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Mechanisms of Brown Planthopper Resistance in Mudgo Variety of Rice (Hemiptera : Delphacidae)

Kazushige SŌGAWA[1] and M. D. PATHAK[2]

The International Rice Research Institute, Los Baños, Laguna, The Philippines

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Mudgo, an *indica* rice variety, is highly resistant to brown planthoppers. The insects exhibited strong non-preference for this variety in greenhouse and field experiments. This reaction was evident primarily as a gustatory response and not as an alighting response. The insects caged on Mudgo had high mortality, a slow growth rate, small body size, and low fecundity. Newly emerged female planthoppers caged on Mudgo had underdeveloped ovaries that contained few mature eggs. Planthoppers did not exhibit any difficulty in inserting their stylets or reaching the vascular bundles in Mudgo plants. Still when caged on this host they lost weight and excreted very little honeydew. These results indicated that Mudgo plants either lacked feeding stimuli or possessed one or more taste repellents for the planthoppers. The sugar content of susceptible and resistant plants was not significantly different but resistant plants contained smaller quantities of amino acids, particularly of asparagine. In separate tests, female brown planthoppers showed strong attraction to this amino acid. Thus, lower asparagine content in Mudgo is suggested as a factor of its brown planthopper resistance.

INTRODUCTION

The brown planthopper, *Nilaparvata lugens* STÅL is serious pest of rice (*Oryza sativa* L.) throughout Asia (HINCKLEY, 1963; KISIMOTO, 1965; MIYAKE and FUJIWARA, 1962; NASU, 1964; PATHAK, 1968; and SUENAGA, 1963). The insect is present in varying populations on most rice crops, but often its damage is noticed only after the crop suffers hopperburn. It is not generally realized that even low populations can cause reduced tillering, reduced crop vigor, fewer panicles, and higher percentages of unfilled grains (BAE and PATHAK, 1969). Also, the insect has recently been recorded as the vector of the grassy stunt virus disease of rice (RIVERA et al., 1966). Furthermore, heavily fertilized fields planted with high-tillering, short-statured rice varieties (which signify improved plant type), are apparently more susceptible to this pest than the conventionally cultivated fields.

Currently, control is by insecticides sprayed on the foliage or applied to the paddy water (PATHAK, 1968). However, recent studies at The International Rice Research Institute (IRRI) have identified some rice varieties that possess high natural resistance to this insect.

The resistance of one variety, Mudgo, is outstanding. Insects caged on

[1] Present address: Laboratory of Applied Entomology, Faculty of Agriculture, Nagoya University, Chikusa, Nagoya, Japan.

[2] Present address: Cornell University, Ithaca, New York, 14850, U.S.A.

Mudgo suffer high mortality so their populations do not build up, they cause little plant damage and the resistance in Mudgo is transferable to more desirable plant types (PATHAK et al., 1969). This paper reports the interactions between the brown planthopper and the Mudgo plants with emphasis on causes of planthopper resistance in this variety.

MATERIALS AND METHODS

Three rice varieties were used in these experiments: Mudgo (highly resistant), IR 8 (susceptible but somewhat tolerant), and Taichung (Native) 1 (highly susceptible). The brown planthoppers used were from a colony originally collected from IRRI experimental plots but reared for several generations in a greenhouse. The details of various techniques used are described along with the results of the corresponding experiments.

RESULTS

Preference of the Planthoppers for Different Rice Varieties

Twenty potted plants each of IR 8, Taichung (Native) 1, and Mudgo were at 30 days after transplanting placed in a completely randomized design in a field plot. These were exposed to natural infestations of brown planthoppers. The pots were spaced 80 cm apart. On 10 random plants of each variety, daily records were made for the number of planthoppers present. The number of insects on the remaining 10 plants was counted at 5-day intervals. The insects on all plants were removed after each count.

Daily observations of the migration of planthoppers to the plants were made. The results showed that only IR 8 received significantly larger numbers of insects (at the 5 per cent level) than Mudgo plants. Taichung (Native) 1 had more insects than Mudgo, but the differences were not significant.

The results of the counts every 5 days, however, showed that nearly 90 per cent of the insects were clustering on IR 8 and Taichung (Native) 1 plants, reflects the insect's ability to locate a host and then stay on it. Of the total population recorded, only 7 per cent of the females and 12 per cent of the males were recovered from Mudgo plants (Table 1). These indicated that the planthoppers exhibited little difference in alighting on these varieties but then moved off Mudgo plants for sustained feeding.

Similarly, when adult planthoppers were introduced into a cage containing these varieties in a greenhouse, almost all females settled on either IR 8 or Taichung (Native) 1 within 24 hours after their release (Fig. 1). Again, the differences in varietal preference were not apparent within the first 6 hours after release. Generally the male insects exhibited similar trends in host preference but were more mobile than the females. These results show that male and female planthoppers much preferred the IR 8 and Taichung (Native) 1 varieties for sustained feeding.

Table 1. Number of Planthoppers Collected on Potted Plants of Different Rice Varieties in Field Experiments (IRRI, 1968)

Total number of insects collected per observation	Percentages of insects collected on Mudgo	IR8	T(N) 1
Daily collections[a]:			
206 (female)	21	47	32
30 (male)[b]	30	53	17
Collections made at 5-day intervals[c]:			
1034 (female)	7	49	45
309 (male)	12	48	40

[a] Average of daily smaples collected during 16 days.
[b] Possibly the total number of insects attracted is too small to show any trend for host preference.
[c] Average of three samples collected during 15 days.

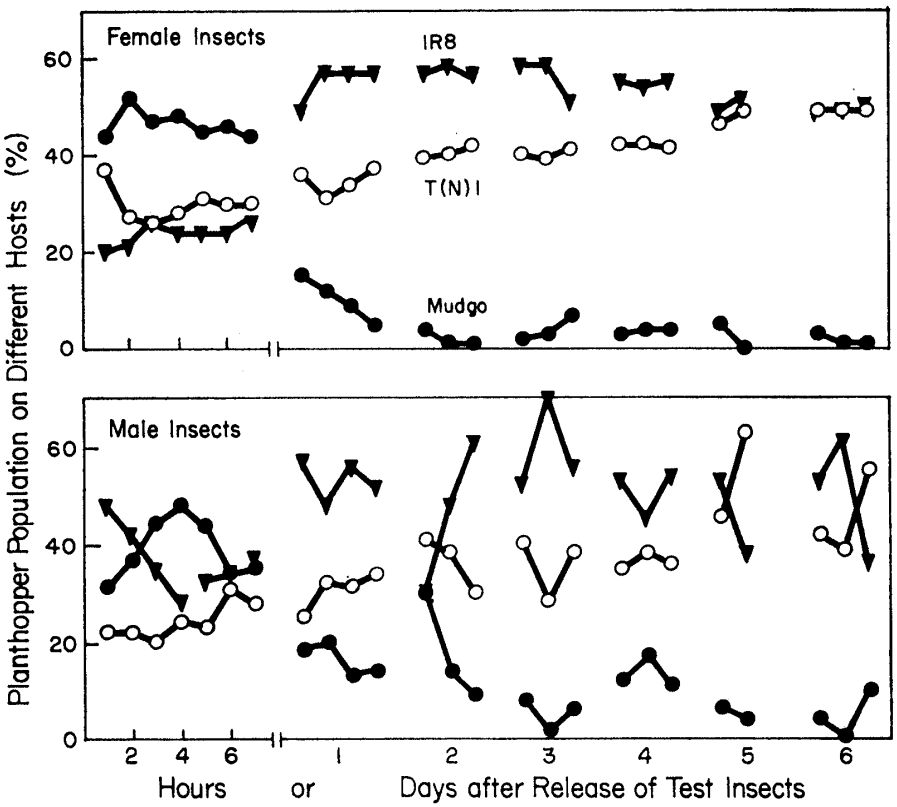

Fig. 1. Distribution of brown planthoppers on resistant and susceptible hosts. Macropterous adults were released in a cage containing the three varieties in a greenhouse experiment. (IRRI, 1968).

Survival of and Population Build-up by Brown Planthoppers on Susceptible and Resistant Varieties

In another greenhouse experiment, newly hatched planthopper nymphs were caged on individual seedlings of IR 8, Taichung (Native) 1, and Mudgo. Cylindrical

plastic cages (8 × 57 cm) with fine mesh cloth windows were used for this purpose. Ten nymphs were placed in each cage. The insects caged on Mudgo had higher mortality and slower rates of growth than those caged on IR 8 and Taichung (Native) 1 plants. Also, the adults that developed on Mudgo were smaller in size, weighed less, and had higher percentages of alates than those on other hosts.

The survival and fecundity of the adults on these varieties was also investigated in two additional experments by caging adults on potted plants in a greenhouse. In one experiment five pairs of newly emerged adults were caged on 1-month-old plants using 16-×69-cm cylindrical plastic cages. In the other experiment, 10 mated females were caged on 2-month-old plants using 35-×125-cm cylindrical cages suported by an iron frame and covered with fine mesh nylon cloth. In both experiments, the cages enclosed the plant completely.

The adult insects caged on Mudgo suffered higher mortality and produced

Table 2. Number of Adult Planthoppers Produced by Ten Mated Females at 1 Month after Their Caging on Individual Plants of Resistant and Susceptible Rice Varieties

Variety	Number of replications	Number of adults per plant			Remarks
		Minimum	Average	Maximum	
Mudgo	9	10	91	204	A few scattered nymphs present. No visible plant damage.
IR8	8	91	312	573	Numerous nymphs present. Hopperburn symptoms beginning to show.
T(N) 1	9	80	267	725	

The plants were infested at 60 days after transplanting. IRRI, 1968.

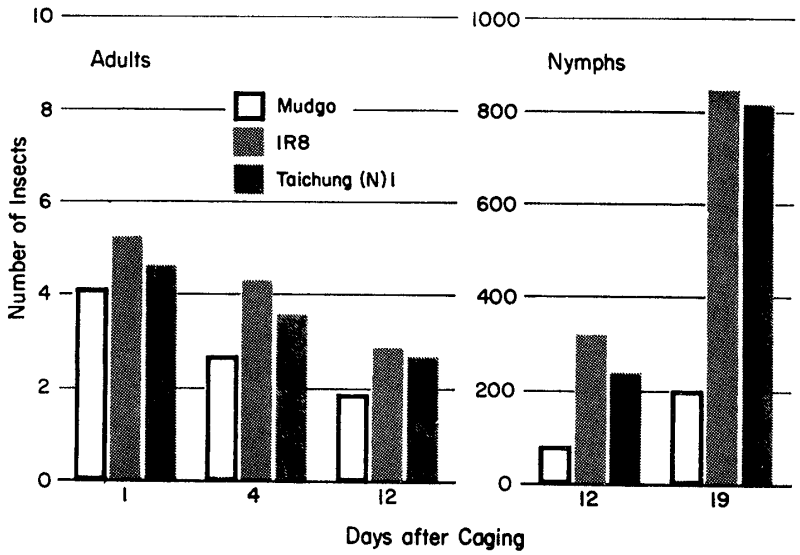

Fig. 2. Number of the brown planthopper adults and their progenies 30-day old plants Mudgo, IR8, and Taichung (Native) 1 rice varieties.

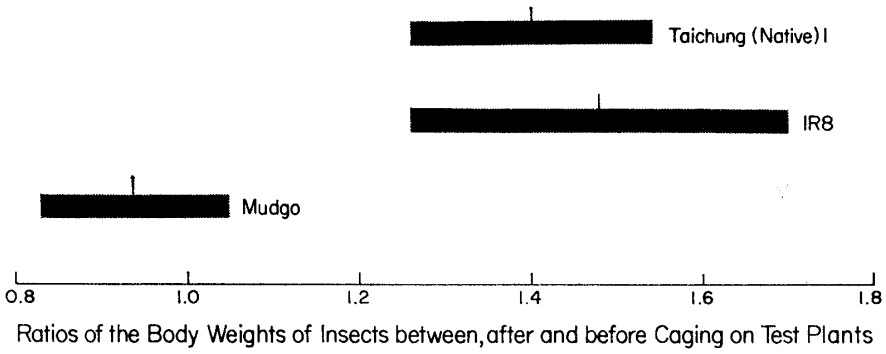

Fig. 3. Rate of change in body weights of female brown planthoppers when caged for 2 days on the different rice varieties. (IRRI, 1968).

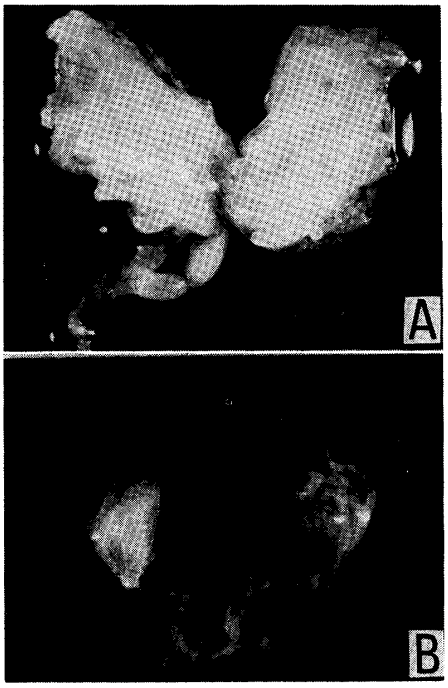

Fig. 4. Differences in the ovary development of newly emerged brown planthoppers after being caged for 3 days on Taichung (Native) 1 (A) and Mudgo (B) plants. (IRRI, 1968).

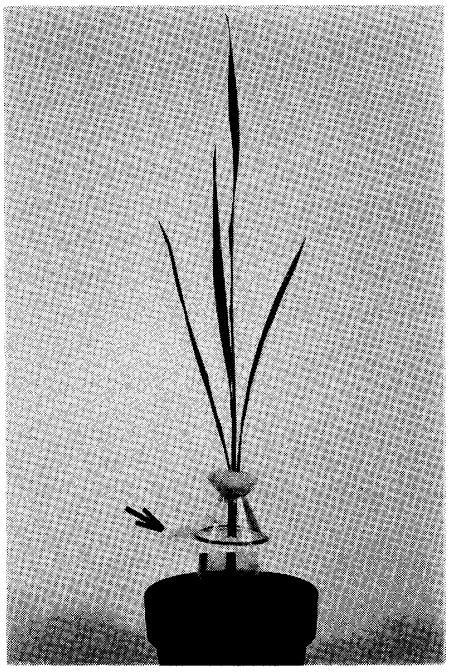

Fig. 5. Arrangements for collecting honeydews excreted by brown planthoppers on rice plants. (IRRI, 1968).

about one-fourth as many nymphs as those on IR 8 and Taichung (Native) 1 plants (Fig. 2). Nineteen days after infestation, plants of the latter two varieties were becoming heavily damaged so records on population development could not be made. However, a similar population trend was also obtained on comparatively older plants that supported the adults and their progenies up to 1 month after caging (Table 2). Furthermore, in simultaneous experiments, insects caged on Mudgo plants lost weight while those caged on susceptible hosts gained significantly

(Fig. 3). Also, females caged on resistant and susceptible hosts exhibited dramatic difference in the development of their ovaries (Fig. 4). Thus, these results confirm earlier records of the high resistance of Mudgo to brown planthoppers (PATHAK et al., 1969) and indicate that the pest population should continually decline on Mudgo plants.

Causes of Resistance

Ability of insects to feed on Mudgo plants:

One possible explanation of the insect's high mortality and low fecundity on Mudgo is that it probably did little feeding on this host. This was supported by results showing that even when caged for short periods on Mudgo plants, planthoppers lost weight while those on IR 8 and Taichung (Native) 1 gained significantly (Fig. 3).

The relative amounts of feeding by the planthoppers on these hosts was assessed by measuring the honeydew excreted by them when caged on different hosts. The honeydew was collected on a filter paper at the bottom of a conical plastic cage placed around the base of the test plant (Fig. 5). Five adult insects were introduced into each cage. These were removed 48 hours later. Five filter paper was also taken out and air-dried in the laboratory. The honeydew on the filter paper was visible as pale blue spots under ultraviolet light. It could be also stained by dipping the filter paper in ninhydrin. The amino acids in the honeydew produced purplish red spots on ninhydrin treatment. Besides these qualitative assessments, a more quantitative measurement was also made by spectrophotometric assay of sugars in the honeydew.

The results showed that both male and female insects excreted very little honeydew on Mudgo as compared with those on IR 8 and Taichung (Native) 1

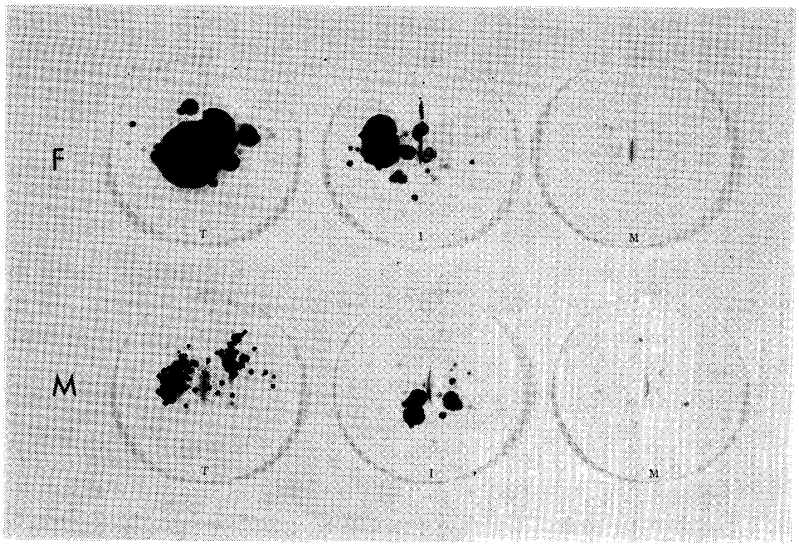

Fig. 6. Honeydew excreted by brown planthopper females (top row) and males (bottom row) when caged on Mudgo (M), IR8 (I) and Taichung (Native) 1 (T) rice varieties. The honeydew absorbed on filter paper was stained with ninhydrin. (IRRI, 1968).

Table 3. Measurement of Total Sugars Contained in the Honeydew Excreted by Female Brown Planthoppers on Different Rice Varieties

Replications	Total sugar contained in the honeydow (absorbance at 625 mμ) Mudgo	IR 8	T (N) 1
1	0.05	0.30	0.18
2	0.02	2.43	0.68
3	0.01	1.35	1.22
4	0.00	3.00	1.00
5	0.01	2.52	3.80
Average	0.02	1.94	1.38
Ratio	1	97	69

Five adult insects were caged on each variety for 24 hours. IRRI, 1968.

Table 4. Relative Concentrations of Sugars and Free Amino Acids in Different Rice Varieties as Determined by Their Light-Absorbance in a Spectrophotometer (IRRI, 1968)

Rice Variety	Sugars		Free amino acids	
	Absorbance at 625 mμ	Ratio	Absorbance at 570 mμ	Ratio
Mudgo	0.24	1.0	0.09	1.0
IR8	0.24	1.0	0.16	1.8
T(N) 1	0.19	0.8	0.33	3.7

plants (Fig. 6). On the latter two hosts, the female insects excreted more honeydew than the males. However, no distinct difference in quantity of honeydew excreted by male and female insects on Mudgo plants was found. Quantitatively compared, the total honeydew excreted by insects feeding on IR 8 and Taichung (Native) 1 contained 97 and 69 times more sugar respectively than the honeydew of insects feeding on Mudgo plants (Table 3). The total sugar content of Mudgo plant itself was not lower than those of IR 8 and Taichung (Native) 1 plants (Table 4).

Accessibility of insects' stylet sheaths to feeding sites:

These results thus established that the planthoppers did less feeding on Mudgo than on IR 8 and Taichung (Native) 1 plants. Whether this was because of the inability of their proboscises to reach the proper feeding sites was investigated by microtomic sectioning of the stylet sheaths in different varieties. For this study, individual planthopper adults were confined for 24 hours using 2×2×5 cm rectangular cages on leaf sheaths near the base of the plants. A total of five insects were caged on each variety and the experiment was repeated five times. The feeding marks on the plant surface were counted after staining the exposed plant parts with a 2 per cent erythrocin solution. In experiments designed to investigate the path of stylets in the plant tissues, the insects were allowed to feed for 2 days on a leaf sheath near the plant base. This leaf sheath part was fixed in a mixture of formalin, ethanol and acetic acid and, following

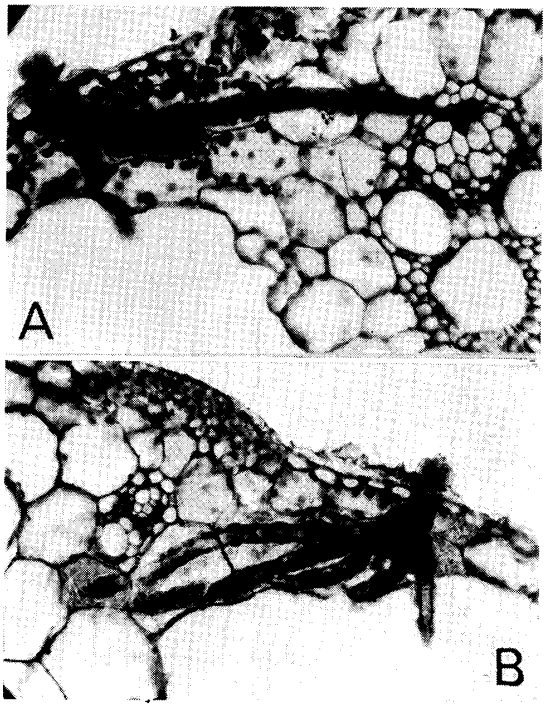

Fig. 7. The salivary sheaths produced by brown planthopper adults in Taichung (Native) 1 (A), and IR8 (B) plants. (IRRI, 1968).

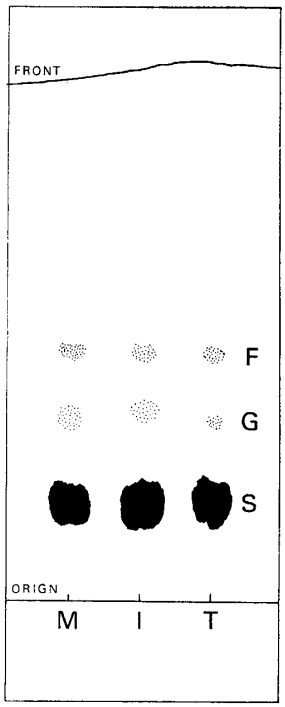

Fig. 8. Paper chromatogram of sugars in the three rice varieties, Mudgo (M), IR8 (I), and Taichung (Native) 1 (T). S=Sucrose; G=Glucose; and F=Fructose. (IRRI, 1968).

Table 5. COMPARISON OF THE FEEDING BEHAVIOR OF BROWN PLANTHOPPER ADULTS ON DIFFERENT RICE VARIETIES (IRRI, 1968)

Observation	Mudgo	IR8	T(N) 1
Average feeding marks per insect per day			
Female	50.8	15.8	15.4
Male	31.0	15.6	17.2
Sites of stylets penetration[a] (%)			
Fiber layer	45	22	10
Parenchyma	55	78	90
Termination of salivary sheaths[a] (%)			
Vascular bundles[b]	79	47	60
Non-vascular tissues	21	53	40

[a] Numbers of the salivary sheaths studied in Mudgo, IR8, and T(N) 1 were 457, 153, and 425 respectively.

[b] Based on at least one branch of the salivary sheath entering the vascular bundles.

standard procedures, then was microtomed into 15 μ-thick cross sections. The were stained with safranin 0 and fast green.

Planthoppers, like other plant-feeding homoptera, secrete a coagulable salivary

fluid when they puncture plant tissues (SŌGAWA, 1967). This secretion leaves a circular spot on the plant surface, called the feeding mark, and a salivary sheath within the plant tissues (Fig. 7). These were used to estimate the probing frequency by the planthoppers and to study the course taken by their stylets within the plant tissues.

On IR 8 and Taichung (Native) 1 one male or female planthopper produced an average of about 15 feeding marks in 24 hours, while on Mudgo plants the male and female insects produced 31 and 50 feeding marks, respectively (Table 5). Furthermore, stylet punctures through the fiber tissues were distinctly less frequent in IR 8 and Taichung (Native) 1 than in Mudgo plants. Conversely, stylet punctures through the parencyhma were less ferquent in Mudgo than in IR 8 and Taichung (Native) 1 plants. Also higher percentages of the salivary sheaths terminated in vascular bundles of Mudgo than of IR 8 and Taichung (Native) 1.

Thus no mechanical barrier to the insects' feeding was apparent in Mudgo plants. In addition, the insects had better access to feeding sites in Mudgo than in IR 8 and Taichung (Native) 1 plants. That the insects nevertheless did much less feeding on Mudgo than on IR 8 and Taichung (Native) 1 plants suggested that Mudgo plants probably contained a feeding inhibitor or lacked feeding stimulus (or stimuli) for this insect. Thise aspects were further explored by

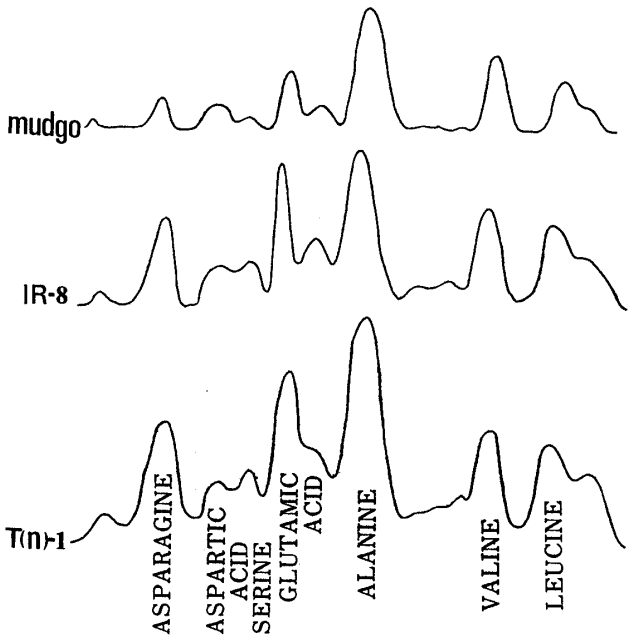

Fig. 9. Amino acid composition of the three rice varieties Mudgo, IR8, and Taichung (Native) 1, Patterns of paper chromatogram were recorded with demsitometer (Photvolt Corporation, Model No. 52-c).

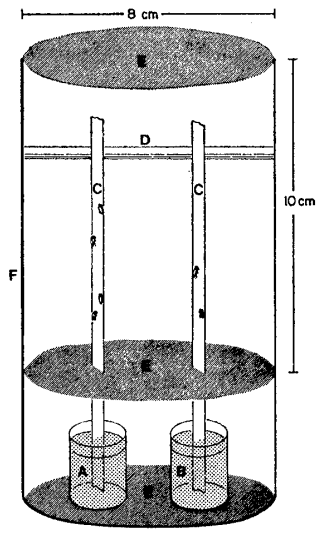

Fig. 10. Apparatus used to study the feeding preference of planthoppers for different solutions. A : Test solutions; B : Distilled water; C : Filter paper; D : Glass rod to suspend the filter papers; E : Wire gauze; F : Translucent plastic cylinder.

analyzing the plants for their sugar and amino acid contents.

Sugar and amino acid contents of the test varieties:

Samples of one-month-old plants of Mudgo, IR 8, and Taichung (Native) 1 were dried at room temperature and then ground to a fine powder, which was then extracted with chloroform to remove lipoidal materials, and finally extracted with 80 per cent ethanol. The ethanol extract was dried, redissolved in distilled water, and centrifuged to remove insoluble materials. Qualitative analysis of sugars and amino acids in the supernatant was done by chromatography. A mixture of butanol, acetic acid, and water (4 : 1 : 2 v/v), was used as the solvent. Anilinehydrochloride was used for detecting sugars and ninhydrin for detecting amino acids. The relative concentration of these constituents in different varieties was determined colorimetrically using anthrone for sugars and ninhydrin stannous chloride for amino acids.

The main sugar in these varieties was sucrose, with traces of glucose and fructose (Fig. 8). The Taichung (Native) 1 plants had a somewhat lower sugar content than Mudgo and IR 8. The sugar contents of the latter two varieties were identical (Table 4). Thus, the results suggested that the differences in the planthopper-susceptibility of the varieties were not related to their sugar contents. On the other hand, total amino acid concentration of these varieties differed and was particularly low in Mudgo plants (Table 4). Qualitatively, however, all three varieties contained the same amino acids (Fig. 9). The major amino acids were alanine, glutamic acid, valine, leucine, asparagine, aspartic acid, and serine. The asparagine content of Mudgo plants was much lower than that of the other host varieties (Fig. 9).

Table 6. PREFERENCE OF BROWN PLANTHOPPERS FOR DIFFERENT SOLUTIONS OVER DISTILLED WATER

Compounds Tested	Ratio of insects recorded on treated filter paper over insects on filter paper dipped in distilled water	
	Female	Male
Sucrose	2.4	3.0
Alanine	1.2	0.6
Arginine	1.2	1.2
Asparagine	2.2	1.2
Aspartic acid[a]	0.2	0.3
Glutamic acid[a]	0.7	0.4
Glycine	0.8	1.2
Isoleucine	1.3	1.5
Lysine	0.8	0.6
Serine	1.5	0.8
Valine	1.0	1.7

Ten pairs of insects were released in each cage containing a test compound and distilled water. IRRI, 1968.

[a] pH 3.5.

Preference of the Brown Planthoppers for Sucrose and Amino Acids

In another experiment, the stimulatory effect of sucrose and 10 amino acids on the feeding by brown planthoppers was tested using the apparatus shown in Fig. 7. The lower tip of a filter paper strip inside the plastic cylinder was dipped in the test compound while the lower tip of a second strip was dipped in distilled water. The strips stayed moist by capillary action. Twenty brown planthopper adults (10 males and 10 females) were then introduced into each cylinder and the number of insects on each filter paper was recorded at desired intervals. Five per cent sucrose and one per cent solutions of the 10 amino acids were thus evaluated, each in separate experiments.

Of the compounds tested, sucrose and asparagine exhibited a distinct stimulatory effect on insect's feeding (Table 6).

DISCUSSION

In experiments on screening of rice varieties for resistance to the brown planthopper, Mudgo, a variety from India, suffered no apparent damage even under insect populations high enough to kill 80 to 90 per cent of the plants of the test varieties planted in adjacent rows (IRRI 1967). In subsequent studies Mudgo was found to be highly resistant to this pest (PATHAK et al., 1969). The experimetnts described in this paper were undertaken to investigate the causes of planthopper resistance in this variety.

In field experiments, the flying-in planthoppers exhibited non-preference for Mudgo plants, Because this was more distinct in observations made every 5 days than in daily recordings, the non-preference apparently was the outcome of gustatory rather than visual or olfactory responses. Mudgo plants are tall, they have elongated internodes, comparatively few tillers, and light colored leaves. IR 8 and Taichung (Native) 1 plants are short, heavy tillering, and dark-leaved. But that non-preference was not evident as alighting response on these plants and that the differences in non-preference were detectable even during the seedling stage when the plants were identical morphologically, plant morphological characters do not appear to be of singificance in determining the preference of the pest. This has been further confirmed by transferring the resistance of Mudgo to short, heavy tillering and dark-leaved plants (IRRI, 1968).

Planthoppers caged on Mudgo had lower survival and prolonged nymphal periods, and were smaller and lighter in weight than those on IR 8 and Taichung (Native) 1 plants. Furthermore, planthoppers caged on Mudgo lost weight while those on IR 8 and Taichung (Native) 1 gained weight significantly. The females caged on Mudgo plants had retarded ovaries.

These results show strong antibiosis effects of Mudgo plants on the brown planthopper and provide new information on this pest and resistant rice variety host plant interrelationships. SUENAGA (1963), MIYAKE and FUJIWARA (1962), and KISIMOTO (1965) reported that nymphs reared on such unsuitable hosts as *Panicum crusgalli* var. *hispidulum*, *Zizania latifolia*, and *Leersia japonica* generally developed into macropterous adults.

The possible causes of Mudgo's antibiosis to brown planthoppers could be

one or more of the following: The insects did not feed enough to ingests appropriate quantities of required nutrients, the plants lacked nutrients vital for the insect or the plants contained materials toxic to the pest. That the insects caged on Mudgo even for a day or two lost weight and excreted very little honeydew indicated that they did much less feeding on Mudgo than on susceptible hosts. Their body-weight gain of 140 to 150 per cent during a 48-hour caging on the latter hosts is comparable to the normal body weight gains by female planthoppers during the preoviposition periods (Kisimoto, 1965). Furthermore, newly emerged females caged on Mudgo for 3 days (which corresponds with their preovipositional periods) had underdeveloped ovaries without matured eggs. Insects caged for the same period on susceptible hosts had normal ovaries with fully developed eggs. It is known that the development of internal reproductive organs of this insect is almost completed during the last nymphal instar but the egg formation (yolk and chorion) takes place after adult emergence (Suenaga, 1963). Since the insects did little feeding on Mudgo, their ovarial underdevelopment was problably due to lack of nutrients.

Similar differences in the amounts of food taken from resistant and susceptible hosts by certain species of aphids have been recorded (Pathak and Painter, 1958; Maxwell and Painter, 1959; Auclair, 1959; and McMurty and Stanford, 1960). McMurty and Stanford (1960) also reported that the stylets of spotted alfalfa aphid reached the phloem of susceptible varieties less frequently than they did the phloem of resistant varieties. Jayaraj (1967) suggested the anomalous thickening around vascular bundles in resistant castor bean plants as the cause of leafhopper resistance. However, in our studies the planthoppers did not exhibit problems either in puncturing the plants surface or in reaching the vascular bundles thereby indicating the absence of any mechanical barrier to their feeding on Mudgo.

This leaves the possibilities of the presence of one or more taste repellent or the absence of feeding stimulus (or stimuli) in Mudgo for the planthopper. The hypothesis is further supported by the fact that the insects, probably in an effort to locate palatable spots, punctured Mudgo plants more frequently than they did the susceptible varieties IR 8 and Taichung (Native) 1. This reaction could be compared to the restless behavior and frequent change of feeding sites by spotted alfalfa aphids caged on resistant plants (Howe and Smith, 1957; McMurty and Stanford, 1960).

Thus the contents of plant sap appeared to adversely affect the feeding of planthoppers on Mudgo. Auclair et al. (1967) and Maltais and Auclair (1957) recorded that aphid-resistant pea varieties contained low concentrations of free and total amino acids. For *Myzus persicae* (Sulzer), sucrose and amino acids played important roles in probing response and feeding rate (Mittler and Dadd, 1965; and Mittler, 1967 a), and several dietary amino acids, especially methionine, enhanced feeding rates (Mittler, 1967 b, c). Dorothy and Beck (1963) reported that sugars, amino acids, and an unidentified stimulant in the seedcoat controlled the continuity of feeding by the large milkweed bug. Resistance to the brown planthopper does not appear to be due to differences in sucrose contents of resistant and susceptible varieties (Table 5). However, the resistant variety Mudgo contained lower concentrations of amino acids (particularly of asparagine)

than the susceptible varieties. In separate tests, female planthoppers were strongly attracted to this amino acid. Thus it suggests that the non-preference of Mudgo for feeding by brown planthppers could be due to its lower asparagine content. However, this does not explain the non-preference response of the males.

The biochemical basis of insect resistance is often a complex phenomenon and lower asparagine contents in Mudgo plants may be just one of the fectors of resistance. These aspects are being further investigated.

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