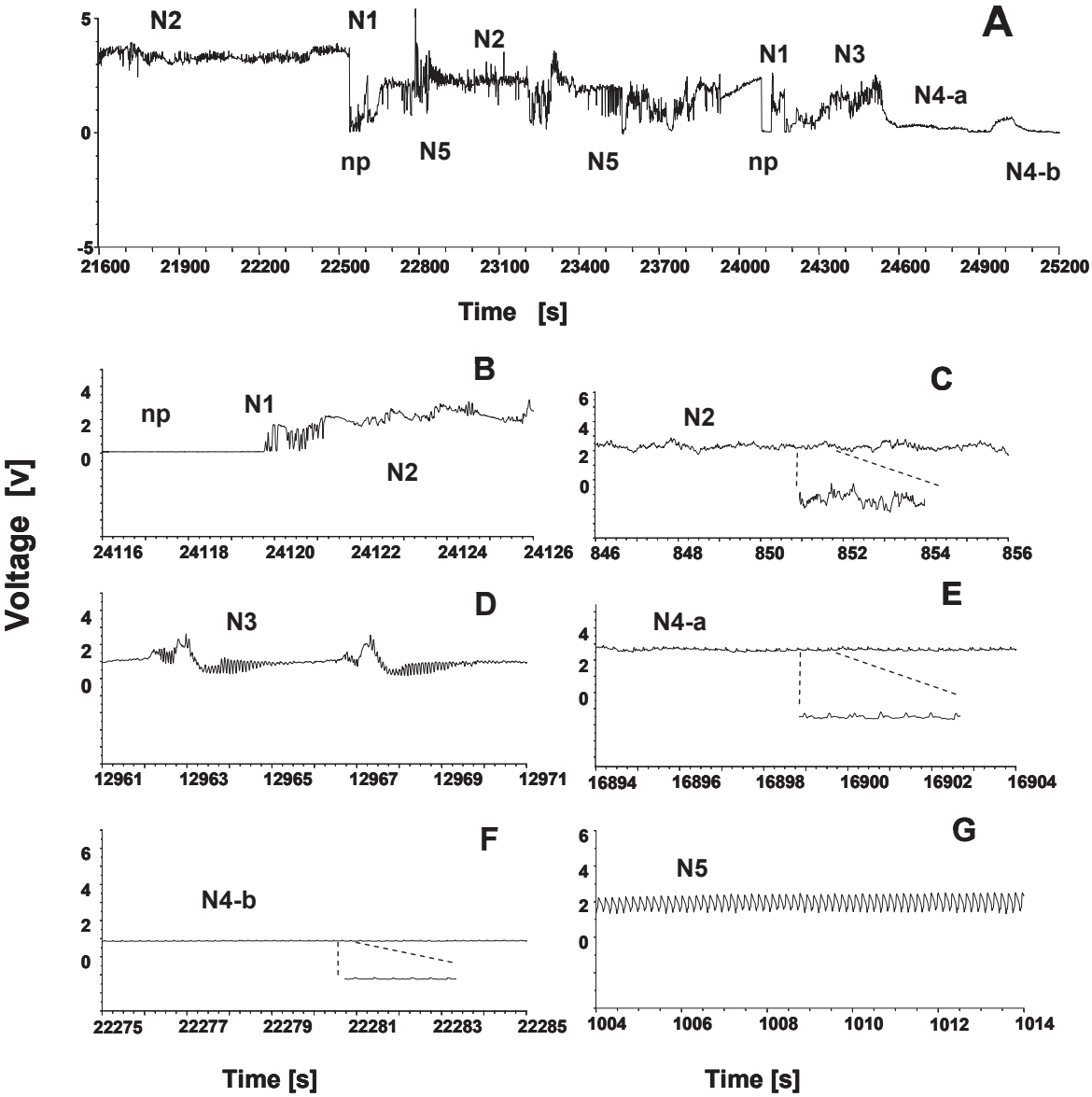

Fig. 2. Typical EPG waveforms of BPH on rice plant. (A) Overview of each waveform for 1 h; (B) np: non-penetration of stylets, N1: penetration initiation; (C) N2: salivation and stylet movement; (D) N3: mechanical puncture near the phloem region; (E) N4-a: secrete water-soluble components to damage the defense system of rice; (F) N4-b: phloem sap ingestion; (G) N5: activity in the xylem region.

of BPH decreased from 115.34 min (control) to 30.41, 7.63, and 0.36 min, respectively. However, plants treated with 0.1 mg/ml MA did not significantly affect the BPH feeding behaviour. With the increase of the MA concentration, the phenomena became more and more obvious (Table II). BPH exposed to MA delayed the first probing (the stylets punctured the plant epidermis) and increased the number of probings. The portion of the np waveform within the total recording time (8 h) showed a significant increase (from 43% to 62%), when the MA concentration increased (from 0.1 mg/ml to 1.0 mg/ml) (Fig. 3). On the other hand, the total duration of N4 and

Table II. Probing and feeding behaviours of BPH on MA-treated rice recorded with EPG for 8 h.

Stylet penetration behaviour	Control (Kimura B only)	Treatment (Kimura B + MA [mg/ml])		
		0.1	0.5	1.0
Total time of each activity per BPH [min]				
Pathway*	172.66 ± 20.51 ab	143.61 ± 21.30 a	231.65 ± 28.29 b	249.50 ± 32.48 b
Phloem	115.34 ± 23.99 a	30.41 ± 18.99 b	7.63 ± 4.63 b	0.36 ± 0.128 b
Xylem	50.44 ± 16.19 a	34.85 ± 11.79 ab	19.89 ± 9.72 ab	3.05 ± 2.28 b
Time to first occurrence [min]				
Probe**	0.32 ± 0.07 a	0.34 ± 0.11 a	0.60 ± 0.16 a	1.22 ± 0.35 b
Phloem	103.18 ± 10.93 a	66.18 ± 12.47 a	170.92 ± 65.59 a	112.49 ± 84.99 a
Number of probes	3.33 ± 0.59 a	4.00 ± 0.41 a	5.56 ± 0.47 b	7.11 ± 0.29 c
Portion of BPH performing (%)				
Phloem	100	46	46	8
Xylem	92	77	62	45

Values (means ± SE) followed by the same letter within a row are not significantly different; Duncan's multiple range test ($P < 0.05$); Kruskal-Wallis one-way ANOVA by ranks.
* Pathway: stylet movement in rice tissue; ** probe: the stylet punctured the plant epidermis.

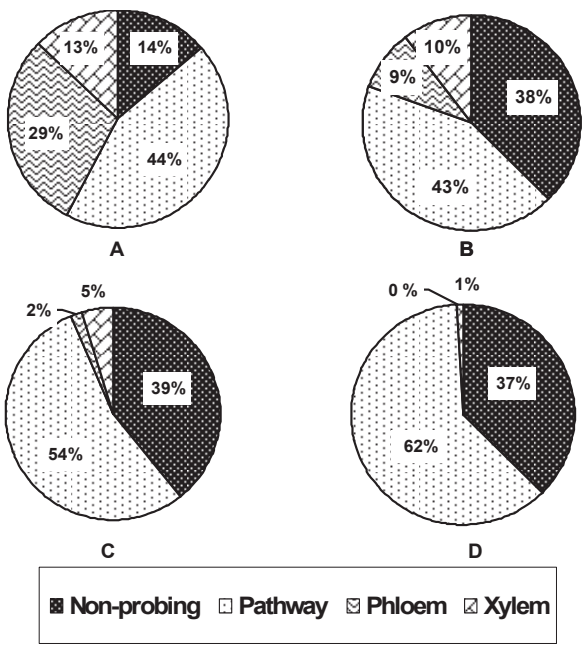

Fig. 3. The portions of each EPG waveform against the total recording time (8 h) from BPH on MA-treated plants. (A) Control (Kimura B only); (B) Kimura B + 0.1 mg/ml MA; (C) Kimura B + 0.5 mg/ml MA; (D) Kimura B + 1.0 mg/ml MA.

N5 decreased with the increase of the MA concentration; especially when MA reached the concentration of 1.0 mg/ml, the total time of N4 and N5 accounted for no more than 2.0% (Fig. 3D). These results indicated that MA acted as an antifeedant to BPH.

A previous study found shorter periods of N4 and N5 for BPH on resistant as compared to susceptible rice varieties (Kimmins, 1989). Several compounds isolated from leaf sheaths of rice have been identified as potent sucking inhibitors against BPH. This study certified that exogenous MA absorbed by rice plants acts as a sucking inhibitor on BPH, and the antifeedant effect was apparent at lower MA concentrations than the lethal effect.

Enzyme assay

GST and GPX are major enzymes involved in detoxification reactions and the metabolic resistance of insect pests to insecticides (Eaton and Bammler, 1999; Zhou *et al*., 2003). At 96 h, the enzyme activity of GST in the control BPH group was 74.46 μmol/(min mg prot), while in the BPH group treated with 0.1 mg/ml MA, the enzyme activity was raised to 90.00 μmol/(min mg prot) (Fig. 4), and at 1.0 mg/ml MA the GST activity was 100.51 μmol/(min mg prot).

GSTs form a group of ubiquitous enzymes that catalyze the conjugation between GSH and another substrate, and thus play a critical role in the cellular detoxification mechanism of both endogenous and xenobiotic compounds (Tang and Bi, 2003). A previous study revealed that the GST activity significantly increases when BPH feed on the resistant rice varieties ASD7 or Ruthu Heenati (RH) for one generation (Zhou *et al*., 2003).

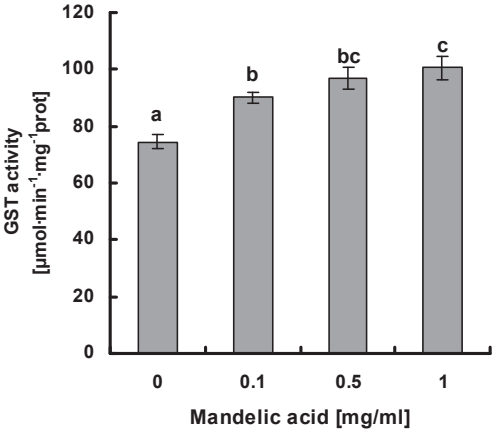

Fig. 4. GST activity of BPH treated with different concentrations of MA dissolved in 5% sucrose.

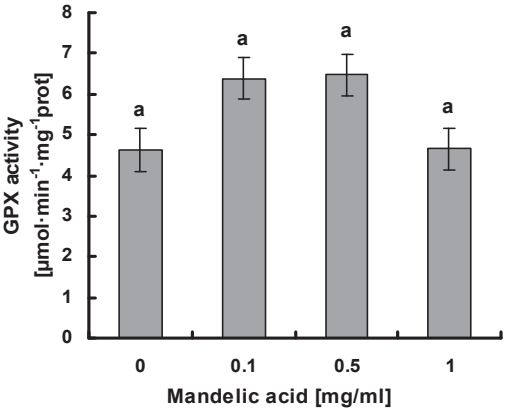

Fig. 5. GPX activity of BPH treated with different concentrations of MA dissolved in 5% sucrose.

Therefore, it was suggested that there are some compounds in ASD7 or RH accounting for the rice resistance and provoking an increase of the GST activity in BPH. The significant enhancement of the GST activity in BPH in response to MA showed that MA was recognized as a xenobiotic compound by BPH.

MA appeared to cause an increase in the GPX activity (Fig. 5), but the changes were statistically not significant.

In conclusion, our findings suggest that exogenous MA absorbed by rice plants acts as a feeding deterrent, which results in shorter ingestion duration and more probing times. The increased GST activity and decreased survival rate of BPH indicate that MA is toxic to BPH. The increased GST activity is indicative of a counteraction of BPH against MA.

Commonly used insecticides such as pymetrozine, thiamethoxam, and imidacloprid usually do not have satisfactory effects in controlling the BPH due to the development of insecticide resistance. Application of synergistic agents and additives in insecticides may be a way to enhance the efficacy of insecticides by reducing the BPH resistance to insecticides, and may aid in controlling the BPH. MA could confer resistance to the rice plants against BPH, so it has the potential to be investigated as an additive in insecticides. Furthermore, it may be possible to improve the chemical structure of MA by chemical modification, such as hydroxylation, glycosylation, and acetylation. MA was shown to have some antimicrobial activity in some microorganisms, such as, *Enterococcus* spp. and *Escherichia coli* (Putten, 1979). Some symbiotic bacteria and endofungi have been found in BPH (Tang *et al*., 2010; Dong *et al*., 2011), therefore, the next step is to explore the effects of these derivatives on BPH and its symbionts, in order to develop better synergistic agents or additives for insecticides.

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