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A new gene for resistance to green leafhopper *Nephotettix virescens* (Distant) in rice

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Abstract. The mode of inheritance of resistance to green leafhopper in 12 cultivars of rice *Oryza sativa* L. was studied. Seedlings of parent and hybrid populations were artificially infested with second- and third-instar virus-free green leafhopper nymphs. Seedling reaction was scored when TN1, the susceptible check, was completely killed. The results revealed that single dominant genes confer resistance in six varieties, two independent dominant genes in four varieties, and single recessive genes in two varieties. The single dominant genes in Sri Gaya, ARC 7320, and T23 and one of the two genes in Aswina and Bhura Rata 2 are allelic to *Glh-1*; while Bhawalia has *Glh-5* gene. The second gene of Bhura Rata 2 is allelic to IR28 gene. Resistance in Chamar is controlled by two independent genes one of which is allelic to *Glh-5* and the other allelic to IR28 gene. Bazal has *Glh-2* and *Glh-5*. The single recessive gene in ARC 7012 is allelic to *glh-4* but the single recessive gene in DV85 is nonallelic to and independent of *glh-4*. This new recessive gene is designated as *glh-8*. The single dominant genes of Dumai, Gadur, and the second gene of Aswina are nonallelic to all the known genes for resistance.

Keywords. *Oryza sativa* L.; green leafhopper; allelic genes; varietal resistance.

1. Introduction

The green leafhopper (GLH) is known to occur in most major rice-growing countries and can cause serious damage by direct feeding. But more often, it damages the rice crop by transmitting viral diseases. For some years, GLH has been controlled by the use of insecticides. However, in recent years, emphasis has shifted to the development of resistant varieties as a component of integrated pest management strategies.

Rice cultivars with high levels of resistance have been identified at the International Rice Research Institute (IRRI) and elsewhere (Pathak *et al* 1969; Pathak 1970, 1972; Shastry *et al* 1971; Rezaul Karim and Pathak 1982; Heinrichs *et al* 1985). The inheritance of resistance has been investigated and seven genes for resistance (*Glh-1*, *Glh-2*, *Glh-3*, *glh-4*, *Glh-5*, *Glh-6*, and *Glh-7*) have been identified (Athwal *et al* 1971; Siwi and Khush 1977; Rezaul Karim and Pathak 1982; Avesi and Khush 1984; Ruangsook and Khush 1987). The resistance genes *Glh-1*, *Glh-2*, *Glh-3*, and *glh-4* have been incorporated into improved varieties which are now widely grown (Khush 1977, 1984). Populations of GLH adapt to resistant varieties in 3–5 years; thus breeders need to incorporate new genes, into breeding materials so that, if cultivars carrying specific genes become susceptible, new cultivars with different genes can be released. This study was undertaken to identify additional genes for resistance to GLH.

2. Materials and methods

Twelve rice cultivars resistant to GLH and of diverse geographical origin (table 1) were used in this study. Each cultivar was crossed with susceptible cultivar TN1 and with resistant cultivars/lines IR5491, IR5492, IR8, Ptb 8, and ASD8 which are homozygous for *Glh-1*, *Glh-2*, *Glh-3*, *glh-4*, and *Glh-5* genes, respectively. The cultivars were also crossed with IR28, an improved plant type cultivar found to have a single dominant gene which is nonallelic to the aforementioned genes (Avesi and Khush 1984). F_1, F_2, and F_3 progenies of these crosses were tested for their reaction to GLH using the population from Luzon Island in the Philippines. This population has been maintained by culturing continuously on the susceptible cultivar TN1.

To test for resistance to GLH, test materials were grown in rows, 5 cm apart, in $60 \times 45 \times 10\ cm^3$ wooden seedboxes filled with soil to a depth of 5 cm. Each seedbox could accommodate 13 rows, 45 cm long, which were divided into 26 subrows, about 20 cm long. Out of these, two rows were planted to the susceptible check (TN1) and another two to the resistant check (IR28). At one leaf stage, the seedlings were uniformly infested with second- to third-instar virus-free nymphs of GLH with five or six insects per seedling. The reaction was recorded when the susceptible check was completely killed (generally 7–8 days after infestation). The F_1 and F_3 were scored on a row basis while each F_2 seedling was classified as resistant or susceptible. The F_3 lines were scored as homozygous resistant, segregating, or homozygous susceptible. The study was conducted at the International Rice Research Institute (IRRI) in Los Baños, Philippines during 1986–87.

3. Results

3.1 *Mode of inheritance*

The F_1 progenies of the crosses of TN1 with ten cultivars were resistant (table 2), indicating that resistance in these cultivars is dominant. However, the F_1 progenies of the crosses of TN1 with ARC 7012 and DV85 were susceptible showing that resistance in these two cultivars is recessive. The F_2 populations from the crosses of

Table 1. *N. virescens*-resistant rice cultivars.

Cultivar	IRRI Acc. no.	Country of origin
Chamar	26320	Bangladesh
Bhawalia	26307	Bangladesh
Bazal	26301	Bangladesh
Aswina	26289	Bangladesh
Dumai	25852	Bangladesh
Sri Gaya	25149	Indonesia
ARC 7320	20599	India
Gadur	16246	Nepal
ARC 7012	12314	India
DV85	8839	Bangladesh
T23	6433	India
Bhura Rata 2	3673	India

Table 2. Reaction to *N. virescens* (Distant) of F_1 and F_2 populations and F_3 families from the crosses of TN1 with test cultivars of rice.

Cross	F_1 reaction[a]	F_2 reaction (No. of seedlings)				Reaction of F_3 families (No. of families)				
		Total	*S* (%)	*P* value 3:1	*P* value 15:1	*R*	Seg.	*S*	*P* value 1:2:1	*P* value 7:8:1
TN1/Chamar	*R*	411	8·52	–	0·10–0·20	74	71	8	–	0·50–0·30
TN1/Bhawalia	*R*	364	28·02	0·20–0·10	–	45	74	35	0·50–0·30	–
TN1/Bazal	*R*	388	7·73	–	0·30–0·20	55	84	15	–	0·10–0·05
TN1/Aswina	*R*	403	7·69	–	0·30–0·20	52	83	12	–	0·20–0·10
TN1/Dumai	*R*	647	27·67	0·20–0·10	–	22	86	46	0·20–0·10	–
TN1/Sri Gaya	*R*	498	28·11	0·20–0·10	–	28	84	41	0·20–0·10	–
TN1/ARC 7320	*R*	993	23·77	0·50–0·30	–	32	86	36	0·50–0·20	–
TN1/Gadur	*R*	944	24·68	0·90–0·80	–	44	75	35	0·70–0·50	–
TN1/ARC 7012	*S*	847	74·5	0·80–0·70[b]	–	29	81	44	0·20–0·10	–
TN1/DV85	*S*	733	72·7	0·20–0·10[b]	–	34	69	47	0·20–0·10	–
TN1/T23	*R*	491	27·49	0·30–0·20	–	41	72	41	0·80–0·70	–
TN1/Bhura Rata 2	*R*	418	7·89	–	0·20–0·10	66	81	7	–	0·70–0·50

[a]*R* = resistant, Seg. = segregating, *S* = susceptible; [b]The ratio is 1*R*:3*S*.

six cultivars (Bhawalia, Dumai, Sri Gaya, ARC 7320, Gadur, and T23) with TN1 segregated in a ratio of 3 resistant to 1 susceptible (table 2), indicating that resistance to GLH in each of them is governed by a single dominant gene. These conclusions were further confirmed by the reaction of F_3 lines of these crosses wherein a ratio of 1:2:1 expected for monogenic control of resistance was observed (table 2).

The F_2 populations from the crosses TN1/ARC 7012 and TN1/DV85 segregated in a ratio of 1 resistant to 3 susceptible, thereby showing that single recessive genes confer resistance in these two cultivars. These conclusions were confirmed by the reaction of F_3 families which segregated in the ratio of 1:2:1 expected for monogenic control of resistance (table 2).

The F_2 populations from the crosses of four cultivars (Chamar, Bazal, Aswina, and Bhura Rata 2) with TN1 segregated in a ratio of 15 resistant:1 susceptible, indicating that two dominant genes govern resistance in each of these cultivars. The F_3 lines from these crosses segregated in a ratio of 7 resistant:8 segregating:1 susceptible (table 2), thereby confirming that each of these cultivars has two independent dominant genes for resistance.

3.2 *Allele tests*

Crosses with IR5491: Data on the reaction of F_1 hybrids and F_2 and F_3 populations from the crosses of IR5491 (*Glh-1*) with test cultivars are given in table 3. All the F_1 hybrids were resistant. No segregation for susceptibility was observed in the crosses of IR5491 with Aswina, Sri Gaya, ARC 7320, T23, and Bhura Rata 2. A few susceptible seedlings were observed in the F_2 populations of these four crosses but none of the F_3 families was susceptible. A similar number of susceptible seedlings were also observed in the resistant checks. Earlier workers have also

Table 3. Reaction to *N. virescens* (Distant) of F_1 and F_2 families from the crosses of IR5491 with test cultivars of rice.

Cross	F_1 reaction[a]	F_2 reaction (No. of seedlings) Total	S (%)	P value 15:1	P value 63:1	Reaction of F_3 families (No. of families) R	Seg.	S	P value 7:8:1	P value 37:26:1
IR5491/Chamar	R	423	1·89	–	0·70–0·50	80	69	4	–	0·30–0·20
IR5491/Bhawalia	R	339	4·72	0·30–0·20	–	63	85	6	0·30–0·20	–
IR5491/Bazal	R	467	3·0	–	0·05–0·01	80	69	5	–	0·20–0·10
IR5491/Aswina	R	857	1·75	–	–	148	6	0	–	–
IR5491/Dumai	R	466	8·15	0·10–0·05	–	87	60	7	0·50–0·30	–
IR5491/Sri Gaya	R	687	1·31	–	–	149	1	0	–	–
IR5491/ARC 7320	R	425	2·12	–	–	154	0	0	–	–
IR5491/Gadur	R	523	7·84	0·20–0·10	–	57	86	11	0·30–0·20	–
IR5491/ARC 7012	R	436	15·14	0·10–0·05[b]	–	66	77	10	0·90–0·80	–
IR5491/DV85	R	788	20·94	0·20–0·10[b]	–	67	74	13	0·70–0·50	–
IR5491/T23	R	420	0·48	–	–	149	4	0	–	–
IR5491/Bhura Rata 2	R	481	1·04	–	–	152	2	0	–	–

[a] R = resistant; Seg = segregating; S = susceptible; [b] P value for 13R:3S ratio.

reported the occurrence of a few dead seedlings in the F_2 populations of crosses between two parents having allelic genes for resistance (Athwal *et al* 1971; Siwi and Khush 1977; Avesi and Khush 1984; Ruangsook and Khush 1987). The death of these seedlings was attributed to unusually heavy insect population or attack of soil-borne fungi. These results show that Sri Gaya, ARC 7320, and T23 have *Glh-1* for resistance. The two dominant genes of Aswina and Bhura Rata 2 are also allelic to *Glh-1*. In the crosses of Bhawalia, Dumai, and Gadur a segregation ratio of 15 resistant:1 susceptible in the F_2 and 7 resistant:8 segregating:1 susceptible in the F_3 was observed showing that the single dominant genes of these three varieties segregated independently of *Glh-1*. In the F_2 populations of IR 5491/ARC7012 and IR5491/DV85, a segregation ratio of 13 resistant:3 susceptible was observed. The F_3 families of these two crosses segregated in a ratio of 7 resistant: 8 segregating: 1 susceptible, thereby showing that recessive genes of ARC7012 and DV85 segregate independently of *Glh-1*. The F_2 populations and F_3 families from the crosses IR5491/Chamar and IR5491/Bazal segregated in a ratio of 63 resistant:1 susceptible and 37 resistant:26 segregating:1 susceptible, respectively, thus showing that the two dominant genes of these cultivars are independent of *Glh-1*.

Crosses with IR5492: The data on F_1, F_2, and F_3 populations of the crosses of IR5492 with test cultivars are given in table 4. The F_1s of all the crosses were resistant. No segregation for susceptibility was observed in the cross IR5492/Bazal indicating that one of the two genes of Bazal is *Glh-2*. The crosses of IR5492 with Bhawalia, Dumai, Sri Gaya, ARC 7320, Gadur, ARC 7012, DV85, and T23 segregated in a digenic fashion, thereby showing that the single genes of these varieties are nonallelic to *Glh-2*. A segregation ratio of 63 resistant:1 susceptible in F_2 and a ratio of 37 resistant:26 segregating:1 susceptible in the F_3 were observed in the crosses of IR5492 with Chamar, Aswina, and Bhura Rata 2, thereby showing that the two dominant genes of these three varieties are independent of *Glh-2*.

Table 4. Reaction to *N. virescens* (Distant) of F_1 and F_2 populations and F_3 families from the crosses of IR5492 with test cultivars of rice.

Cross	F_1 reaction[a]	F_2 reaction (No. of seedlings) Total	S (%)	P value 15:1	P value 63:1	Reaction of F_3 families (No. of families) R	Seg.	S	P value 7:8:1	P value 37:26:1
IR5492/Chamar	R	854	2·46	–	0·05–0·01	88	62	3	–	>0·90
IR5492/Bhawalia	R	323	4·64	0·30–0·20	–	60	78	7	0·70–0·50	–
IR5492/Bazal	R	455	0·66	–	–	153	1	0	–	–
IR5492/Aswina	R	461	2·17	–	0·50–0·30	73	78	2	–	0·80–0·70
IR5492/Dumai	R	470	7·87	0·20–0·10	–	66	75	13	0·70–0·50	–
IR5492/Sri Gaya	R	834	8·27	0·05–0·01	–	77	68	8	0·30–0·20	–
IR5492/ARC 7320	R	810	7·78	0·10–0·05	–	75	74	5	0·30–0·20	–
IR5492/Gadur	R	946	7·51	0·20–0·10	–	71	71	12	0·70–0·50	–
IR5492/ARC 7012	R	908	16·19	0·05–0·01[b]	–	75	68	10	0·50–0·30	–
IR5492/DV85	R	943	19·19	0·80–0·70[b]	–	49	92	13	0·30–0·20	–
IR5492/T23	R	437	7·55	0·30–0·20	–	69	75	6	0·50–0·30	–
IR5492/Bhura Rata 2	R	417	2·40	–	0·20–0·10	74	63	3	–	0·50–0·30

[a] R = resistant, Seg = segregation, S = susceptible; [b] P value for 13R:3S ratio.

Crosses with IR8: The data on the F_1, F_2, and F_3 populations of the crosses of IR8 with test cultivars are given in table 5. The F_1s of all the crosses were resistant. Crosses of IR8 with Bhawalia, Dumai, Sri Gaya, ARC 7320, Gadur, ARC 7012, DV85, and T23 showed digenic segregation in the F_2 and F_3 thus showing that single resistance genes of these cultivars are nonallelic to *Glh-3*. Similarly a trigenic segregation ratio was observed in the F_2 and F_3 populations in the crosses of IR8 with Chamar, Bazal, Aswina, and Bhura Rata 2, thereby showing that the two dominant genes of these cultivars segregate independently of *Glh-3*.

Table 5. Reaction to *N. virescens* (Distant) of F_1 and F_2 populations and F_3 families from the crosses of IR8 with test cultivars of rice.

Cross	F_1 reaction[a]	F_2 reaction (No. of seedlings) Total	S (%)	P value 15:1	P value 63:1	Reaction of F_3 families (No. of families) R	Seg.	S	P value 7:8:1	P value 37:26:1
IR8/Chamar	R	416	2·40	–	0·20–0·10	96	55	2	–	0·50–0·30
IR8/Bhawalia	R	400	7·75	0·30–0·20	–	48	72	12	0·20–0·10	–
IR8/Bazal	R	499	2·40	–	0·10–0·05	92	57	5	–	0·20–0·10
IR8/Aswina	R	450	2·44	–	0·10–0·05	89	60	5	–	0·30–0·20
IR8/Dumai	R	478	7·32	0·50–0·30	–	65	79	10	>0·50	–
IR8/Sri Gaya	R	460	8·26	0·10–0·05	–	84	63	7	0·50–0·30	–
IR8/ARC 7320	R	487	7·60	0·30–0·20	–	96	46	9	0·90–0·80	–
IR8/Gadur	R	374	9·63	<0·01	–	53	89	10	0·10–0·05	–
IR8/ARC 7012	R	483	15·73	0·10–0·05[b]	–	71	79	4	0·20–0·10	–
IR8/DV85	R	459	20·26	0·20–0·10[b]	–	68	71	15	0·20–0·10	–
IR8/T23	R	679	7·81	0·10–0·05	–	77	90	6	0·10–0·05	–
IR8/Bhura Rata 2	R	490	2·24	–	0·20–0·10	60	87	5	–	0·10–0·05

[a] R = resistant; Seg. = segregating, S = susceptible; [b] P value for 13R:3S ratio.

Table 6. Reaction to *N. virescens* (Distant) of F_1 and F_2 populations and F_3 families from the crosses of Ptb 8 with ARC 7012 and DV85.

Cross	F_1 reaction[a]	F_2 reaction (No. of seedlings) Total	S (%)	P value 7:9	Reaction of F_3 families (No. of families) R	Seg.	S	P value 7:8:1
Ptb 8/ARC 7012	R	501	1·20	—	154	9	0	—
Ptb 8/DV85	S	470	47·87	<0·01	66	74	13	0·70–0·50

[a]R = resistant; Seg. = segregating; S = susceptible.

Crosses with Ptb 8: The two cultivars with recessive genes (ARC 7012 and DV85) were crossed with Ptb 8 which has *glh-4* for resistance. The F_1 progeny of Ptb 8/ARC 7012 was resistant and no segregation for susceptibility was observed in the F_2 or F_3 populations of this cross (table 6). These results show that ARC 7012 also has *glh-4* for resistance. The F_1 progeny of Ptb 8/DV85 was susceptible and the F_2 population segregated in a ratio of 7 resistant:9 susceptible. The F_3 families of this cross segregated in a ratio of 7 resistant:8 segregating:1 susceptible. The results show that the recessive gene of DV85 is nonallelic to and independent of *glh-4*.

Crosses with ASD8: The data on the F_1, F_2, and F_3 populations from the crosses of ASD8 with test cultivars are given in table 7. The F_1 populations of all the crosses were resistant. No segregation for susceptibility was observed in the F_2 and F_3 populations of the crosses of ASD8 with Chamar, Bhawalia, and Bazal. These results show that a single dominant gene of Bhawalia is allelic to *Glh-5* and one of the two dominant genes of Chamar and Bazal are allelic to *Glh-5*. The F_2 and F_3 populations of the crosses of ASD8 with Dumai, Sri Gaya, ARC 7320, Gadur, ARC

Table 7. Reaction to *N. virescens* (Distant) of F_1 and F_2 populations and F_3 families from the crosses of ASD8 with test cultivars of rice.

Cross	F_1 reaction[a]	F_2 reaction (No. of seedlings) Total	S (%)	P value 15:1	P value 63:1	Reaction of F_3 families (No. of families) R	Seg.	S	P value 7:8:1	P value 37:26:1
ASD8/Chamar	R	725	1·10	–	–	150	4	0	–	–
ASD8/Bhawalia	R	703	1·71	–	–	154	0	0	–	–
ASD8/Bazal	R	421	1·19	–	–	145	1	0	–	–
ASD8/Aswina	R	470	2·55	–	0·10–0·05	102	49	2	–	0·10–0·05
ASD8/Dumai	R	452	5·09	0·50–0·30	–	73	70	8	0·70–0·50	–
ASD8/Sri Gaya	R	797	7·78	0·50–0·30	–	81	66	7	0·10–0·05	–
ASD8/ARC 7320	R	451	8·20	0·10–0·05	–	55	88	11	0·20–0·10	–
ASD8/Gadur	R	879	7·67	0·10–0·05	–	58	83	8	0·50–0·30	–
ASD8/ARC 7012	R	495	21·41	0·10–0·05[b]	–	70	73	11	0·80–0·70	–
ASD8/DV85	R	462	21·43	0·20–0·10[b]	–	63	85	5	0·20–0·10	–
ASD8/T23	R	394	4·31	0·20–0·10	–	59	85	10	0·50–0·30	–
ASD8/Bhura Rata 2	R	517	2·32	–	0·20–0·10	78	72	4	–	0·20–0·10

[a]R = resistant; Seg = segregating; S = susceptible; [b]P value for 13R:3S ratio.

7012, DV85, and T23 segregated in a digenic fashion, thus showing that single resistance genes of these cultivars segregate independently of *Glh-5*. The F_2 and F_3 populations of the crosses of ASD8 with Aswina and Bhura Rata 2 gave trigenic ratios and showed that the two dominant genes of these cultivars are independent of *Glh-5*.

Crosses with IR28: The data on the F_1, F_2 and F_3 populations from the crosses of IR28 with test cultivars are given in table 8. The F_1 progenies of all crosses were resistant. No segregation for susceptibility was observed in the F_2 and F_3 populations of the crosses of IR28 with Chamar and Bhura Rata 2. These results show that one of the two dominant resistance genes of these cultivars is allelic to the dominant gene of IR28. The F_2 and F_3 populations of the crosses of IR28 with Bhawalia, Dumai, Sri Gaya, Gadur, ARC 7012, DV85, and T23 segregated in a digenic fashion, thus showing that single resistance genes of these cultivars are nonallelic to and independent of the dominant resistance gene of IR28. The F_2 and F_3 populations of the crosses of IR28 with Bazal and Aswina gave trigenic ratios and showed that the two dominant genes of these cultivars are nonallelic to and independent of the dominant resistance gene of IR28.

4. Discussion

The results of this study show that resistance in rice cultivars Bhawalia, Dumai, Sri Gaya, ARC 7320, Gadur, and T23 is governed by single dominant genes but single recessive genes convey resistance in ARC 7012 and DV85. Two dominant genes convey resistance in each of Chamar, Bazal, Aswina, and Bhura Rata 2.

The analysis for allelic relationships shows that resistance in Chamar is governed by *Glh-5* and another dominant gene which is allelic to the dominant gene of IR28. The two dominant genes of Bazal are allelic to *Glh-2* and *Glh-5*, respectively.

Table 8. Reaction to *N. virescens* (Distant) of F_1 and F_2 populations and F_3 families from the crosses of IR28 with test cultivars of rice.

Cross	F_1 reaction[a]	F_2 reaction (No. of seedlings): Total	S (%)	P value 15:1	P value 63:1	Reaction of F_3 families (No. of families): R	Seg.	S	P value 7:8:1	P value 37:26:1
IR28/Chamar	R	932	1·07	–	–	152	2	0	–	–
IR28/Bhawalia	R	287	7·67	0·20–0·10	–	68	73	12	0·70–0·50	–
IR28/Bazal	R	990	2·12	–	0·20–0·10	88	59	3	–	0·90–0·80
IR28/Aswina	R	448	2·46	–	0·20–0·10	109	41	4	–	0·50–0·30
IR28/Dumai	R	470	7·66	0·30–0·20	–	67	71	16	0·10–0·05	–
IR28/Sri Gaya	R	302	–	0·90–0·80	–	72	77	5	0·30–0·20	–
IR28/Gadur	R	914	4·92	0·10–0·05[b]	–	77	66	11	0·30–0·20	–
IR28/ARC 7012	R	477	15·72	0·10–0·05[b]	–	76	67	11	0·30–0·20	–
IR28/DV85	R	965	20·83	0·10–0·05[b]	–	72	63	9	0·30–0·20	–
IR28/T23	R	894	5·93	0·70–0·50	–	86	62	6	0·30–0·20	–
IR28/Bhura Rata 2	R	886	1·81	–	–	146	4	0	–	–

[a] R = resistant; Seg = segregation; S = susceptible; [b] P value for 13R:3S ratio.

Table 9. Summary of information on genes for resistance to GLH in 12 rice varieties.

Variety	Nature of resistance	Gene for resistance
Chamar	Digenic, dominant	*Glh 5*+IR28 gene
Bhawalia	Monogenic, dominant	*Glh 5*
Bazal	Digenic, dominant	*Glh 2*+*Glh 5*
Aswina	Digenic, dominant	*Glh 1*+1 dominant gene[a]
Dumai	Monogenic, dominant	1 dominant gne[a]
Sri Gaya	Monogenic, dominant	*Glh 1*
ARC 7320	Monogenic, dominant	*Glh 1*
Gadur	Monogenic, dominant	1 dominant gene[a]
ARC 7012	Monogenic, recessive	*glh 4*
DV8	Monogenic, recessive	1 recessive gene[b]
T23	Monogenic, dominant	*Glh 1*
Bhura Rata 2	Digenic, dominant	*Glh 1*+IR28 gene

[a]Nonallelic to *Glh 1*, *Glh 2*, *Glh 3*, *Glh 5* and IR28 gene; [b]Nonallelic to *glh 4* gene.

Aswina has *Glh-1* and another dominant gene which is nonallelic to all the other known genes for resistance. Bhura Rata 2 has *Glh-1* and another gene which is allelic to the dominant gene of IR28. Resistance in Bhawalia is conveyed by *Glh-5* but Sri Gaya, ARC 7320, and T23 have *Glh-1*. The single dominant genes of Dumai and Gadur are nonallelic to all the known genes for resistance. The recessive gene of ARC 7012 is allelic to *glh-4*. The single recessive gene of DV85 is nonallelic to and independent of *glh-4*. Following the standard rules for gene nomenclature, the recessive gene of DV85 is designated *glh-8*. Although, the single dominant genes of Dumai and Gadur are nonallelic to *Glh-1*, *Glh-2*, *Glh-3*, and *Glh-5*, their allelism with *Glh-6* and *Glh-7* should be tested before a gene symbol can be assigned to them. Information on the allelic relationships of the genes in 12 cultivars investigated is given in table 9.

Leafhopper-resistant rice cultivars have been grown in the Philippines and other Asian countries for many years. When cultivars with high levels of resistance are grown for 3–5 years, the insect populations become adapted to these cultivars. Although no hopperburn is observed, the insects have a longer life span and can multiply faster on these cultivars. Moreover, they are able to transmit tungro virus disease. Thus we need to release cultivars with different genes for resistance every 3–5 years. Differential patterns of virulence in GLH populations from different countries have been noted. For example, GLH populations in Bangladesh are highly virulent to *Glh-1* and *Glh-3* genes (Rezaul Karim and Pathak 1982). Similar differences have been noted in GLH populations in India, Indonesia, and Malaysia.

We have carried out genetic analysis of several GLH-resistant cultivars during the last 18 years and several genes for resistance have been identified (Athwal *et al* 1971; Siwi and Khush 1977; Rezaul Karim and Pathak 1982; Avesi and Khush 1984; Ruangsook and Khush 1987). In this study at least four cultivars have been identified which have genes nonallelic to *Glh-1*, *Glh-2*, *Glh-3*, *glh-4*, and *Glh-5*. These should serve as useful donors in the host-resistance breeding programs.

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