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Wu Jung-Tsung
International Rice Research Institute

E. A. Heinrichs
International Rice Research Institute, eheinrichs2@unl.edu

F. G. Medrano
International Rice Research Institute

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Wu Jung-Tsung, E. A. Heinrichs, and F. G. Medrano

International Rice Research Institute, Manila, Philippines

Corresponding authors – The current address of Wu Jung-Tsung is the South China College of Agriculture, Guangzhou, Guandong Province, China. The current address of E. A. Heinrichs is the Department of Entomology, 402 Life Sciences Building, Louisiana State University, Baton Rouge, LA 70803-1710.

Abstract
Of 36 wild rices screened, 19 accessions were resistant or moderately resistant to three biotypes of the brown planthopper, *Nilaparvata lugens* (Stål), and 9 were resistant or moderately resistant to at least one biotype. Resistant accessions were nonpreferred and *N. lugens* caged on resistant accessions had low food ingestion rates, slow nymphal development, reduced longevity, low fecundity, and consequently low populations. Two wild rice species decreased the percent hatchability of *N. lugens* eggs. Some moderately resistant accessions have tolerance to *N. lugens*, as indicated by low plant damage ratings and plant loss and high percentage *N. lugens* survival and weight gain. Wild rices are possible sources of new genes for *N. lugens* resistance.

The brown planthopper, *Nilaparvata lugens* (Stal), damages rice plants by sucking plant sap and by transmitting grassy stunt and ragged stunt virus (Ling 1975, Ling et al. 1978). It is effectively and economically controlled by the use of resistant cultivars (Heinrichs 1980). However, the development of *N. lugens* biotypes capable of surviving on and damaging resistant cultivars is a constant threat (Pathak & Heinrichs 1982).

Wild rices are potential sources of new resistance genes to cope with the *N. lugens* biotype problem. The world collection of 1,100 wild rice accessions at the International Rice Research Institute is being evaluated for resistance to the major rice insect pests, and

accessions with resistance to one or more *N. lugens* biotype have been identified. Many are resistant to three *N. lugens* biotypes (Heinrichs et al. 1985). Selected accessions have been further evaluated to determine the mechanisms of resistance, and the results of these studies are herein reported.

Materials and Methods

Seedbox Screening Test and Preference

To confirm their resistance, 36 wild rice accessions were screened to biotypes 1, 2, and 3 of *N. lugens* in the greenhouse. *N. lugens* biotypes 1, 2, and 3 were reared as described by Heinrichs et al. (1985). About 20 seeds of each test entry were sown in rows (15 cm long) in wooden seedboxes (60 by 40 by 7 cm) filled with fine soil 5 cm deep. Each seed box served as a replication and each treatment was replicated three times using a split plot design with biotype as the main plot and rice accession as the subplot. At 7 days after sowing, weeds were removed and seedlings were thinned to 15 per row and then infested with between three and five third-instar *N. lugens* per seedling. After infestation, each seedbox was enclosed with a mylar film cage (65 by 45 by 70 cm). Grading for plant damage began when 95% of the susceptible check plants were killed and was repeated twice at 2-day intervals. A final rating was based on an average of the three gradings. To determine preference, *N. lugens* nymphs on 10 randomly selected seedlings per row in the seedbox screening test were counted at 48 h after infestation.

Population Growth

In this and the following tests, one accession each of *Oryza punctata*, *O. latifolia*, *O. rufipogon*, *O. nivara*, and *O. perennis* were used to determine the nature of resistance. The selected accessions had damage ratings based on previous studies (Heinrichs et al. 1985) that ranged from resistant to susceptible. Plants with damage ratings of 1.0–3.9 were considered resistant, 4.0–6.9 as moderately resistant, and 7–9 as susceptible. All experiments were conducted in the greenhouse with a temperature range of 20–35°C using *N. lugens* biotype 2 as test insects.

In the population growth test, four 7-day-old seedlings were transplanted into a clay pot (16-cm diam), with five pots for each rice species; each pot served as a replication. Treatments were arranged in a randomized complete block design (RCBD). Thirty days after transplanting (DAT) the plants in each pot were enclosed within a mylar film cage (13 cm diam by 90 cm high) and then infested with three pairs (male and female) of 3-day-old *N. lugens* adults. At 20 days after infestation (DAI), third, fourth, and fifth instars and adults were counted to determine the number in each development stage.

Quantity of Food Ingested and Metabolic Utilization

Six seedlings of each species were transplanted into each of five clay pots (12 cm diam) arranged in a RCBD. Each pot represented a replication. Six 5-day-old *N. lugens* female adults per replication were individually weighed on a balance (Mettler ME-30) (1 μg sensitivity) before infestation to determine their initial weight (W1) and again 24 h after infestation for their respective final weights (W2). Each test insect was placed within an airtight

parafilm sachet on the stem of a 45-day-old test plant as described in Pathak et al. (1982). Similarly, six control insects per replication were individually weighed before infestation for their initial weights (C1) and 24 h after starvation inside a parafilm sachet containing water-soaked cotton for their final weights (C2). The increase in weight of the insect, or the amount of food assimilated was calculated as:

$$W1 \times \frac{C1 - C2}{C1} + (W2 - W1)$$

The sum of the assimilated food and fresh weight of the excreta or honeydew gave the total weight of the food ingested by the insect. The amount of honeydew excreted was determined by first weighing the parafilm sachet containing the honeydew and then removing the honeydew with blotting paper and reweighing the parafilm sachet (Saxena & Pathak 1977).

Longevity, Fecundity, and Egg Hatchability

One 7-day-old seedling of each species was planted in each of 10 clay pots (16 cm diam); each pot served as a replication. At 20 DAT, each potted plant was covered with a mylar film cage (13 cm diam by 90 cm high) infested with one pair of 3-day-old adults. Dead adults and newly hatched nymphs were recorded daily and removed from the cage. The unhatched eggs were stained as described by Gifford & Trahan (1969) and counted 10 days after the death of the last adult in each cage.

Ovariole Development and Copulation

Test plants were grown in clay pots (16 cm diam) maintained inside rearing cages (50 by 50 by 50 cm). About 150 pairs of newly emerged *N. lugens* adults were placed on the plants in each cage when they were 30 days old. Nine days after infestation, reproductive organs from 15 to 20 randomly selected females were dissected in a physiological saline solution under a microscope (40×). The ovariole with the most advanced development was selected to determine the number of fully developed eggs and the length of the ovariole.

Successful copulation of females was also recorded. In mated females the bursa copulatrix was saccular in shape and opaque white, and spermatozoa moved outside the spermatheca during dissection in physiological saline solution. In unmated females, the bursa copulatrix was flat, small, and transparent.

Tolerance

Each species was planted in five clay pots (16 cm diam); each pot served as a replicate. When the plants were 30 days old, the secondary tillers of the plants were removed, and then the plants were enclosed with a mylar film cage (13 cm diam by 90 cm high). Test plants were infested with 100 second instars per cage. At 14 DAI, damage ratings were recorded on individual plants and insects were counted. The insects and the test plants were dried in an oven at 75°C for 72 h and weighed on a balance (Mettler). Plant height was measured before and after infestation.

Tolerance was evaluated as functional plant loss index (FPLI) on plant dry weight and plant height using the following equations (Panda Heinrichs 1983):

$$\text{FPLI (\%) (plant weight)} = \left[1 - \left(\frac{\text{dry weight of infested plants}}{\text{dry weight of uninfested plants}}\right) \cdot \left(1 - \frac{\text{damage rating}}{9}\right)\right] \times 100$$

$$\text{FPLI (\%) (plant growth)} = \left[1 - \left(\frac{\text{increased height of infested plants}}{\text{increased height of uninfested plants}}\right) \cdot \left(1 - \frac{\text{damage rating}}{9}\right)\right] \times 100$$

Results

Screening for Varietal Resistance and Preference

Of the 36 wild rice accessions tested, 20 exhibited resistant or moderately resistant reactions to *N. lugens* biotypes 1, 2, and 3 (Table 1). Two *O. officinalis* accessions (101155 and 101414) from Malaysia and India, respectively, had consistent damage ratings of 1 to all three biotypes. *O. punctata* (acc. no. 100892) and *O. nivara* (acc. no. 101973), both from India, reacted like *bph* 2 gene cultivars ('ASD7'), whereas *O. barthii* reacted like a *Bph* 1 gene cultivar ('IR26') (Pathak & Heinrichs 1982). Only *O. rufipogon* (acc. no. 100910) was rated as moderately resistant to all three biotypes. Eight other accessions exhibited moderate resistance to at least one biotype.

Table 1. Levels of resistance of wild rices to three *N. lugens* biotypes

Species			Damage rating[a]		
Name	IRRI acc. no.	Origin	Biotype 1	Biotype 2	Biotype 3
O. barthii	101243	Mali Republic	R[b]	S	MR[b]
O. latifolia	100168	Costa Rica	R	R	R
O. latifolia	100172	Guatemala	R	R	R
O. latifolia	100895	USA	R	R[b]	MR[b]
O. latifolia	100914	Mexico	R	R	R
O. latifolia	100956	India	R	R	R
O. latifolia	100962	Guatemala	R	R	R
O. latifolia	100964	Guatemala	R	R	R
O. latifolia	100965	Costa Rica	R	MR[b]	R[b]
O. latifolia	100966	Panama	R	R[b]	MR[b]
O. latifolia	102481	Nicaragua	R	R[b]	R[b]
O. longista-minata	100930	Sudan	S	S	S
O. minuta	100887	India	MR[b]	S	S
O. minuta	101081	Philippines	R	R	R
O. nivara	100197	Burma	S	S	S
O. nivara	101970	India	MR[b]	S	S
O. nivara	101973	India	R[b]	MR[b]	S
O. nivara	101979	India	S	S	S
O. nivara	102165	India	R	R	R
O. nivara	102185	India	R[b]	R[b]	R[b]
O. nivara	102467	Bangladesh	S	S	S
O. officinalis	101155	Malaysia	R	R	R
O. officinalis	101414	India	R	R	R
O. perenis	100844	Madagascar	S	S	S
O. punctata	100892	India	R	R	S
O. punctata	100937	China	R	R	R
O. punctata	100954	Japan	R	R	R
O. punctata	101409	Ghana	R	R	R
O. rufipogon	100184	Cuba	S	S	S
O. rufipogon	100910	Thailand	MR[b]	MR[b]	MR[b]
O. nivara × *rufipogon*	101966	—	S	S	S
O. sativa f. *spontanea*	100901	India	MR	S	S
O. sativa f. *spontanea*	100902	Japan	S	S	S
O. sativa f. *spontanea*	100920	Malaysia	S	S	S
O. sativa f. *spontanea*	100942	India	S	S	S
O. sativa f. *spontanea*	100943	India	S	S	S
'TN1' (S check)	105	—	S	S	S
'IR 26' (check)	6303	—	R	S	R
'ASD7' (check)	24154	—	R	R	S

[a]Based on a plant damage rating of 1–9: 1.0–3.9, resistant (R); 4.0–6.9, moderately resistant (MR); 7.0–9, susceptible (S). Data are the means of four replications.
[b]Tolerant accession because it has an equal or higher *N. lugens* population than that of the susceptible check but has resistant or moderately resistant damage ratings.

Differences in susceptibility and resistance were noted among accessions of the same species. Of the seven *O. nivara* and four *O. punctata* accessions tested, only two (acc. no. 102165 and 102185) and three (acc. no. 100937, 100954, and 101409) accessions, respectively, were resistant to the three biotypes.

Significant differences in number of *N. lugens* settled on the different wild rices were observed at 48 h after infestation (Fig. 1). Five accessions (101081, 101155, 100937, 100954, and 100962) rated as resistant in screening tests had generally lower densities of all·three biotypes than susceptible *O. perennis* (acc. no. 100844) and *O. rufipogon* (acc. no. 100184). The number of insects on *O. rufipogon* (acc. no. 100910) that had moderately resistant reactions to the three biotypes in the screening test was not significantly different from those on susceptible 'TNI,' *O. perennis*, and *O. rufipogon* (acc. no. 100185).

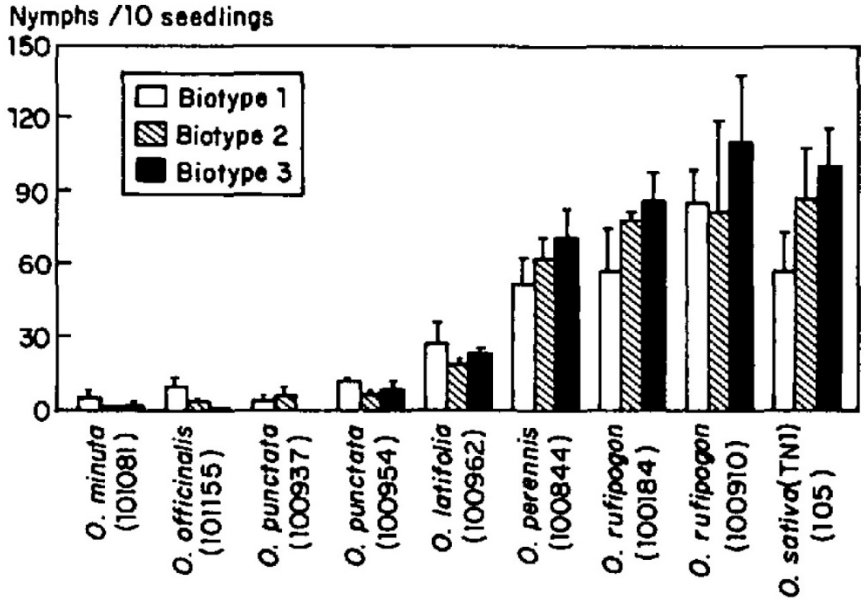

Figure 1. Preference of *N. lugens* nymphs for selected wild rices 48 h after infestation. Standard deviations are indicated on the bars. IRRI accession numbers are in parentheses.

Population Growth

Populations were lowest on the resistant accessions (Table 2). Population growth in 20 days on susceptible *O. perennis* was 31- and 6-fold higher than on resistant *O. punctata* and *O. latifolia*, respectively, but it did not significantly differ from that on moderately resistant *O. rufipogon*.

Development was delayed on the resistant species. There was a significantly higher percentage of third and fourth instars and lower percentage of fifth instars and adults on resistant ('ASD7,' *O. punctata*, and *O. latifolia*) than on moderately resistant and susceptible accessions.

Table 2. Population growth and developmental stages of *N. lugens* biotype 2[a] on selected wild rices

Species	IRRI accession no.	Resistance rating[b]	*N. lugens* population (no. per cage)	Developmental stage (%)	
				3rd and 4th instars	5th instars and adults
O. punctata	100954	R	18 ± 17.2c	85.3 ± 15.9a	14.7 ± 15.9b
O. latifolia	100962	R	91 ± 73.8bc	82.3 ± 9.0a	17.7 ± 9.0b
O. rufipogon	100910	MR	595 ± 15.9a	45.6 ± 11.6b	54.4 ± 11.6a
O. perennis	100844	S	566 ± 34.3a	42.5 ± 27.7b	57.5 ± 27.7a
O. sativa, 'ASD7'	6303	R	237 ± 92.8b	90.5 ± 5.4a	9.5 ± 5.4b

[a]Based on an initial population of three pairs (males and females) of adult *N. lugens*. In a column, means followed by a common letter are not significantly different ($P > 0.05$; Duncan's multiple range test [Gomez and Gomez 1984]).

[b]Rating in seedbox test: R, resistant; MR, moderately resistant; S, susceptible.

Quantity of Food Ingested and Metabolic Utilization

Amount of food ingested was lowest on the resistant accessions (Table 3). The quantity of food ingested by the insects from moderately resistant *O. rufipogon* and susceptible *O. perennis* and 'IR26' ranged from 8 to 17 mg per day. On resistant accessions 'ASD7,' *O. punctata*, and *O. latifolia* food ingested was only ca. 3 mg per day (Table 3).

Food assimilation was related to amount of food ingested. Food assimilation on susceptible accessions was ca. 1 mg per day, while on resistant accessions it was about one-half that amount (Table 3).

The increase in insect body weight on resistant accessions was also significantly lower as compared with the moderately resistant and susceptible accessions (Table 3). The increase in body weight on susceptible *O. perennis* in 24 h was 33%, while it was only 9% on the resistant *O. punctata*. The amount of food ingested and increase in body weight were significantly correlated ($r = 0.918$; $P < 0.05$). The computed regression equation of percent gain in body weight and the amount of food ingested was $y = 6.31 + 1.59x$, indicating a 1.59% increase in body weight for each mg of food ingested.

Table 3. Ingestion and metabolic utilization of food by *N. lugens* biotype 2 female adults[a] on selected wild rices

Species	IRRI accession no.	Resistance rating[b]	Food ingested (mg/♀/day)	Food assimilated (mg/♀/day)	Increase in body wt (%)
O. punctata	100954	R	2.6 ± 4.5c	0.4 ± 0.3c	9.1 ± 13.6e
O. latifolia	100962	R	3.4 ± 5.2b	0.5 ± 0.3c	15.8 ± 13.6d
O. rufipogon	100910	MR	10.1 ± 15.3b	0.8 ± 0.7ab	19.9 ± 22.1c
O. perennis	100844	S	17.9 ± 19.2a	1.1 ± 0.6a	33.4 ± 25.7a
O. sativa, 'IR26'	24154	(S check)	7.8 ± 7.3b	0.8 ± 0.5b	25.1 ± 20.3b
O. sativa, 'ASD7'	6303	(R check)	2.1 ± 5.3c	0.3 ± 0.4c	5.3 ± 19.9f

[a]Data are based on the means of six *N. lugens* female adults in each of five replications. In a column, means followed by a common letter are not significantly different ($P > 0.05$; Duncan's multiple range test [Gomez and Gomez 1984]).

[b]Rating in seedbox screening test: R, resistant; MR, moderately resistant; S, susceptible.

Longevity, Fecundity, and Hatchability

Adults lived significantly shorter and laid fewer eggs on resistant *O. punctata* than on the other resistant and susceptible accessions (Table 4). Longevity and fecundity on moderately resistant *O. rufipogon* did not significantly differ from that on the susceptible accessions.

Fecundity and longevity were significantly correlated ($r = 0.935$; $P < 0.05$). The regression equation of the number of eggs laid and longevity was $y = 24.69x - 114.38$, indicating that for every day increase in longevity there was a corresponding increase of 24.7 eggs laid by a female starting at 6 days after emergence. Egg hatchability was lowest on *O. punctata* (55%) and *O. latifolia* (75%); both differed significantly from the susceptible check (94%) and the resistant check (98%).

Table 4. Longevity and fecundity of *N. lugens* biotype 2 female adults[a] and egg hatchability on selected rices

Species	IRRI accession no.	Resistance rating[b]	Longevity (days)	Eggs laid (no./♀)	Hatchability (%)
O. punctata	100954	R	5.8 ± 1.7c	28 ± 44.4c	55.4 ± 29.5c
O. latifolia	100962	R	14.9 ± 4.9b	169 ± 113.7bc	74.5 ± 27.6bc
O. rufipogon	100910	MR	18.3 ± 6.8ab	401 ± 305.1a	81.6 ± 12.8ab
O. perennis	100844	S	23.2 ± 6.9a	421 ± 234.5a	79.7 ± 29.1ab
O. sativa, 'IR26'	24154	(S check)	17.3 ± 6.6ab	359 ± 222.6a	94.2 ± 8.4a
O. sativa, 'ASD7'	6303	(R check)	13.1 ± 7.9b	222 ± 274.8ab	98.1 ± 2.5a

[a]Data derived from one female in each of the replications. Means in a column followed by the same letter are not significantly different ($P > 0.05$; Duncan's multiple range test [Gomez and Gomez 1984]).
[b]Rating in seedbox screening test: R, resistant; MR, moderately resistant; S, susceptible.

Ovariole Development and Copulation

The ovaries of adults on resistant *O. punctata* had significantly fewer fully developed eggs and shorter ovarioles than those on moderately resistant *O. rufipogon*, and susceptible *O. perennis* and 'IR26' (Table 5). The percent females that had copulated was positively correlated ($r = 0.989$; $P < 0.05$) with ovariole development. The percentage copulation on resistant *O. punctata* was 53%, while it ranged from 80 to 89% on moderately resistant and susceptible accessions at 9 days after adult emergence (Table 5).

Table 5. Ovariole development of *N. lugens* females[a] on selected wild rices

Species	IRRI accession no.	Resistance rating[b]	Fully developed eggs (no.)	Length of ovariole (μm)	Copulation (%)
O. punctata	100954	R	0.7 ± 1.0c	1,389 ± 181.6b	53.3 ± 11.6b
O.rufipogon	100910	MR	15.6 ± 10.5ab	2,017 ± 514.4a	80.0 ± 20.0a
O. perennis	100844	S	20.8 ± 11.7a	2,013 ± 472.2a	88.9 ± 19.2a
O. sativa, 'IR26'	24154	(S check)	11.9 ± 12.2b	2,036 ± 581.6a	82.2 ± 15.7a

[a]Data are based on a mean of 15–20 females per rice species. Means in a column followed by a common letter are not significantly different ($P > 0.05$; Duncan's multiple range test [Gomez and Gomez 1984]).
[b]Rating in seedbox screening test: R, resistant; MR, moderately resistant; S, susceptible.

Tolerance

N. lugens survival (62–73%) and body weight (0.67–0.79 mg) were not significantly different among test accessions, indicating that the plants had no antibiosis effect (Table 6). However, damage ratings and FPLI (both plant weight and height) of the moderately resistant *O. rufipogon* and *O. nivara* were significantly lower than those of *O. perennis* and 'IR26.'

Table 6. Damage ratings and functional plant loss index (FPLI) of selected wild rices infested with 100 biotype 2 *N. lugens* per 30-day-old plant

Species	IRRI accession no.	Resistance rating[a]	Damage rating	FPLI (%)		*N. lugens* survival (%)	Body wt (mg/insect)[b]
				Plant dry wt	Plant ht		
O. rufipogon	100910	MR	3.4 ± 1.7c	69.0 ± 14.4b	38.9 ± 63.2b	69.4 ± 13.7a	0.79 ± 0.2a
O. nivara	101973	MR	3.8 ± 1.10c	58.6 ± 9.2b	53.2 ± 34.6b	62.4 ± 8.2a	0.67 ± 0.2a
O. perennis	100844	S	6.6 ± 1.7b	85.0 ± 14.1a	84.4 ± 15.3a	62.2 ± 12.9a	0.67 ± 0.0a
O. sativa, 'IR26'	24154	(S check)	8.2 ± 1.8a	96.0 ± 9.1a	96.1 ± 8.7a	73.0 ± 10.4a	0.75 ± 0.1a

Means in a column followed by a common letter are not significantly different ($P > 0.05$; Duncan's multiple range test [Gomez and Gomez 1984]).

[a]Rating in seedbox screening test: R, resistant; MR, moderately resistant; S, susceptible.

[b]Based on 50 biotype 2 *N. lugens* per plant, the weight of *N. lugens* on the susceptible check was significantly less than that on the moderately resistant species because the plants were hopperburned and the insects starved.

Discussion

This study indicated that *N. lugens* on the highly resistant wild rice species developed low populations and had a retarded developmental rate, underdeveloped ovaries, low fecundity, and reduced adult longevity. These factors were attributed to a low quantity of food ingested and assimilated on the resistant wild rices.

Development of the reproductive organ of *N. lugens* was severely retarded on *O. punctata* (acc. no. 100954). The number of fully developed eggs was 3% of that on a susceptible wild rice 9 days after infestation. According to Wigglesworth (1964), maturation of oocytes is highly dependent on nutrition in most insects. Katayama (1975), using *O. sativa* as a test plant, reported on the influence of food intake on the development of *N. lugens* ovarioles.

It is significant to note that two wild rices, *O. punctata* (acc. no. 100954) and *O. latifolia* (acc. no. 100962), significantly reduced percentage egg hatching. As indicated in Table 4 and in our previous studies (E.A.H. & F.G.M., unpublished data), *N. lugens*-resistant *O. sativa* accessions have not been observed to reduce the hatchability of eggs.

Although nonpreference appeared to be a major mechanism involved in the highly resistant *O. punctata* and *O. latifolia* accessions, neither nonpreference nor antibiosis were involved in the resistance of moderately resistant *O. rufipogon* (acc. no. 100910). This is indicated by the fact that the *N. lugens* population, food ingestion and body weight increase, adult longevity and number of eggs laid, and ovariole development on *O. rufipogon* were similar to that of the susceptible check. Tolerance of both *O. rufipogon* and *O. nivara* (acc. no. 101973) was evident because both species were moderately resistant in the seedbox screening test in spite of maintaining *N. lugens* populations equal to that on the

susceptible check. Further evaluation using the FPLI indicated that these two moderately resistant wild rices had less plant dry weight loss and plant height reduction than susceptible accessions when infested with the same number of *N. lugens* per plant.

Both *O. nivara* and *O. rufipogon* have 24 chromosomes and have the AA genome groups as does *O. sativa* and can be utilized as donor sources for *N. lugens* resistance in a hybridization program with *O. sativa*. *O. latifolia* and *O. punctata* have different genome groups than that of *O. sativa* (Chang 1976) and, thus, cannot be crossed with *O. sativa* using conventional breeding methods. The development of genetic engineering techniques may someday allow the utilization of these wild rices in breeding programs for insect resistance.

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