Some aspects of induced resistance to rice blast fungus, *Magnaporthe grisea*, in rice plant infested by white-backed planthopper, *Sogatella furcifera*

Hiroo KANNO,[1,*] Masaru SATOH,[1] Takashi KIMURA[1] and Yoshikatsu FUJITA[2]

[1] Kyushu Okinawa National Agricultural Research Center; Kumamoto 861–1192, Japan
[2] Hokkaido National Agricultural Research Center; Sapporo 062–8555, Japan

Abstract

The effect of previous rice plant infestation of the white-backed planthopper, *Sogatella furcifera*, on the incidence of rice blast disease caused by the fungal pathogen, *Magnaporthe grisea*, was investigated. The fungal pathogen *M. grisea* was less likely to cause symptoms of leaf blast on rice plants that had been previously infested with *S. furcifera* than on uninfested plants. This indicates that resistance to *M. grisea* was induced in rice plants by infestation of *S. furcifera*. The number of blast lesions per plant decreased with increasing numbers of infesting *S. furcifera* from 0 to 10 pairs. The active period of induced resistance was maintained for a relatively long time being greater than 15 d. The difference in the incidence of leaf blast between *S. furcifera* infested and uninfested plants in the booting stage became smaller than that in the tillering stage, although there was a still significant difference in blast incidence between both infested and uninfested plants in booting stage. There was no significant difference in the incidence of leaf blast between damaged plants treated with needling and untreated control plants. This suggests that the simple mechanical effect to the plants caused by stylet insertion (penetration) and subsequent probing with the feeding behavior of *S. furcifera* was not related to the observed phenomenon. In *S. furcifera* infested plants, the expression of two genes regarding β-1,3-glucanase, *Gns4* and *Gns5*, was confirmed by RT-PCR analysis. These results show that infestation of *S. furcifera* apparently induced physiological changes including gene expression that were related to pathogen resistance to *M. grisea* in rice plants.

Key words: Induced resistance; rice; *Sogatella furcifera*; *Magnaporthe grisea*; β-1,3-glucanase

INTRODUCTION

Many of the studies on herbivorous insects and also on pathogens have been conducted to clarify the relationship of insects to plants and of pathogens to plants. However, studies on the relationship between insects and pathogens through host plants have seldom been conducted (Karban et al., 1987; Kanno and Fujita, 2003).

The white-backed planthopper, *Sogatella furcifera*, and the rice blast disease caused by *Magnaporthe grisea*, are economically important insect pest and disease respectively, of rice, *Oryza sativa*, throughout Southeast and Far-East Asia, including Japan. In general, *S. furcifera* does not hibernate in Japan. All of the original *S. furcifera* population emigrates from Mainland China into Japan during the rainy season from early June to early July. Then the population of the next generation of *S. furcifera* increases rapidly in rice fields, and the highest peak of the population appears at around late July or early August (Watanabe et al., 1991; Watanabe, 1996). At the same time, the rice blast disease caused by *M. grisea* also commonly develops in rice fields in Japan, especially those in the Kyushu area, and occasionally causes serious damage to the rice plants (Iwano, 1999). The authors, therefore, were interested in the interspecific relationships between *S. furcifera* and *M. grisea* through the host plants, and recently found that the resistance to the rice blast disease caused by *M. grisea* in the rice is induced by previous infestation of *S. furcifera*. Furthermore, it was confirmed that the induced resistance in the rice is systemic and is caused by the feeding behavior of *S. furcifera* (Kanno and Fujita, 2003). In this paper, the results

of studies on some other important aspects of this phenomenon are introduced and discussed.

MATERIALS AND METHODS

Test plants. Japonica rice variety Hinohikari, containing blast-resistant genes Pi-a and Pi-i (Iwano, 1999), was used in all experiments. Plants were grown under glasshouse conditions (25±1°C, 60–80% RH) from seeds planted in plastic pots containing a commercial potting soil, Hinokuni-shodo (Japan Agricultural Co.), mixed with fertilizers (nitrogen: 0.02%, phosphoric acid: 0.05%, potassium: 0.04%). Tests were conducted on plants grown to around the 5-leaf-stage, about 4 weeks post seeding.

Test insects. S. furcifera was from a laboratory-reared culture originating from adults collected in 1990 from a rice field in Chikugo, Fukuoka Prefecture, Japan. The susceptible Japonica rice variety "Reihoh" to S. furcifera was used for insect rearing. Adults of S. furcifera were allowed to oviposit on rice plants grown to the 2-leaf-stage in an insect rearing cage (25 cm×30 cm×25 cm). The rearing cages containing approximately 1,000 planthoppers individually were put in a controlled environment chamber (25°C, 50–70% RH, L14 : D10) until adults emerged 20 d after oviposition. These adults were used for all experiments.

Test fungal inoculums. The colony of M. grisea (race number: 007) used for this experiment was established in 1995 from a diseased rice paddy in Nishigoshi, Kumamoto Prefecture, Japan. The colony was incubated on oatmeal sucrose agar (OMSA) at 25°C in the dark for 2 weeks. The OMSA plates were then flooded with a 0.02% Tween 20 (surfactant) solution. The conidial suspension of M. grisea was prepared by softly scraping the mycelia from the surface of the plates using a paintbrush. A suitable concentration of conidia in suspension (about 500 per mm^2) was carefully determined by microscopic observation at a magnification of ×150, by adding distilled water.

Test 1: Effect of number of infested S. furcifera on incidence of rice blast disease caused by M. grisea. Test 1 was conducted to verify the effect of the number of infested S. furcifera on the incidence of rice blast disease caused by M. grisea. Forty rice plants at the 5-leaf-stage covered with transparent plastic cylinders (15 cm in diameter

and 70 cm in height) were divided into four equal groups. Each group of 10 plants was infested with a different number of S. furcifera, specifically 0, 2, 5 or 10 pairs of adults per plant. The first, 0, category was the uninfested control. These adults were released into a cylinder, and allowed to feed and oviposit on the plant. Two days later, all treated and control plants were removed from the cylinders, and sprayed with 2 ml/plant of conidial suspension using an airbrush sprayer (PIECE COM: PC-WIDE 308). Plants were incubated in a dew chamber (25°C, 100% RH) for 18 h before being transferred to the glasshouse. The number of typical blast lesions, called S-lesion (susceptible lesion), on the plants was counted and compared among the treatments at 7 d post inoculation. The experiment was replicated three times. The data were analyzed by Tukey-Kramer test (SAS, 2000).

Test 2: The stability of induced resistance over time. Test 2 was designed to investigate the stability of the induced resistance in rice over time. Fifty rice plants at the 4-leaf-stage were prepared for the test, and divided into five equal groups. Groups of 10 plants each were assigned to one of five categories, 0, 5, 10 and 15 d after S. furcifera infestation for 48 h and another group for the uninfested control. Firstly, the ten rice plants of the 15 d group were set in a cage (50×50×50 cm, plastic rod frame covered with a fitted cotton mesh net), then 100 pairs of newly emerged S. furcifera adults were released into the cage, and allowed to feed and oviposit on the plant. Two days later, the test plants were removed from the cage and put in the glasshouse condition. The other three groups, 10, 5 and 0 d, received the same treatment every 5 d. The 10 plants in the uninfested control group were placed in a second cage for 48 h with no additional insects, when the 0 d group was treated. Then, all of the test plants were inoculated with M. grisea and incubated as described in Test 1. After 7 d, the number of S-lesions of rice blast on the plants was counted. The experiment was replicated two times. The data were analyzed by Tukey-Kramer test (SAS, 2000).

Test 3: Effect of plant stage on induced resistance. Test 3 was conducted to confirm the effect of plant stage on induced resistance. Twenty rice plants at the 4-leaf-stage (tillering stage: vegetative stage) and another 20 plants at the 8-leaf-stage (booting stage: reproductive stage) were prepared

and used in this experiment. The test plants in both leaf stages were divided into two groups, *S. furcifera* infested group and uninfested control group. The groups infested with *S. furcifera* at both leaf stages containing 10 plants each were put in the cage mentioned above, then 100 pairs of newly emerged *S. furcifera* adults were released into the cage, and allowed to feed and oviposit on the plant. The other two groups consisting of the uninfested category in both leaf stages were also placed in two other cages (same size, but no insects) for use as control plants. Two days later, these infested and uninfested plants were removed from the cages and then inoculated with *M. grisea* by the same method described above. We counted the number of S-lesions on the plants at 7 d after inoculation. The experiment was replicated two times. The data were analyzed by Tukey-Kramer test (SAS, 2000).

Test 4: Effect of mechanical damage on the incidence of rice blast disease caused by *M. grisea*. This test was conducted to clarify the effect of mechanically simulating *S. furcifera* feeding on induced resistance to *M. grisea*. Twenty rice plants at the 5-leaf-stage were prepared and divided into two groups for the test. The leaves of one of the groups of 10 plants were mechanically damaged by puncture using a sewing needle. The plant was punctured 50 times every 12 h for 48 h, so that the total number of needle punctures was 250 per plant. Another group of 10 plants was used as the untreated control. The test plants were then inoculated with *M. grisea*. Inoculation, incubation and investigation were conducted by the same methods described above. The test was replicated twice. The data obtained was analyzed by Tukey-Kramer test (SAS, 2000)

Test 5: Genes expression coding PR-protein, *β*-1,3-glucanase, in rice plant infested by *S. furcifera*. This test was conducted to investigate the gene expression coding for one of the PR-proteins, *β*-1,3-glucanase, in rice plants infested by *S. furcifera*. Sixty rice plants at the 5-leaf-stage were prepared and divided into two groups, *S. furcifera* infested and uninfested plants. In this test, *S. furcifera* infestation was restricted to the stems of the test plants, which were encased in transparent plastic cylinders (5 cm in diameter and 15 cm in height). Ten pairs of *S. furcifera* were released into each cylinder in the infested group. Twenty four hours later, the leaves of all test plants were cut off

from the stems using scissors, and immediately frozen in liquid nitrogen and stored at $-80°C$. For isolation of total RNA, 2 g of frozen material were ground in liquid nitrogen and resuspended in 20 ml of extraction butter [2% cetyltrimethylammonium bromide, 0.1 M Tris-HCl (pH 9.5), 20 mM EDTA, 1.4 M NaCl, 1% *β*-mercaptoethanol] and incubated at 65°C for 10 min. The aqueous phase was extracted twice with an equal volume of chloroform/isoamyl alcohol (24 : 1). LiCl precipitation with 1/4 volume 10 M LiCl was repeated twice, followed by resuspension in DEPC-treated water. The mRNA was isolated from the total RNA using an Oligotex-dT30 mRNA Purification Kit (TaKaRa). For RT-PCR analysis, cDNA was synthesized from 1 μg of mRNA using a First-strand cDNA Synthesis Kit (TaKaRa). One or 4 μl of the diluted cDNA (1/230) was used for analysis of a rice actin mRNA or two types of *β*-1,3-glucanase mRNAs respectively. The expression of a rice actin gene (GenBank accession number X16280 and AC091532) was used as the control. The amplification conditions were as follows: 2 min at 94°C; 32 cycles of 30 s at 94°C, 30 s at 55°C, 1 min at 68°C. Primer pairs were as follows: *Gns4*, 5′-gctctgat-cattggagcatttgc and 5′-tggcgtagttgaggctgatgtcg; *Gns5*, 5′-ttggagttgcggccattcctac and 5′-gagcgcg-tagttgatgtcgatc; actin gene, 5′-tcaagtaccccatcgag-catgg and 5′-caatccacatctgctggaatgt.

RESULTS

Effect of number of infested *S. furcifera* on incidence of rice blast disease caused by *M. grisea*

The symptom of rice blast disease initially appears as lesions on the rice leaves that are confirmed with the naked eye on the rice leaves from around 4 d after inoculation of the conidial suspension of *M. grisea* in the glasshouse condition, 25°C and 70–80% RH. The number of S-lesion indicating typical symptoms of rice blast disease differed significantly between *S. furcifera* infested rice and uninfested rice. In the infested rice group, S-lesions were seldom found on the plant, although many S-lesions were observed on uninfested control plants. A decreasing tendency in the number of S-lesions per plant was apparently observed with increasing numbers of infested insects, and the difference among the treatments was significant ($p < 0.05$), as shown in Fig. 1. The incidence of leaf
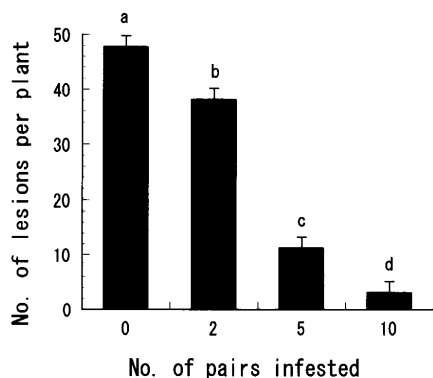
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Fig. 1.　Incidence of rice blast disease caused by *Magnaporthe grisea* on rice (Japonica variety: Hinohikari) previously infested by different numbers of the white-backed planthopper, *Sogatella furcifera*. Standard bars (SB) indicate mean number of blast lesions per plant, and vertical bars on the SB indicate standard errors. Means accompanied by different letters are significantly different at $p<0.05$ (Tukey-Kramer test; SAS, 2000).
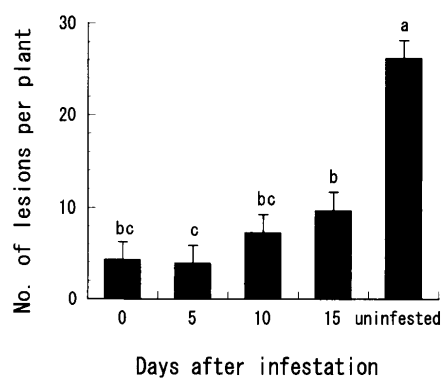

Fig. 2.　Effect of the dates elapsed after infestation of *Sogatella furcifera* on incidence of rice blast disease caused by *Magnaporthe grisea* on rice (Japonica variety: Hinohikari). Standard bars (SB) indicate mean number of blast lesions per plant, and vertical bars on the SB indicate standard errors. Means accompanied by different letters are significantly different at $p<0.05$ (Tukey-Kramer test; SAS, 2000).

blast in rice infested by *S. furcifera* was significantly lower than that in uninfested control plants, even with the low density infestation of only two pairs of *S. furcifera*.

The stability of induced resistance over time

The number of S-lesions on *S. furcifera* infested plants 1 d after infestation was quite small compared with that on uninfested control plants. The lesions gradually increased over time from 0 to 15 d after infestation. However, the number of lesions on plants infested by *S. furcifera* was still significantly smaller ($p<0.05$) than that on uninfested control plants, even at 15 d after infestation, as shown in Fig. 2.

Effect of plant stage on induced resistance

The incidence of rice blast varied greatly according to the plant stage. In the case of plants at the tillering stage (vegetative stage) 4 weeks after planting, the difference in lesion numbers between *S. furcifera* infested and uninfested plants was highly significant ($p<0.05$). On the other hand, in the case of plants at the booting stage (reproductive stage) 8 weeks after planting, the incidence of leaf blast was apparently lower than that in the tillering stage in both *S. furcifera* infested and uninfested control plants, as shown in Fig. 3. The difference of incidence of leaf blast between *S. furcifera* infested and uninfested plants was much smaller than that in the tillering stage, although the difference
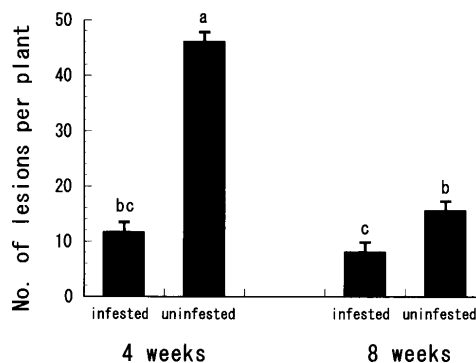

Fig. 3.　Effect of plant stages, such as tillering stage and booting stage, on incidence of rice blast disease caused by *Magnaporthe grisea* on rice (Japonica variety: Hinohikari) previously infested by the white-backed planthopper, *Sogatella furcifera*. Standard bars (SB) indicate mean number of blast lesions per plant, and vertical bars on the SB indicate standard errors. Means accompanied by different letters are significantly different at $p<0.05$ (Tukey-Kramer test; SAS, 2000).

between the two groups was still significant.

Effect of mechanical damage on the incidence of rice blast disease caused by *M. grisea*

There was no significant difference ($p<0.05$) in the incidence of leaf blast between damaged plants treated with needling and untreated control plants, although the mean value of the S-lesions in the plants treated with needling was slightly lower than that in untreated control plants, as shown in Fig. 4.

Expression of β-1,3-glucanase genes in plants infested by *S. furcifera*

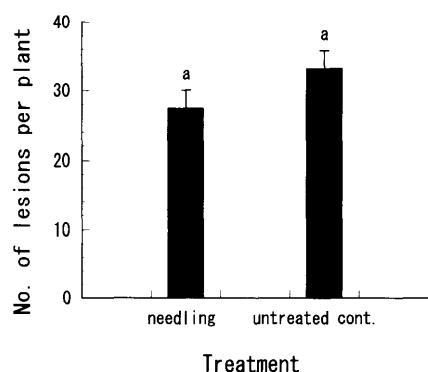The β-1,3-glucanase is well-known as a defense-

Fig. 4. Effect of mechanical wounding by needling on the incidence of blast disease caused by *Magnaporthe grisea* on rice (Japonica variety: Hinohikari). Standard bars (SB) indicate mean number of blast lesions per plant, and vertical bars on the SB indicate standard errors. Means accompanied by different letters are significantly different at $p<0.05$ (Tukey-Kramer test; SAS, 2000).

+ : *S. furcifera* infested plant
— : uninfested control plant

Fig. 5. Effect of *S. furcifera* infestation on the expression of β-1,3-glucanase genes. Two genes, *Gns4* and *Gns5*, were investigated by RT-PCR analysis. The expression of a rice actin gene was used as an internal control.

related gene induced in plants against fungi. RT-PCR method was applied to detect the expression of β-1,3-glucanase genes, *Gns4* and *Gns5* (Romero et al., 1998). Amplification of genomic DNA was distinguishable from that of cDNA because of the presence of an intron. No contamination of genomic DNA occurred in the cDNA sample. Both genes were more expressed in *S. furcifera* infested plants compared with uninfested control plants. In particular, the induction of *Gns5* expression was clearly significant, as shown in Fig. 5.

DISCUSSION

The interspecific relationship between two kinds of insects has been studied in several species. Attacks by herbivorous insects induce chemical and physical changes in many host plants (Green and Ryan, 1972; Tallamy and Raupp, 1991; Baldwin, 1994; Dicke, 1994; Schoonhoven et al., 1998). In several systems host changes caused by herbivore damage have had deleterious effects on subsequent herbivores. Herbivores that fed on damaged plant tissue had lower survival rates, reduced individual growth rates, and reduced adult weight or fecundity, or both (Karban and Myers, 1989; Denno et al., 1995). However, the interspecific relationship between insects and pathogens has seldom been studied (Karban et al., 1987; Kanno and Fujita, 2003). The negative interspecific effects between an herbivorous insect and a fungus were first observed in both the spider mite, *Tetranychus urticae*,
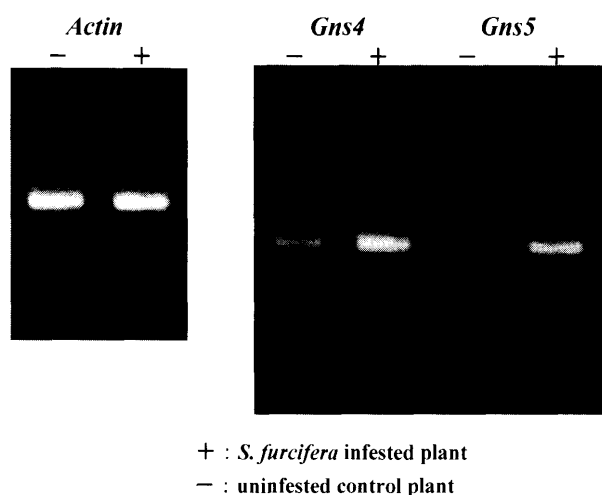
and the fungal pathogen, *Verticillium dahliae*. It was reported that changes in cotton seedlings caused by previous exposure to spider mites reduced the probability of infection and severity of symptoms caused by the vascular wilt fungus, *V. dahliae* (Karban et al., 1987).

Kanno and Fujita (2003) recently demonstrated the following phenomenon in rice plants. Rice plants that had previously been infested with *S. furcifera* were less likely than controls to develop the blast disease caused by *M. grisea*. The number of blast lesions, especially S-lesions, on the leaves of rice plants that were infested with *S. furcifera* was significantly lower than that on the uninfested plants. Further, the blast incidence was strongly suppressed by infestation with either male or female adults of *S. furcifera*, and no significant difference between the two sexes was observed. There was also a significant difference in the number of lesions between *S. furcifera* infested and uninfested plants when the infestation was restricted only to the rice plant stems. In this case, the lesion number on the plants that were previously infested with *S. furcifera* was around 40% lower than that of uninfested control plants.

The results of Kanno and Fujita (2003) show that *S. furcifera* infestation can strongly inhibit the development of rice blast symptoms. *S. furcifera* was no longer present in the first experiment when rice plants were inoculated with conidia, therefore infestation of *S. furcifera* must have induced physi-

ological changes in the plant that reduced its susceptibility to the fungus, *M. grisea*. The incidence of blast disease did not significantly differ in the presence of either all-male or all-female *S. furcifera*, thus they hypothesize that the lower disease incidence was induced by the feeding behavior of either sex rather than the oviposition behavior of females. The incidence of rice blast is also suppressed by restricted infestation of *S. furcifera* to only the stems of the host plant. This result indicates that induced physiological changes in the plants, reducing susceptibility to *M. grisea*, are a systemic phenomenon.

We also report here on the induced systemic resistance in rice to *M. grisea*, the causal agent of the rice leaf blast. The results of our present experiment basically support those of the studies described above, and more detailed phenomena were further elucidated. The incidence of the leaf blast is negatively correlated with the number of *S. furcifera* infested on the plants, and the results indicate that strong resistance is induced in rice by *S. furcifera* infestation, because the lesion number on the plants infested by even two pairs (two males and two females) was significantly smaller than that in uninfested control plants. This induced resistance continues for a relatively long time of more than 15 d, and is strongly enhanced in the vegetative stage compared to the reproductive stage of the plants. An important implication of this result is that the susceptibility to *M. grisea* in rice must be reduced with growth of the plant from the vegetative stage to reproductive stage. Furthermore, the blast incidence was not affected by mechanical wounding. This result suggests that the simple mechanical effect to the plants caused by stylet insertion (penetration) and subsequent probing with feeding behavior of *S. furcifera* is not related to the phenomenon.

Several possible mechanisms could produce a general resistance pattern. Resistance may result from a physiological change in the plant, which requires no mechanism of recognition or response to a unique component of the attacking pathogen. Such a physiological change need not be adaptive for the plant but may reflect wounding or deterioration of metabolic functions. The first species attacking the plant may deplete the most desirable nutrients or plant parts. Alternatively, resistance may be caused by metabolites that undergo activa-

tion or *de novo* synthesis and accumulate in the plant after attack. Chemicals that accumulate after damage may have activity against a variety of organisms. For example, phytoalexin isoflavonoids reduce fungal growth and also deter feeding by herbivorous insects (Karban et al., 1987).

Recently, technological advances of molecular biology have clarified the mechanism of such induced resistance in plants at the molecular level. For example, in the tomato plant, it has been demonstrated that mechanical wounding, herbivore attack and pathogen attack can elicit a defense system, such as the jasmonic acid pathway, salicylic acid pathway, etc., and then some phytoalexins and pathogenesis related proteins (PR-proteins) against pathogens and herbivores are finally induced in the plants (Fidantsef et al., 1999; Sivasankar et al., 2000; Orozco-Cardenas et al., 2001). In rice plants, Schweizer et al. (1997, 1998) also confirmed that some PR-proteins are produced in the rice with activation of the jasmonic acid pathway by pathogen attack and also mechanical wounding. The authors also confirmed in this study that two genes, *Gns4* and *Gns5*, coding for one of the PR-proteins, β-1,3-glucanase, which indicates a strong antimicrobial activity, were expressed in rice plants infested by *S. furcifera*. We now speculate that these two genes may not have been expressed in rice plants by mechanical wounding with treatment of needling, and are presently trying to verify this.

The present results also indicate that some physiological changes may occur in rice plants fed on by *S. furcifera*. One of the possible mechanisms of the phenomenon is speculated to be as follows. 1) Saliva of *S. furcifera* contains an elicitor regarded as a trigger of the phenomenon; 2) in the rice plant fed on by *S. furcifera*, defense systems, such as the jasmonic acid pathway and the salicylic acid pathway, are activated by the elicitor; 3) then the phytoalexins and PR-proteins, not only β-1,3-glucanase but also others, that protect against pathogens are finally produced in the rice. This hypothesis regarding the mechanism will be investigated as the next step of this research series.

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