Resistance to Whitebacked Planthopper in Elite Lines of Cultivated × Wild Rice Crosses

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ABSTRACT

Wide hybridization is an important breeding tool for incorporating alien genetic variation and transfer of useful traits from wild species of *Oryza* to commercial rice (*O. sativa* L.) cultivars. We evaluated two elite lines, 'IR54742-23-1-29-18' (hereafter called IR54742) and 'IR54751-2-41-10-5' (hereafter called IR54751), selected from 243 lines derived from BC_2F_6 progenies of crosses between cultivated rice and wild rice (*O. officinalis* Wall) for resistance to the whitebacked planthopper *Sogatella furcifera* (Horváth). The insect's behavioral and physiological responses were tested on the two elite lines and their parents 'IR31917-45-3-2' (hereafter called IR31917) and wild rice. 'IR2035-117-3' (hereafter called IR2035) was the resistant check, while 'Taichung Native 1' (TN1) was the susceptible check. Insect food intake and assimilation, growth, longevity and fecundity, and population increase were least on wild rice. The level of insect resistance of IR54751 was comparable to that of IR2035, but insect growth was significantly more on IR54751. IR54742 was comparably less resistant than IR54751. There was no significant difference in insect responses to IR31917 and TN1. The interspecific transfer of gene(s) for planthopper resistance from wild rice to cultivated rice was confirmed.

THE WHITEBACKED PLANTHOPPER (WBPH) is an important pest of rice. It is widely distributed throughout South and Southeast Asia, China, the South Pacific Islands, and the northern part of Australia. Under favorable conditions, the insect can completely destroy rice plants, a condition known as hopperburn (Suenaga, 1963). In the last decade, WBPH outbreaks and occurrences have been frequently reported from both temperate and tropical countries such as Japan (Hirano, 1981), China (Dung, 1981), India (Verma et al., 1979), and Malaysia (Ooi et al., 1980). Fortunately, unlike other hoppers that infest rice, WBPH is not known to be a vector of any rice virus.

Because of the high cost of insecticides and the problem of insecticide-induced WBPH resurgence (Nagata, 1979), varietal resistance is considered as the most promising and practical approach in the integrated control of this pest (Khan and Saxena, 1986a). Breeding programs at the International Rice Research Institute (IRRI) and in several countries focus on the development of pest-resistant rice varieties. So far, about 300 resistant varieties have been identified from the screening of more than 40 000 rice cultivars (Heinrichs and Rapusas, 1983). Genetic analysis of resistant varieties has identified five genes for WBPH resistance. Four of the genes are dominant and designated as *Wbph* 1, *Wbph* 2, *Wbph* 3, and *Wbph* 5; the other one is recessive and designated as *wbph* 4 (Angeles et al., 1981; Saini et al., 1982; Wu and Khush, 1985).

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In the event of a possible exhaustion and limitation of the genetic variability of cultivated rice, plant breeders at the IRRI have resorted to wide hybridization as an important plant breeding tool for incorporating alien genetic variation and transfer of useful traits from wild species of *Oryza* to commercially useful varieties.

The chromosomes of cultivated rice (AA genome) and the wild rice (CC genome) are morphologically similar (Kurata and Omura, 1984), but there is very little pairing between the two species. Using embryo rescue techniques, interspecific hybrids were successfully produced between wild rice and a cultivated breeding line IR31917 (Jena and Khush, 1986). Wild rice accessions from several locations show high resistance to three biotypes of the brown planthopper, *Nilaparvata lugens* (Stål), and WBPH but they possess undesirable agronomic characteristics. IR31917 has a good plant type with high yield potential, but is highly susceptible to planthoppers. Genetic evaluation of the BC_2F_3 progenies of the above mentioned cross has demonstrated that genes for resistance to *N. lugens* have been transferred from wild into cultivated rice (Jena and Khush, 1986). A preliminary test of the BC_2F_4 progenies also has shown that some of the progenies are resistant to WBPH (K.K. Jena, 1987, personal communication).

The objectives of this study were to investigate elite lines of BC_2F_6 progenies of wild × cultivated rice crosses for resistance to WBPH and to examine the behavioral and physiological responses of WBPH to the resistant lines.

MATERIALS AND METHODS

Progenies derived from wide hybridization between wild rice (IRRI Accession no. 100896) and an improved rice breeding line IR31917 were screened for WBPH resistance using the conventional, free-choice seedling bulk test (Pablo, 1977; Saxena and Khan, 1984). Of 600 elite lines, 243 lines showing uniform resistance or segregating resistance in BC_2F_4 progenies were selected. Lines showing resistance to WBPH in preliminary screening were retested thrice using seeds derived from BC_2F_6 progenies along with wild rice and IR31917 in each replicate and TN1 and IR2035 as the resistant and susceptible checks, respectively. Damage was graded on a 0 to 9 scale as soon as susceptible TN1 seedlings were killed; 0 = highly resistant, 1 = resistant, 3 = moderately resistant, 5 = moderately susceptible, 7 = susceptible, and 9 = highly susceptible (Pathak and Saxena, 1980).

Insect Responses to Resistant Lines

Behavioral and physiological responses of WBPH to plants of two selected lines (IR54742 and IR54751 and their parents), wild rice, and IR31917 were tested in a greenhouse; TN1 and IR2035 were the susceptible and resistant checks, respectively.

Orientational and Settling Responses

Test plants were randomly but equidistantly planted in a circle at 8-cm distance from the center of a plastic tray and covered with a transparent, cylindrical mylar-film cage (40

cm high, 20 cm diam.). The cage had a nylon-mesh top with a median hole through which 100 brachypterous females (1- or 2-d-old) were introduced. The number of females that settled on the plants was recorded at 1, 4, 8, 24, and 48 h after release. The percentage of females that settled on each cultivar at different time intervals was calculated.

Ingestion and Assimilation of Food

Newly emerged brachypterous females (starved but water-satiated for 2 h) were weighed individually on a microbalance and then enclosed singly in air-tight parafilm sachets (5 by 5 cm) through which the leaf sheath of a test plant passed. Five such females were observed for each test entry. After 24 h, the weight of each female and its excreta were recorded separately. To assess the loss in insect body weight due to catabolism, a control was similarly established in which the insect was given access to a moist cotton swab to prevent desiccation. The amount of food being ingested and assimilated by the insect was calculated according to the following formula derived from Saxena and Pathak (1977):

$$\text{Food assimilated} = W2 - W1\ (C2/C1)$$
$$\text{Food ingested} = \text{Food assimilated} + \text{Weight of excreta},$$

where $W1$ = initial weight of insect, $W2$ = final weight of insect, $C1$ = initial weight of control insect, and $C2$ = final weight of control insect.

Nymphal Growth

Potted plants were covered with mylar-film cages (75 cm high, 10 cm diam.) in an iron tray filled with water. Each plant was infested with 10 first-instar nymphs that were observed daily until the adult stage. Nymphal growth on resistant and susceptible entries was compared based on the number of nymphs that became adults and the time taken by the nymphs to reach the adult stage. The growth index was calculated as the ratio of percentage of nymphs that developed into adults to mean growth period in days (Saxena et al., 1974) and was referred to as a parameter indicating the suitability of plants for WBPH growth.

Adult Longevity

Newly emerged males and brachypterous females were caged on potted plants of the test entries at a rate of 10 pairs per pot. Insect survival was recorded daily until the last individual died.

Fecundity and Hatchability

Fecundity of brachypterous females and hatchability of their eggs were determined on selected entries. Potted plants were enclosed with 3 pairs of newly emerged adults per pot using mylar-film cages. The caged adults were observed daily and their mortality recorded. At 7 d after caging, surviving adults were transferred to fresh plants and the same procedure was repeated. Emerging nymphs were counted daily, with total number of nymphs being referred to as the number of viable eggs produced by females during their lifetime. At the end of nymph emergence, the unhatched eggs were located in the plants by staining (Khan and Saxena, 1986b). Leaf sheaths of the plants were cut, labeled and bleached in boiling water for 7 to 8 min to coagulate the yolk of unhatched eggs. The boiled plant tissues were further bleached and kept in 950 mL L^{-1} ethyl alcohol for 3 d. They were then rinsed in water and immersed in 1 mL L^{-1} aqueous acid fuchsin solution. After 2 d, the treated leaf sheaths were destained under running water until stained eggs could be easily differentiated from the plant tissues. Unhatched eggs were counted under a binocular microscope. Nymphs and unhatched eggs were combined as total eggs laid by females. Egg hatchability was calculated as the ratio of viable eggs to total eggs.

Ovipositional Response

Test plants in each pot were infested with five gravid brachypterous females reared on TN1 plants. The females were allowed to deposit eggs on the test plants for 24 h. After oviposition, the leaf sheaths of the plants were removed and eggs laid in them were stained and counted, as described above.

Population Increase

Potted plants were covered by mylar cages and infested at a rate of four pairs of newly emerged adults per pot. Nymphs and adults were counted 30 d after infestation.

A completely randomized design was used in all tests for insect responses except for orientation and settling where a randomized-complete block was designed. Data were analyzed by analysis of variance and means were compared using Duncan's (1951) multiple range test (DMRT) at the 5% level of probability. All data in percentages were transformed to arcsine $\sqrt{X/100}$ or arcsine $\sqrt{X/100 + 0.05}$ if zero appeared in the observations before analysis of variance.

RESULTS

Most of the 243 lines screened were susceptible or moderately susceptible to WBPH. Only 13 lines showed resistance to the insect. However, due to poor agronomic traits, 3 of the 13 lines were discarded from BC_2F_6 progenies; only 10 were further evaluated for resistance (Table 1). According to the final damage grading in the retest, two elite lines, IR54742-6-20-3-22 and IR54751-2-41-10-5, were consistently resistant to WBPH; these were selected for studies of insect responses. Wild rice seedlings were not preferred by WBPH nymphs, as also observed in preliminary screening and confirmed by retesting.

Initially, WBPH females oriented to and settled uniformly on all test entries but 4 h after release significantly more females settled on seedlings of the susceptible TN1 and IR31917. Differences in settling response became clearer at 8 and 24 h after release; by 48 h after release, about 60% of the total females settled down on susceptible TN1 and IR31917, but not a single individual settled on wild rice (Table 2).

Food intake by WBPH females on IR54742 and IR54751 was not significantly different from that on the resistant IR2035 and on wild rice, but was significantly lower than on susceptible TN1 plants (Table 3). Females gained significantly more body weight on TN1 plants than on other entries. Insect food intake and assimilation on IR54742 and IR54751 did not differ significantly. However, significantly more food was assimilated on IR54742 as compared with the resistant IR2035, although IR54751 was not statistically different from the resistant check. On wild rice, WBPH ingested and assimilated the least amount of food.

Significantly fewer nymphs became adults on IR54742 and IR54751 than on susceptible TN1 (Table 4). Insect growth on the two elite lines was not significantly different from that on the resistant IR2035. The mean development period also varied among entries; being longer on resistant and shorter on susceptible plants. Due to longer growth period and reduced

Table 1. Re-evaluation of final grading of damage by WBPH nymphs and percent nymphs settled on seedlings of ten lines derived from cultivated × wild rice crosses, their parents, and check cultivars.†

Genotype	IRRI accession no.	Damage rating‡	Resistance‡ rating	Nymphs settled on§ seedlings at	
				42 HAI¶	48 HAI
		Mean ± SE		%	
IR54742-6-20-3-22	100896	4.3 ± 0.7	MS	8.1a	7.7a
IR54742-18-17-20-15	100896	4.3 ± 0.7	MS	6.6a	7.3a
IR54742-23-1-29-18	100896	2.3 ± 0.7	R	6.8a	6.7a
IR54742-23-11-19-6	100986	4.3 ± 1.3	MS	7.8a	7.2a
IR54742-31-16-25-22	100896	6.3 ± 0.7	S	8.0a	7.3a
IR54742-38-37-16-10	100896	6.3 ± 0.7	S	7.4a	7.1a
IR54745-2-34-3-10	100896	6.3 ± 0.7	S	7.1a	7.7a
IR54745-2-45-3-24	100896	5.7 ± 0.7	MS	6.9a	7.5a
IR54751-2-41-10-5	100896	1.7 ± 0.7	R	6.8a	7.2a
IR54743-1-10-3-20	1001150	5.7 ± 0.7	MS	7.0a	7.7a
Wild rice (resistant parent)	100896	0.3 ± 0.3	HR	1.9b	0.6c
IR31917-45-3-2 (susceptible parent)		7.7 ± 0.7	S	6.8a	7.5a
IR2035-117-3 (resistant check)		1.0 ± 0.0	R	5.8a	4.8b
TN1 (susceptible check)		9.0 ± 0.0	HS	7.8a	8.2a

† Values in a column followed by the same letter are not significantly different at the 0.05 level of probability by Duncan's new multiple range test.
‡ Average of three replicates, based on the 0 to 9 scale; HR = highly resistant, R = resistant, MS = moderately susceptible, S = susceptible, HS = highly susceptible.
§ Average of three replicates, 6720 nymphs per seedbox; percentages calculated on total number of nymphs released in a seedbox; remaining insects on the soil below.
¶ HAI = hours after infestation.

Table 2. Percentages of WBPH females recorded on plants of selected elite lines derived from cultivated × wild rice crosses and control genotypes at 48 h after release in a free-choice test.†

Genotype	Females settled on plants at 48 h after release‡
	no.
IR54742-23-1-29-18	18b
IR54751-2-41-10-5	13bc
Wild rice (resistant parent)	0d
IR31917-117-3 (susceptible parent)	23ab
IR2035-117-3 (resistant check)	2cd
TN1 (susceptible check)	34a

† Values followed by the same letter are not significantly different at the 0.05 probability level by Duncan's multiple range test. Average of five replicates, 100 females per cage.
‡ Percentages based on total number of females released in a cage; remaining females on the soil below seedlings.

Table 3. Ingestion and assimilation of food by WBPH females on plants of selected elite lines derived from cultivated × wild rice crosses and control genotypes.†

Genotype	Food ingested by one female	Food assimilated by one female
	mg d^{-1}	
IR54742-23-1-29-18	2.61bc	0.29bc
IR54751-2-41-10-5	1.74bc	0.21cd
Wild rice (resistant parent)	0.39c	0.11e
IR31917-45-3-2 (susceptible parent)	4.24b	0.33b
IR2035-117-3 (resistant check)	0.78c	0.14de
TN1 (susceptible check)	13.51a	0.64a

† Values followed by the letter in each column are not significantly different at the 0.05 probability level by Duncan's multiple range test. Average of five replicates, five females per replicate.

adult emergence, the growth index on the two elite lines was significantly lower than that on susceptible TN1 and IR31917, but higher than that on resistant IR2035. The TN1 plants were therefore the most suitable and wild rice plants the least suitable for WBPH growth; the two elite lines were intermediate.

The survival period of WBPH males and females on

Table 4. Growth and development of WBPH nymphs on plants of selected elite lines derived from cultivated × wild rice crosses and control genotypes.†

Genotype	Nymphs becoming adults	Mean developmental period	Growth‡ index
	%	d	% d^{-1}
IR54742-23-1-29-18	66bc	11.7	5.7b
IR54751-2-41-10-5	66bc	11.6	5.7b
Wild rice (resistant parent)	2d	13.0	0.2d
IR31917-45-3-2 (susceptible parent)	78ab	10.2	7.7a
IR2035-117-3 (resistant check)	50c	13.2	3.8c
TN1 (susceptible check)	92a	10.1	9.1a

† Values followed by the same letter in a column are not significantly different at the 0.05 probability level by Duncan's multiple range test. Average of five replicates, 10 first-instar nymphs per replicate.
‡ Growth index = percent nymphs becoming adults divided by mean developmental period.

the two elite lines was significantly shorter than on TN1 but not significantly different from that on resistant IR2035 (Table 5). Longevities of males were significantly longer on the two elite lines than on wild rice but shorter than that on susceptible breeding line IR31917; female longevities on the elite lines did not differ from that on susceptible IR31917.

WBPH fecundity varied widely on the test entries (Table 5). The females laid significantly fewer eggs on elite lines IR54742 and IR54751 than on susceptible TN1 and IR31917; only a few eggs were laid on resistant IR2035 and wild rice. However, hatchability of WBPH eggs on test entries was uniformly high, except on wild rice. Regardless of susceptibility or resistance, the number of eggs laid by gravid WBPH females in 24 h on cultivated rices did not differ significantly, but fewer eggs were laid on wild rice, indicating its lower suitability for WBPH oviposition (Table 5).

Increase in WBPH population comprising nymphs and adults generated from 4 pairs of males and females at 30 d after infestation differed significantly on the test entries (Table 5). Population increase was

Table 5. The WBPH longevity, fecundity, egg hatchability, ovipositional response, and population increase on plants of selected elite lines derived from cultivated rice × wild rice crosses and control genotypes.†

Genotype	Longevity‡		Fecundity§				
	Male	Female	Eggs by 1 female	Hatchability§	Eggs laid¶ by 5 females	Population# increase
	d		no.	%	no. d^{-1}	no.
IR54742-23-1-29-18	5.5b	6.4bc	111b	92ab	62a	241b
IR54751-2-41-10-5	5.3b	6.2bc	68bc	90ab	68a	89c
Wild rice (resistant parent)	2.4c	2.7d	10c	85b	24b	12c
IR31917-45-3-2 (susceptible parent)	7.5a	8.7ab	186a	98a	72a	368a
IR2035-117-3 (resistant check)	3.8bc	4.9cd	15c	88ab	43ab	45c
TN1 (susceptible check)	8.2a	11.2a	194a	97a	70a	395a

† Values followed by the same letter in each column are not significantly different at the 0.05 probability level by Duncan's multiple range test.
‡ Average of five replicates, 10 pairs of newly emerged adults per replicate.
§ Average of five replicates; three pairs of newly emerged adults per replicate; percentage hatchability calculated as the ratio of viable eggs (number of nymphs emerged) to the total number of eggs per female multiplied by 100.
¶ Average of five replicates.
# Based on number of nymphs and adults recovered. Average of five replicates; four pairs of 1-d-old males and females were caged on 30-d-old plants in each replicate.

Table 6. Relative intensity of WBPH responses on selected elite lines derived from cultivated rice × wild rice crosses and control genotypes.†

Genotype	Insect response at various stages during development										
	Orientation‡	Settling¶	Food intake	Food assimilated	Growth index	Survival		Fecundity	Oviposition	Hatch-ability	Average
						Male	Female				
IR54742	1.1	0.5	0.2	0.5	0.6	0.7	0.6	0.6	0.9	1.0	0.66
IR54751	0.7	0.4	0.1	0.3	0.6	0.6	0.6	0.4	1.0	0.9	0.56
Wild rice (resistant parent)	0.5	0.0	0.03	0.2	0.02	0.3	0.2	0.1	0.4	0.9	0.25
IR31917 (susceptible parent)	1.0	0.7	0.3	0.5	0.8	0.9	0.8	1.0	1.0	1.0	0.81
IR2035 (resistant check)	0.9	0.05	0.06	0.2	0.4	0.5	0.4	0.1	0.6	0.9	0.42
TN1 (susceptible check)	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.00

† Calculated as the ratio of insect response to test plant : insect response to susceptible check, TN1.
‡ At 1 h after release.
§ At 48 h after release.

highest on susceptible TN1 and IR31917 parent and lowest on wild rice, followed by the resistant check IR2035, and the resistant wide cross elite line IR54751. The WBPH population increase on IR54742 was significantly less than on susceptible TN1 and IR31917 but greater than on wild rice, resistant IR2035, and IR54751.

DISCUSSION

Wild rice is considered a rich source of tolerance or resistance to a number of abiotic and biotic stresses, including insect pests (Heinrichs et al., 1985). In the present study, wild rice (IRRI Accession no. 100896) was found to be highly resistant to WBPH. Even at the seedling stage, wild rice deterred the settling response of WBPH nymphs. A comparison of the relative intensity of behavioral and physiological responses of WBPH to the test entries showed that wild rice was less suitable for WBPH establishment (Table 6). This was also reflected in the low population build-up of the insect at 30 d after infestation. Thus, wild rice is a rich source of resistance to WBPH.

The interspecific transfer of gene(s) for resistance to WBPH from wild rice to an improved breeding line of cultivated rice was confirmed in the present study. The two elite lines selected, specially IR54751, showed consistent resistance to the insect, but resistance in other lines was not stable. In the BC_2F_4 progenies, 230 lines graded as resistant or segregating-resistant were found to be susceptible to WBPH in the mass screening test. This indicated that about 90% of the lines tested lost their resistance in BC_2F_5 progenies. In BC_2F_6 progenies, consistent resistance remained in only 2 of 10 promising lines selected for retesting. It seems that WBPH resistance in the elite lines has been lost in some progenies. The cause of this instability is not known, although such a phenomenon is not commonly associated with interspecific gene transfer. A more detailed characterization of the extent and nature of alien introgression would be valuable. Further examination and evaluation of pest resistance in elite lines also is necessary. Elucidation of causes of resistance, whether physical or chemical, would greatly help breeding for resistance and ensure long-term stability.

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