11. FEEDING BEHAVIORS OF THE BROWN PLANTHOPPER AND VARIETAL RESISTANCE OF RICE TO THIS INSECT

Kazushige SOGAWA*

Introduction

In Asian and Pacific regions the brown planthopper, *Nilaparvata lugens* (Stål), is well-known as a serious insect pest which outbreaks sporadically and causes destructive damage to rice by sucking the plant sap. Also this insect has recently been identified as a vector of grassy stunt virus in Southeast Asia. The application of insecticides is now the only practical method for controlling this insect, but it is not economical in the tropical regions where overlapping insect generations occur throughout the year and the repeated applications are required to keep the insect population below the economic injury level. Besides, from the ecological standpoint, such a heavy application of insecticides is not always desirable because of destruction of natural enemies, development of insecticide-resistant pests and poisoning to mammals and fish. For the above reasons, a practical significance of the insect-resistant rice varieties is being increasingly realized as an alternative control measure in the multicropping rice areas. Recently several rice varieties that possess high level of resistance to the brown planthopper have been screened out and the projects of varietal improvement using them are now under way (IRRI, 1967–1969).

In the present report, the feeding behaviors of the brown planthopper are previously described, and the main subject is centered on the biological and biochemical aspects on the causes of varietal resistance of rice plants to this insect.

Feeding Behaviors of the Brown Planthopper

The planthoppers as well as other hemipterous insects have the mouth parts specialized for ingestion of a liquid diet. The parts that penetrate into the plant tissues are two pairs of slender chitinous bristles, i.e. the mandibular and maxillary stylets. These stylets are placed in the labial groove from which they protrude by a telescopic action of the labium during feeding. The piercing organ of the brown planthopper is about 550–600 μ in length. In the course of the stylet penetration the brown planthopper ejects a coagulable salivary secretion which rapidly sets to gel encasing the protruded stylets and forms so-called stylet sheath in plant tissues (Fig. 1). This secretion also leaves a circular spot at the site of stylet insertion on the plant surface. The stylet sheaths produced by the brown planthopper show a single or branched tubular structure, being 3.5–5.0 μ in inner diameter and sometimes over 300 μ in length. These stylet sheaths are available to study the feeding behaviors of the planthoppers, since they remain within the plant tissues even after withdrawal of the stylets and easily visualized by histological staining. The stylets are mainly inserted intracellularly passing the parenchyma, and their branches terminate in various tissues in different frequency. However, the sheaths usually curve toward the vascular bundles, indicating that the brown planthopper feeds on them. In the vascular bundles, the sheaths arrive more

* Faculty of Agriculture, Nagoya University, Chikusa-ku, Nagoya, Japan
Fig. 1. Diagram showing the stylet insertion of the brown planthopper.

frequently in the phloem than xylem tissues. Although many branches end in parenchymal cells, it is doubtful that the insects suck those cells. In the course of feeding the planthoppers always excrete a large amount of honeydew from the anus. The frequency of excretion in the female adult of the brown planthopper varies from 7 to 40 droplets per hour, and the total amount of daily excretion estimates about 13μl on an average. The rate of honeydew excretion of the male adults is about one-tenth of that of the female ones. One female adult is also estimated to discharge about 12μg of amino acids and
0.25 mg of sugars per day through excretion on seedlings of *japonica* rice. These data on honeydew output are available index to estimate the ingestive input of this insect. It is of interest that the brown planthopper excretes considerable amount of sugar-free excreta as well as sugar-containing ones. This seems to suggest that the insects ingest both the phloem and xylem sap. Following the brown planthopper feeding, the symptoms of the hopperburn injury first appear on the rice plants as yellowing of the leaf blades of elders, and progress to extent that the entire above-ground parts of the plants turn brown and die. At the same time, the root development and its physiological activities are also drastically reduced. A remarkable accumulation of free amino acids and amides, accompanied by decrease of protein, in the injured leaves is usually noted. It is probably due to the disturbance of protein metabolism in the leaf blades as a result of draining of free amino acids transported through vascular tissues by the intensive sucking of the insects. Concerning this it is estimated that a single female adult takes up more than 20μg of nitrogen from the plant per day and the sustained feeding of 10 to 20 female adults per rice tiller causes nitrogen-deficiency of the host plants in a short period. However further investigations are still necessary on the causes of hopperburn.

**Varietal Resistance of Rice to the Brown Planthopper**

An *indica* rice variety Mudgo is highly resistant to the brown planthopper, which has been found out through the systematic mass screening tests (IRRI, 1968). The following descriptions refer to the nature and mechanism of the brown planthopper resistance of this variety.

In the field and greenhouse experiments, the brown planthopper exhibits strong non-preference behavior for the resistant variety Mudgo through a gustatory response, although the initial alighting response of the immigrant planthoppers to the different varieties including Mudgo is almost identical. When the brown planthopper nymphs are reared on Mudgo, they show a little higher mortality and slower growth, and the emerged adults are usually smaller and largely macropterous (Table 1). In spite of these

<table>
<thead>
<tr>
<th>Observations</th>
<th>Resistant Mudgo</th>
<th>Susceptible T(N)-1</th>
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<tbody>
<tr>
<td>Nymphaal mortality (%)</td>
<td>14.9</td>
<td>8.2</td>
</tr>
<tr>
<td>Nymphaal period (day)</td>
<td>14.2</td>
<td>12.5</td>
</tr>
<tr>
<td>Body weight of newly emerged female adults (mg)</td>
<td>2.8</td>
<td>4.1</td>
</tr>
<tr>
<td>Head width of female adults (mm)</td>
<td>0.79</td>
<td>0.83</td>
</tr>
<tr>
<td>Rate of macropterous form of female adults (%)</td>
<td>45</td>
<td>36</td>
</tr>
<tr>
<td>Rate of increase in body weight of newly emerged female adults</td>
<td>1.0</td>
<td>1.5</td>
</tr>
<tr>
<td>Matured eggs in ovaries²</td>
<td>few</td>
<td>many</td>
</tr>
<tr>
<td>Rate of reproduction³</td>
<td>4–5</td>
<td>13–15</td>
</tr>
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1) Rate of change in body weights of the immature female adults when caged for two days on the test plants.
2) The ovaries were observed after being caged for two days.
3) Numbers of the adult planthoppers produced by ten mated females were counted at one month after their caging on the plants.
adverse effects, Mudgo plants still allow enough high survival rate of individual insect, indicating that Mudgo contains no lethal toxic entity. However, the fecundity of the newly emerged female adults is strikingly inhibited on Mudgo, where their ovaries mature very slowly and poorly. Consequently their reproductive rate is reduced by around one-fourth, which is too low to built-up enough high population to cause hopper burn to the host plants (Table 1). In view of these evidences, it is probable that the non-preference behavior and reduced reproductivity are the contributing factors to resistance phenomena of Mudgo to the brown planthopper.

The laboratory studies on the feeding behavior of the brown planthopper on the different rice varieties represent available informations to understand the causes of non-preference and reduced reproductive rate of the insects on Mudgo. The stylet sheaths deposited in the Mudgo tissues terminate in the vascular bundles at higher percentages than those in the susceptible plants, and no mechanical barrier within the Mudgo plants prevents the insertion of the styles and feeding site location; nevertheless the insects excrete much reduced amount of honeydew on Mudgo (Table 2). Also the insects try to probe more frequently on Mudgo. This suggests that the chemical nature of the plant sap of Mudgo appears adversely affect the maintenance of insect feeding, and that the non-preference response and lowered fecundity of the planthopper could be due to the repellency of Mudgo's sap and subsequent failure of satisfactory ingestion of nutrients.

Table 2. Comparison of the feeding behaviors of the brown planthopper and total free amino acid contents in the resistant and susceptible rice varieties.

<table>
<thead>
<tr>
<th>Observations</th>
<th>Resistant Mudgo</th>
<th>Susceptible T(N)-1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Preference behavior</td>
<td>Not prefered</td>
<td>Preferred</td>
</tr>
<tr>
<td>Probing frequency (No./insect/day)</td>
<td>50.8</td>
<td>15.4</td>
</tr>
<tr>
<td>Termination of stylets in vascular bundles (%)</td>
<td>79</td>
<td>60</td>
</tr>
<tr>
<td>Stylets penetration through fiber layer (%)</td>
<td>45</td>
<td>10</td>
</tr>
<tr>
<td>Honeydew excretion (ratio)</td>
<td>1</td>
<td>69</td>
</tr>
<tr>
<td>Total free amino acid contents</td>
<td></td>
<td></td>
</tr>
<tr>
<td>in whole plant (ratio)</td>
<td>1</td>
<td>3.7</td>
</tr>
<tr>
<td>in xylem exudate (ratio)</td>
<td>1</td>
<td>2.5</td>
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The chemical analysis of whole plant extracts and xylem exudate reveals that the free amino acid concentration varies significantly among the different rice varieties, being particularly low in Mudgo (Table 2). The whole plant extracts commonly contain aspartic acid, glutamic acid, alanine, and valine. However, the concentrations of aspartic acid and glutamic acid are considerably lower in Mudgo. Furthermore, the xylem exudate of Mudgo contains \( \gamma \)-aminobutyric acid as a major constituent instead of asparagine and glutamic acid occurring in the xylem exudates of susceptible rice varieties. It is a well-established evidence that the rate of sap uptake of aphids is significantly influenced by the quantity and quality of free amino acid constituents in the host plant. This is also true for the brown planthopper. In the separate experiments, it has been demonstrated that specific amino acids such as aspartic acid, glutamic acid, alanine, asparagine and valine evoke significantly stimulated feeding response. Generally they cause a reduction in the probing frequency and enhance the honeydew excretion. Also, their
phagostimulatory activity is synergized by sucrose. Excepting those amino acids, a number of other amino acids including γ-aminobutyric acid have no effect or somewhat deteriorate the ingestion. Basing on these experimental data it is possible to say that the free amino acids naturally occurring in the rice plants play an important role in the feeding behavior of the brown planthopper. In case of Mudgo, its plant sap seems to be less acceptable to the brown planthopper, because of lacking or lowered concentration of phagostimulative amino acids; and this is at least partially responsible for the suppression of insect feeding on Mudgo. In this regard, it is of interest to note that the feeding behavior of the brown planthopper on Mudgo is quite similar to that on the nitrogen-deficient rice plants. So far there is no available informations indicating the presence of specific secondary plant substances which regulate the planthopper feeding.

On the basis of informations presented above, it is concluded as follows: One of the resistant factor of Mudgo is located in the chemical quality of the plant sap, probably lowered concentration of phagostimulative amino acids. It has a primary influence on the planthopper feeding through the gustatory response. Such influence is manifested as non-preference behavior or reduction of food uptake. The reduced ingestion is responsible for lowered fecundity and subsequent failure in population building-up. It may be also concluded that the field resistance phenomena of Mudgo result mainly from the non-preference behavior and reduced fecundity of the planthopper. In this respect, the non-preference behavior seems to be more closely related to the host selection behavior of the macropterous adults, while the reduced rate of food uptake is more important in suppression of high reproductive potential of the brachypterous females. These explanations are summarized in Figure 2.

Unfavourable gustatory factors in Mudgo
(Deficiency of phagostimulative amino acids)

↓

Inhibition of sustained insect feeding

↓

Non-preference behavior

↓

Decrease of sap uptake

Reduction of adult fecundity

↓

Lower insect population

↓

Lighter damage to Mudgo

↓

Resistance phenomena of Mudgo

Fig. 2. The interaction between the brown planthopper and resistant rice variety Mudgo.

Finally, the evidence that some kinds of amino acid derivatives, i.e. tyramine, tryptamine and met oxytryptamine, act as potential feeding deterrents gives a clue of further investigations on the chemical regulation of the feeding behavior of the brown planthopper.
Discussion

M. B. Kalode, India: You have said that sucrose is not a feeding stimulant to the brown planthopper. I would like to know what type of test you carried out to prove this? Because in my experiment I found sucrose is definitely a feeding stimulant to the brown planthopper.

Answer: The effect of sucrose was also evaluated by means of the same method as that for amino acids. Sucrose was found to accentuate the activity of the phagostimulative amino acids, but it was relatively less phagostimulative itself.

M. B. Kalode, India: You have shown in one of the slides that there is an increase in free amino acids in hopper burn plants. Do you think this increase is due to either direct introduction of amino acids along with salivary secretions or due to introduction of proteases.

Answer: The both possibilities are probably negative, because the amount of amino acids injected into the plant tissues along with salivary secretions is negligible, and the salivary secretions contain no proteases. The increase of amino acids in hopper burn plants seems to be due to the disturbance of protein metabolism in leaf blades.

M. B. Kalode, India: Do you have any information on the type of amino acids presented in the hopper burn plants caused by the brown planthopper?

Answer: Particularly, the increase of asparagine, glutamine and arginine was remarkable in the injured leaves.

M. B. Kalode, India: You mentioned tyramine, tryptamine and metoxytryptamine as potential feeding deterents. Would you please let me know at what concentrations they were tested and how they were tested?

Answer: Their effect was tested at 1,000, 100 and 10 ppm in 5% sucrose solution by using the apparatus described in the amino acid experiments.

M. Sakai, Japan: 1) Did you test GABA for feeding deterrent action to the insect? 2) Is there possibility that tryptophan derivatives such as tryptamine etc. act as feeding deterrent in the plant?

Answer: 1) GABA has no effect on the insect feeding at 1%. 2) There has been no experimental data on the influence of such aromatic amines in the rice plants.

References