ABSTRACT

The inheritance of resistance to the brown planthopper (Nilaparvata lugens Stal.) in three breeding lines of rice (Oryza sativa L.), IR747B2-6, IR1154-243, and IR4-93, was studied. Seven-day-old seedlings were infested with second- and third-instar nymphs of brown planthopper and seedling injury was recorded 7 to 8 days after infestation.

The resistance of IR747B2-6 was conditioned by a single dominant gene which was allelic to the dominant gene of the variety 'Mudgo' (Bph 1). The resistance of IR1154-243 and of IR4-93 was governed by the same recessive gene which was also allelic to the recessive gene conditioning the resistance of 'ASD 7' (bph 2). IR4-93 inherited its resistance from 'H-105.' But both parents of IR747B2-6 and of IR1154-243 were susceptible. We concluded that 'TKM 6,' one of the parents of IR747B2-6, is homozygous for Bph 1 but is also homozygous for a gene, I-Bph-1, which inhibits Bph 1. 'Zenith,' one of the parents of IR1154-243, may also have a similar inhibitor gene.

Additional index words: Insect resistance, Nilaparvata lugens, Inhibitor gene, Hopper burn, Grassy stunt virus.

THE brown planthopper (Nilaparvata lugens Stal.) is one of the most serious insect pests of rice (Oryza sativa L.) throughout Asia. Light infestations of planthoppers reduce tillering, plant height, number of productive tillers per plant, and general vigor of the crop and increase the number of unfilled grains. Heavy infestations can destroy the crop completely, a condition known as "hopperburn" (10). The brown planthopper also transmits the grasy stunt virus (11) which causes serious damage to rice in some areas. Improved cultural practices (heavy application of nitrogen fertilizer, for example) which are used with high-yielding, high-tillering cultivars have favored the build-up of brown planthopper populations. Because chemical control of high insect populations for prolonged periods is expensive, the development of insect-resistant cultivars is receiving increased attention at International Rice Research Institute (IRRI), Los Baños, Philippines (5) and elsewhere.

Several tall tropical cultivars which are highly resistant to the brown planthopper have been identified (10). These cultivars, however, have poor plant type and low yielding ability. The inheritance of resistance in cultivars 'Mudgo,' ‘CO 22,’ ‘MTU 15,’ ‘ASD 7,’ and ‘PTB 18’ has been investigated by Athwal et al. (2) and by Athwal and Pathak (1), and in Mudgo by Chen and Chang (3). The resistance to brown planthopper in Mudgo, ‘MGL 2,’ ‘CO 22,’ and MTU 15 is governed by dominant alleles at the same locus (Bph 1), whereas recessive alleles at bph 2 locus convey resistance in ASD 7 and PTB 18. Bph 1 and bph 2 are either allelic or are very closely linked and no recombination between these two genes has been observed.

In 1969, severe outbreaks of brown planthoppers occurred at the IRRI farm. A yield trial of 55 early-maturing selections with improved plant type was severely attacked and all but two selections suffered hopperburn. These two selections, IR747B2-6 and IR1154-243, suffered little damage in all replications (7). When tested in the greenhouse, they were found again to be resistant to the brown planthopper. Surprisingly, none of the parents of these two selections were resistant to the brown planthopper.

Since IR747B2-6 and IR1154-243 have improved plant type and other desirable agronomic traits, they are used as parents in the IRRI breeding program. Another dwarf selection, IR4-93, which has improved plant type and is resistant to brown planthopper, is also being used in the breeding program. It inherited its resistance from H-105.

The objectives of the studies reported herein were: 1) to determine the mode of inheritance of resistance
### RESULTS

**Segregation for resistance to brown planthopper in parents**

<table>
<thead>
<tr>
<th>Cross</th>
<th>Resistant</th>
<th>Susceptible</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>IR747B2-6 \times TNI</td>
<td>57</td>
<td>109</td>
<td>166</td>
</tr>
<tr>
<td>IR747B2-6 \times IR1154-243</td>
<td>93</td>
<td>54</td>
<td>147</td>
</tr>
</tbody>
</table>

*Note: The data on these F2 segregations are presented as resistant and susceptible in all F2 populations, but fewer seedlings died than expected on the basis of independent assortment of resistance genes. In the Mudgo selections and IR747B2-6 TKM-6/2, the cross was repeated to study the mode of origin of its resistance. TKM 6 was also crossed with IR4-93, ASD 7 Sel. from Karsamba Red, and IR24 for resistance, as parents. Since our studies showed that IR1154-243 and IR4-93 have a recessive gene for resistance, the former was crossed with ASD 7 Sel. from Karsamba Red, TNI and IR1154-243 segregated into 1 resistant: 3 susceptible, thereby confirming that the resistance in IR1154-243 and IR4-93 was recessive.*

**Allele Tests**

<table>
<thead>
<tr>
<th>Allele</th>
<th>P, value,</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>R</td>
<td>0.08</td>
<td>220</td>
</tr>
<tr>
<td>S</td>
<td>1.00</td>
<td>220</td>
</tr>
</tbody>
</table>

*Note: The F1, F2, and F3 progenies of all resistant and the reciprocal crosses showed no differences.*
to have originated through complementary gene action. Therefore, the origin of resistance under monogenic control, not under complementary gene action. If one susceptible parent was homozygous for one gene of the complementary system and the other susceptible parent homozygous for the other gene, resistant plants should be obtained at a predictable frequency in the F2 generation. However, the F2 populations of crosses between TKM 6 and other susceptible varieties, like IR8 and TNI, were found to be susceptible. Moreover, the resistance in both selections is of combination of two complementary genes from two resistant plants at the expected frequency on the basis of genetic recombination between the parents. However, the proportion of resistant seedlings was much lower than expected. This conclusion was confirmed in a study of 219F3 F2 populations of resistant varieties and selections. A small proportion of the seedlings of the resistant parents also died, the latter possibility seems more plausible.

The discovery of a contaminant seed, since the product of a rare recombination event would result in the observed low proportion of resistant seedlings. The logical explanation which the available data permit is that TKM 6 is homozygous for a dominant gene as well as for a gene which inhibits the expression of a gene. Since IR8 was obtained from TKM 6, crossing it with IR24 has resulted in progenies resistant to brown planthopper; and moderate levels of resistance to stem borers and blast. Two such lines with multiple disease resistance were found to be susceptible to brown planthopper which have improved plant type when crossed with dwarf varieties. Since IR8 was obtained from TKM 6, crossing it with IR24 has resulted in progenies resistant to brown planthopper; and moderate levels of resistance to stem borers and blast. Two such lines with multiple disease resistance were found to be susceptible to brown planthopper which have improved plant type when crossed with dwarf varieties.

Finally, the origin of resistance originated through mutation was also considered, but no evidence of genetic recombination between the parents. Moreover, the resistance in both selections is of combination of two complementary genes from two resistant plants at the expected frequency on the basis of genetic recombination between the parents. However, the proportion of resistant seedlings was much lower than expected. This conclusion was confirmed in a study of 219F3 F2 populations of resistant varieties and selections. A small proportion of the seedlings of the resistant parents also died, the latter possibility seems more plausible.
Fig. 2. Field reaction of resistant and susceptible selections to the brown planthopper. Resistant selection IR1541-76-3-65 has suffered no visible damage. Susceptible varieties IR8 and IR20 have been lulled; resistant selection IR1541-76-3-65 has suffered no visible damage. Such cultivars should help suppress the brown planthopper populations which have been increasing alarmingly in recent years. These cultivars are so resistant that they hardly suffer any damage under population pressures high enough to kill susceptible cultivars (Fig. 2). Since brown planthoppers cannot multiply on resistant cultivars, large-scale cultivation of such cultivars would be the most logical and cheapest way to control this serious pest of rice.

Although brown planthopper is a major pest of rice throughout Asia, 25 resistant cultivars identified to date (9) and TKM 6, come from either South India or Sri Lanka. All of these cultivars belong to the indica group. No Japonica cultivar with resistance to this pest is known, although Kaneda (4) has developed resistant lines with japonica traits from crosses of Mudgo and japonica cultivars.

Numerous lines with improved plant type having either \textit{Bph 1} or \textit{bph 2} have been developed at IRRI and distributed to breeders and entomologists throughout Asia. Several breeding programs in Asia are now trying to incorporate these resistance genes into their future cultivars. Several resistant selections with either \textit{Bph 1} or \textit{bph 2} were tested for resistance to local biotypes of brown planthopper in Korea, Taiwan, Vietnam, Sri Lanka, British Solomon Islands, and Fiji by local scientists and were found to be resistant. Thus, no evidence for biotype variation in the natural insect populations has yet been found in Asia, although a laboratory biotype to which \textit{Bph 1 Bph 1} genotypes were susceptible was isolated at IRRI (1). Selections of \textit{bph 2 bph 2} genotype, however, were resistant to this biotype.