

Do Rice Hybrids Have Heterosis for Insect Resistance? A Study with *Nilaparvata lugens* (Hemiptera: Delphacidae) and *Marasmia patnalis* (Lepidoptera: Pyralidae)

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ABSTRACT Antibiosis-based resistance to two insect pests of rice, *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae) and *Marasmia patnalis* Bradley (Lepidoptera: Pyralidae), was compared in 11 F₁ hybrids and their parental lines. Our objective was to determine whether hybrids show heterosis (hybrid vigor) for insect resistance or susceptibility. Heterosis is defined as the amount by which a hybrid exceeds its midparent value or its better parent. Overall, we did not find evidence of heterosis or heterobeltiosis (a type of heterosis in which a hybrid exceeds its better parent) for antibiosis-based resistance or susceptibility to either of the insects. One hybrid, IR64616H, seemed more resistant to *M. patnalis* than its better parent but none of the other hybrids showed heterobeltiosis for resistance or susceptibility to either insect. Three hybrids had resistance to *N. lugens* that exceeded their midparent value, possibly due to dominant resistance in one of the parents. The increased frequency and severity of insect outbreaks on hybrid rice that have been reported in China may be attributable to factors other than diminished antibiosis in hybrids, such as greater attractiveness of hybrids to migrating or dispersing insects or differences in agronomic practices applied to hybrids and inbred rice cultivars.

KEY WORDS heterosis, heterobeltiosis, hybrid rice, host plant resistance, antibiosis

HYBRID CROP SEED IS the F₁ progeny of two inbred parental lines (Fig. 1). Hybrids often have higher yields than their parental lines, a phenomenon known as heterosis or hybrid vigor. Heterosis is defined as the amount by which a hybrid exceeds its midparent value or its better parent, for a trait such as yield or plant height (Mather and Jinks 1971, Virmani 1994). Improvement of the hybrid over the better parent is also referred to as heterobeltiosis. The yield advantage of hybrids has led to the success of hybrid maize, sorghum, and numerous vegetable crops. Concerted efforts to develop hybrid rice began in China in the 1960s, and hybrids now account for ≈50% of China's rice-growing area (Janaiah and Hossain 2001). Increasing amounts of hybrid rice are also being grown in India, the Philippines, the United States, and several other countries. Rice hybrids typically have a 20% higher yield than their inbred parental lines (Virmani 1994). The cultivation of hybrid rice may increase substantially in the coming decade as further progress is made in improving the grain quality and decreasing

the cost of seed production of hybrids suitable for tropical areas (Virmani 2001).

There have been occasional reports in China of increased frequency and severity of insect and disease incidence on hybrid rice in comparison with inbred rice varieties (for reviews, see Mew et al. 1988, Sogawa et al. 2003). The insect pests noted in these reports include two delphacids (Hemiptera): *Nilaparvata lugens* (Stål) and *Sogatella furcifera* (Horvath); and three pyralids (Lepidoptera): *Cnaphalocrocis medinalis* (Guenée) (a leaf folder), and the stem borers *Scirpophaga incertulas* (Walker) and *Chilo suppressalis* (Walker). Earlier planting dates may account for some of the increased insect pest populations on hybrids (Mew et al. 1988). In addition, some studies have reported that hybrids are more susceptible to insects than are inbred varieties. For example, Huang et al. (1985) found that *S. furcifera* population growth was faster on a hybrid than on two inbred varieties under greenhouse conditions, and Tan (1987) found *C. suppressalis* had higher pupal weight and survival to adult on two hybrids than on two inbred varieties. The results of studies such as Huang et al. (1985) and Tan (1987) could suggest that hybrid rice lines are inherently more susceptible to insects than are inbred varieties. However, these studies did not compare insect resistance of rice hybrids with that of their inbred parental lines. Such comparisons are necessary to test the inherent properties of hybrids.

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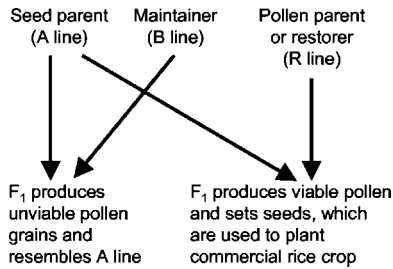


Fig. 1. Production of hybrid rice seed by using a three-line system.

Painter (1951) noted that general vigor and hybrid vigor have a strong effect on tolerance, i.e., the capacity to produce a crop of high quality and yield despite insect infestation. This is exemplified by tolerance to chinch bug, *Blissus leucopterus* (Say) (Hemiptera: Lygaeidae), in F_1 maize hybrids and sorghum hybrids in which both parents are susceptible (Painter 1951). Similarly, a rice hybrid was reported to be more tolerant to *C. suppressalis*, due to its vigorous tillering and consequent ability to compensate for damage (Tan et al. 1983). Whereas tolerance is a measure of the effect of insect feeding on a plant genotype, antibiosis concerns the effect of the plant genotype on the survival, growth rate, or reproduction of insects after the ingestion of host tissue. Two alternative hypotheses can be proposed concerning possible heterosis for the antibiosis type of insect resistance. Hybrids might have increased antibiosis due, for example, to increased levels of constitutive or inducible chemical defenses. In contrast, hybrids might be more suitable hosts for insects due to a possible increase in nutritional quality.

In this study, we compared the resistance of 11 rice hybrids and their parental lines to two insect pests, a planthopper (*N. lugens*) and a pyralid leafroller (*Masmia patnalis* Bradley). We measured insect survival, weight, and developmental time and, in the case of *N. lugens*, the damage rating of plants after insect infestation. Our objective was to determine whether rice hybrids have heterosis or heterobeltiosis for insect resistance or susceptibility.

Materials and Methods

Plants. We studied 11 hybrid lines and their parents, derived from a three-line hybrid rice breeding program (Fig. 1) at International Rice Research Institute (Laguna Province, Philippines). The parental lines in a three-line system are the A line or seed parent, the B line or maintainer, and the R (restorer) line or pollen parent (Virmani 1994). Hybrid seed is produced by crossing the A and R lines. The A line is male sterile and therefore cannot self-fertilize, which facilitates the production of hybrid seed. The B line is used to pollinate the A line to maintain a supply of A line seed. The A and B lines have the same nuclear genome but differ in the cytoplasmic genome. Male sterility results from the interaction of a nuclear allele with a

cytoplasmic allele that is carried only by the A line. A and R lines are selected on the basis of their combining ability, i.e., their performance in hybrid combinations as measured by heterosis and other characteristics of the F_1 produced (Virmani 1994).

There were 11 experimental groups of plants, each containing a unique hybrid and R line but some having the same A and B lines (Table 1). All the hybrids in groups A1 to A5 had IR68897A and IR68897B as A and B lines, respectively. Similarly, all the hybrids in groups B1 to B3 had IR68888A and IR68888B as A and B lines, respectively. Groups C1, D1, and E1 had unique A and B lines.

The plants and insects were reared and the experiments were conducted under ambient conditions in a greenhouse, in which noontime temperatures ranged from 25 to 35°C.

Insects. *N. lugens* were obtained from a greenhouse colony established from rice fields in Laguna Province. The colony was maintained on the susceptible rice variety Taichung Native 1 (TN1). Gravid females were randomly selected from the culture and allowed to oviposit on TN1 plants for 2–3 d. Nymphs were reared to the second or third instar and then used to infest test plants. *M. patnalis* adults were collected from rice fields in Laguna Province. The adults were placed in cages with 45-d-old TN1 plants, brought to the greenhouse, and allowed to oviposit. Neonate larvae were used to infest test plants. We chose to use *M. patnalis* because it has a similar biology to *C. medinalis* (a species for which outbreaks have been reported on hybrid rice in China), and it is easier to collect in sufficient numbers in Laguna Province.

***M. patnalis* Survival, Weight, and Developmental Time.** Seven-day-old seedlings were transplanted into 15-cm-diameter pots, four per pot. When the plants were 35 d old, four pots of a single entry were enclosed in a rectangular plastic cage (96 by 52 by 40 cm) with nylon mesh side windows and tops. Twenty neonate larvae were introduced into each cage. Each cage represented a replicate, and the cages for the entries [(A line, B line, R line(s) and hybrid(s)] of each group A–E were arranged in a randomized complete block design with four replicates. Adults that emerged were collected daily, placed in individual vials, and stored at –20°C. Adults were dried at 60°C for 3 d and weighed individually on a balance with 0.01-mg sensitivity. The percentage of survival of larvae to the adult stage and the weight and developmental time of males and females were recorded.

Modified Seedbox Test for Reaction to *N. lugens* Infestation. Separate seedboxes (110 by 65 by 6 cm) were prepared for each of the groups A–E, with one replicate per seedbox. Fifteen pregerminated seeds of each entry [A line, B line, R line(s), and hybrid(s)] and the susceptible control variety IR26 were sown in rows in a randomized arrangement. There were three replicate seedboxes per group, and the seedboxes were placed in a completely randomized arrangement. The seedboxes were infested with two nymphs per seedling and covered with plastic cages with nylon mesh side windows and tops. When the IR26 plants

Table 1. Survival and development (mean ± SEM) of *M. patnalis* reared on rice hybrids and their parental lines

Group	Line	Survival (%)	Weight (mg)		Developmental time (d)	
			Male	Female	Male	Female
A1	IR60819R	48.8 ± 13.7	4.34 ± 0.19	5.23 ± 0.19	25.5 ± 0.54	25.9 ± 0.54
	IR68897A	65.0 ± 8.4	4.40 ± 0.19	5.23 ± 0.17	24.7 ± 0.52	25.8 ± 0.47
	IR68897B	51.3 ± 2.4	4.40 ± 0.19	5.45 ± 0.17	25.6 ± 0.56	26.2 ± 0.49
A2	IR73868H	48.8 ± 3.1	4.67 ± 0.19	5.80 ± 0.18	25.8 ± 0.54	25.9 ± 0.51
	IR62036R	43.8 ± 10.7	4.20 ± 0.15	5.55 ± 0.21	24.4 ± 0.45	24.3 ± 0.54c
	IR68897A	65.0 ± 8.4	4.39 ± 0.15	5.24 ± 0.16	24.7 ± 0.43	25.8 ± 0.39b
	IR68897B	51.3 ± 2.4	4.38 ± 0.16	5.45 ± 0.17	25.9 ± 0.47	26.3 ± 0.43ab
A3	IR73855H	55.0 ± 7.4	4.38 ± 0.14	5.14 ± 0.18	25.9 ± 0.42	26.3 ± 0.45a
	IR65622R	55.0 ± 16.5	4.65 ± 0.17	4.80 ± 0.23	25.5 ± 0.37	25.4 ± 0.58
	IR68897A	65.0 ± 8.4	4.40 ± 0.18	5.21 ± 0.21	24.8 ± 0.39	25.8 ± 0.49
	IR68897B	51.3 ± 2.4	4.40 ± 0.19	5.44 ± 0.21	25.5 ± 0.45	26.3 ± 0.51
A4	IR75584H	57.5 ± 6.6	4.27 ± 0.18	5.41 ± 0.21	25.7 ± 0.40	26.5 ± 0.51
	IR60199R	53.8 ± 9.7	4.30 ± 0.14	4.99 ± 0.22	24.9 ± 0.42	26.4 ± 0.49
	IR68897A	65.0 ± 8.4	4.39 ± 0.15	5.23 ± 0.18	24.7 ± 0.44	25.8 ± 0.41
	IR68897B	51.3 ± 2.4	4.39 ± 0.16	5.45 ± 0.19	25.6 ± 0.48	26.3 ± 0.45
A5	IR76708H	51.3 ± 6.9	4.26 ± 0.15	5.33 ± 0.21	25.4 ± 0.44	25.5 ± 0.47
	IR68445R	50.0 ± 7.9	4.19 ± 0.18	5.23 ± 0.20	24.3 ± 0.76	26.5 ± 0.52
	IR68897A	65.0 ± 8.4	4.40 ± 0.18	5.21 ± 0.18	24.8 ± 0.73	25.8 ± 0.47
	IR68897B	51.3 ± 2.4	4.40 ± 0.19	5.45 ± 0.19	25.5 ± 0.84	26.2 ± 0.49
B1	IR76713H	62.5 ± 5.9	3.94 ± 0.17	5.33 ± 0.19	25.9 ± 0.66	26.2 ± 0.49
	IR63870R	48.8 ± 8.9	4.23 ± 0.18	5.63 ± 0.17	24.4 ± 0.55	24.9 ± 0.62
	IR68888A	57.5 ± 4.8	4.15 ± 0.16	5.29 ± 0.17	25.9 ± 0.50	26.2 ± 0.60
	IR68888B	58.8 ± 9.7	4.17 ± 0.16	5.13 ± 0.17	25.8 ± 0.47	26.5 ± 0.61
B2	IR73860H	61.3 ± 8.3	4.29 ± 0.15	5.30 ± 0.17	25.9 ± 0.47	26.4 ± 0.60
	IR56381R	67.5 ± 8.3a	4.34 ± 0.15	5.49 ± 0.17	25.3 ± 0.64	25.9 ± 0.49
	IR68888A	57.5 ± 4.8ab	4.15 ± 0.15	5.29 ± 0.18	25.9 ± 0.65	26.2 ± 0.52
	IR68888B	58.8 ± 9.7ab	4.17 ± 0.14	5.13 ± 0.19	25.8 ± 0.62	26.5 ± 0.54
B3	IR73863H	47.5 ± 7.2b	4.14 ± 0.18	5.55 ± 0.19	26.5 ± 0.77	25.9 ± 0.54
	IR62161R	41.3 ± 2.4	4.46 ± 0.19	5.30 ± 0.18	25.3 ± 0.58	26.4 ± 0.71
	IR68888A	57.5 ± 4.8	4.15 ± 0.17	5.29 ± 0.16	25.9 ± 0.51	26.2 ± 0.68
	IR68888B	58.8 ± 9.7	4.17 ± 0.16	5.13 ± 0.17	25.8 ± 0.49	26.6 ± 0.69
C1	IR75207H	42.5 ± 8.3	4.51 ± 0.19	5.45 ± 0.18	24.7 ± 0.56	25.2 ± 0.72
	IR34686R	51.3 ± 11.6	3.68 ± 0.14b	5.02 ± 0.18b	25.5 ± 0.61	26.8 ± 0.51
	IR58025A	50.0 ± 8.9	4.28 ± 0.15a	5.53 ± 0.17ab	25.7 ± 0.62	25.3 ± 0.49
	IR58025B	62.5 ± 6.3	4.33 ± 0.14a	5.87 ± 0.15a	24.7 ± 0.61	26.3 ± 0.41
D1	IR68284H	56.3 ± 14.2	4.32 ± 0.16a	5.19 ± 0.15b	25.9 ± 0.65	25.5 ± 0.42
	IR29723R	48.8 ± 3.1ab	4.45 ± 0.19	5.34 ± 0.19a	25.5 ± 0.67	25.2 ± 0.42
	IR62829A	53.8 ± 4.3ab	4.49 ± 0.18	5.72 ± 0.19a	24.8 ± 0.64	24.6 ± 0.41
	IR62829B	60.0 ± 11.4a	4.70 ± 0.18	5.31 ± 0.18a	25.3 ± 0.64	25.9 ± 0.38
E1	IR64616H	38.8 ± 4.3b	4.15 ± 0.22	4.61 ± 0.20b	26.9 ± 0.75	26.2 ± 0.43
	IR68926R	52.5 ± 7.8ab	4.33 ± 0.15	5.64 ± 0.23	24.3 ± 0.49b	24.8 ± 0.56
	IR68899A	67.5 ± 11.6a	4.41 ± 0.15	5.45 ± 0.23	25.7 ± 0.46ab	26.1 ± 0.55
	IR68899B	40.0 ± 3.5b	4.54 ± 0.18	5.76 ± 0.23	26.5 ± 0.57a	26.5 ± 0.56
	IR75221H	51.3 ± 2.4ab	4.48 ± 0.17	5.36 ± 0.21	24.6 ± 0.55b	26.2 ± 0.52

Means within a column and group sharing the same letter are not significantly different (LSD test, $P > 0.05$). Where means are not followed by letters, the main effect of rice line is not significant ($P > 0.05$).

were all dead, the test entries were rated using the 0–9 scale of the Standard Evaluation System for Rice (Heinrichs et al. 1985).

N. lugens Survival, Weight, and Developmental Time. Seven-day-old seedlings were transplanted into 15-cm-diameter pots, one per pot. Thirty days after sowing, each potted test plant was enclosed with a cylindrical plastic cage with nylon mesh side windows and tops. Thirty newly hatched nymphs were introduced into each cage. Each potted plant represented a replicate, and the plants [A line, B line, R line(s), and hybrid(s)] for each group A–E were arranged in a randomized complete block design with six replicates. Adults emerging in the cages were collected daily, placed in vials, and stored at -20°C . Adults were dried at 60°C for 2 d and weighed on a balance with 0.01-mg sensitivity. The percentage of survival of nymphs to the adult stage and the weight and developmental time of males and females were recorded.

Data Analysis. Data on survival and plant damage ratings were analyzed using PROC analysis of variance (ANOVA) of the SAS package (SAS Institute 1998). Survival data (in percentages) were square root- and arcsine-transformed before analysis. Data on developmental time and adult weight had unequal sample sizes among replicates and were therefore analyzed using PROC MIXED of SAS, and least squares means were compared and are reported for these variables. We used the test of least significant difference (LSD) to compare means but conducted means comparisons only when the main effect of rice entry was significant—a conservative procedure known as Fisher’s protected LSD (Steele and Torrie 1980).

Results

Resistance to *M. patnalis*. In only one of the 11 groups (D1) was there a trend of increased or de-

Table 2. Survival and development (mean \pm SEM) of *N. lugens* reared on rice hybrids and their parental lines

Group	Line	Damage rating	Survival (%)	Weight (mg)		Development time (d)	
				Male	Female	Male	Female
A1	IR60819R	7.7 \pm 1.3	97.1 \pm 1.5a	0.48 \pm 0.01	0.79 \pm 0.02	13.1 \pm 0.05b	13.4 \pm 0.07
	IR68897A	6.3 \pm 0.7	93.0 \pm 2.4ab	0.49 \pm 0.01	0.79 \pm 0.02	12.9 \pm 0.06a	13.1 \pm 0.07
	IR68897B	6.3 \pm 1.8	91.5 \pm 1.9b	0.47 \pm 0.01	0.76 \pm 0.02	13.0 \pm 0.06ab	13.2 \pm 0.08
A2	IR73868H	7.0 \pm 0.0	95.4 \pm 1.0ab	0.50 \pm 0.01	0.80 \pm 0.02	12.8 \pm 0.06a	13.1 \pm 0.07
	IR62036R	3.0 \pm 0.0a	76.5 \pm 7.8b	0.39 \pm 0.01b	0.62 \pm 0.02b	13.6 \pm 0.15c	14.3 \pm 0.15c
	IR68897A	6.3 \pm 0.7b	93.0 \pm 2.4a	0.49 \pm 0.01a	0.79 \pm 0.02a	12.9 \pm 0.15a	13.2 \pm 0.14a
	IR68897B	6.3 \pm 1.8b	91.5 \pm 1.9ab	0.48 \pm 0.01a	0.76 \pm 0.02a	13.0 \pm 0.14b	13.4 \pm 0.15a
A3	IR73855H	3.7 \pm 0.7a	91.9 \pm 3.1ab	0.47 \pm 0.01a	0.75 \pm 0.02a	13.4 \pm 0.14bc	13.9 \pm 0.15b
	IR65622R	7.7 \pm 0.7	94.9 \pm 3.7	0.47 \pm 0.01	0.77 \pm 0.02	12.9 \pm 0.07	13.5 \pm 0.12b
	IR68897A	6.3 \pm 0.7	93.0 \pm 2.4	0.49 \pm 0.01	0.79 \pm 0.02	12.8 \pm 0.07	13.2 \pm 0.12a
	IR68897B	6.3 \pm 1.8	91.5 \pm 1.9	0.48 \pm 0.01	0.76 \pm 0.02	13.0 \pm 0.06	13.4 \pm 0.13ab
A4	IR75584H	8.3 \pm 0.7	94.5 \pm 2.0	0.48 \pm 0.01	0.79 \pm 0.02	12.9 \pm 0.07	13.1 \pm 0.12a
	IR60199R	5.0 \pm 0.0	83.9 \pm 5.5	0.47 \pm 0.01	0.75 \pm 0.02	12.9 \pm 0.07	13.3 \pm 0.11
	IR68897A	6.3 \pm 0.7	93.0 \pm 2.4	0.49 \pm 0.01	0.79 \pm 0.02	12.8 \pm 0.06	13.2 \pm 0.11
A5	IR68897B	6.3 \pm 1.8	91.5 \pm 1.9	0.48 \pm 0.01	0.75 \pm 0.02	13.0 \pm 0.06	13.4 \pm 0.11
	IR76708H	7.7 \pm 0.7	91.1 \pm 2.2	0.47 \pm 0.01	0.76 \pm 0.02	12.9 \pm 0.06	13.3 \pm 0.11
	IR68445R	6.3 \pm 1.3	90.4 \pm 3.1	0.47 \pm 0.01	0.78 \pm 0.02	12.9 \pm 0.06	13.4 \pm 0.07
	IR68897A	6.3 \pm 0.7	93.0 \pm 2.4	0.49 \pm 0.01	0.79 \pm 0.02	12.9 \pm 0.06	13.2 \pm 0.06
B1	IR68897B	6.3 \pm 1.8	91.5 \pm 1.9	0.48 \pm 0.01	0.76 \pm 0.02	13.0 \pm 0.05	13.4 \pm 0.07
	IR76713H	3.7 \pm 0.7	95.8 \pm 1.2	0.49 \pm 0.01	0.78 \pm 0.02	12.8 \pm 0.06	13.3 \pm 0.07
	IR63870R	1.0 \pm 0.0a	90.1 \pm 5.2	0.42 \pm 0.02b	0.70 \pm 0.02	13.8 \pm 0.17b	15.4 \pm 0.21b
	IR68888A	6.3 \pm 1.3b	93.4 \pm 3.5	0.48 \pm 0.01a	0.77 \pm 0.02	12.9 \pm 0.17a	13.3 \pm 0.21a
B2	IR68888B	5.7 \pm 0.7b	96.0 \pm 1.9	0.47 \pm 0.01a	0.75 \pm 0.02	12.9 \pm 0.17a	13.2 \pm 0.21a
	IR73860H	2.3 \pm 2.9a	93.0 \pm 2.7	0.44 \pm 0.01a	0.73 \pm 0.02	13.6 \pm 0.17b	14.8 \pm 0.21b
	IR56381R	7.7 \pm 0.7	91.1 \pm 2.4b	0.47 \pm 0.01	0.77 \pm 0.01	12.9 \pm 0.09	13.2 \pm 0.09
	IR68888A	6.3 \pm 1.3	93.4 \pm 3.5ab	0.48 \pm 0.01	0.77 \pm 0.01	12.9 \pm 0.09	13.3 \pm 0.09
B3	IR68888B	5.7 \pm 0.6	96.0 \pm 1.9a	0.47 \pm 0.01	0.75 \pm 0.01	12.9 \pm 0.09	13.2 \pm 0.09
	IR73863H	5.0 \pm 1.2	93.6 \pm 2.2ab	0.48 \pm 0.01	0.76 \pm 0.01	12.9 \pm 0.09	13.3 \pm 0.09
	IR62161R	5.7 \pm 0.7	91.7 \pm 3.9	0.48 \pm 0.01	0.79 \pm 0.02	13.0 \pm 0.11	13.7 \pm 0.12
	IR68888A	6.3 \pm 1.3	93.4 \pm 3.5	0.48 \pm 0.01	0.77 \pm 0.01	12.9 \pm 0.11	13.3 \pm 0.12
C1	IR68888B	5.7 \pm 0.7	96.0 \pm 1.9	0.47 \pm 0.01	0.75 \pm 0.02	12.9 \pm 0.11	13.2 \pm 0.12
	IR75207H	4.3 \pm 0.7	95.2 \pm 1.9	0.49 \pm 0.01	0.79 \pm 0.02	12.8 \pm 0.11	13.3 \pm 0.12
	IR34686R	7.7 \pm 0.7	91.7 \pm 2.8	0.44 \pm 0.01	0.69 \pm 0.02	13.2 \pm 0.18b	13.8 \pm 0.09b
	IR58025A	9.0 \pm 0.0	90.6 \pm 2.3	0.44 \pm 0.01	0.69 \pm 0.02	12.6 \pm 0.18a	13.1 \pm 0.09a
D1	IR58025B	8.3 \pm 0.7	83.9 \pm 6.4	0.43 \pm 0.01	0.69 \pm 0.02	12.6 \pm 0.18a	13.0 \pm 0.09a
	IR68284H	8.3 \pm 0.7	83.9 \pm 7.1	0.44 \pm 0.01	0.69 \pm 0.02	12.8 \pm 0.18ab	13.3 \pm 0.09a
	IR29723R	1.0 \pm 0.0a	89.4 \pm 4.8ab	0.44 \pm 0.01	0.69 \pm 0.02b	13.2 \pm 0.10ab	13.9 \pm 0.14
	IR62829A	4.3 \pm 0.7b	92.2 \pm 1.6ab	0.42 \pm 0.01	0.63 \pm 0.02a	12.9 \pm 0.10a	13.9 \pm 0.14
E1	IR62829B	5.0 \pm 1.2b	96.7 \pm 1.2a	0.40 \pm 0.01	0.61 \pm 0.02a	12.9 \pm 0.09a	13.8 \pm 0.13
	IR64616H	1.0 \pm 0.0a	86.7 \pm 2.4b	0.40 \pm 0.01	0.63 \pm 0.02a	13.4 \pm 0.10b	13.2 \pm 0.14
	IR68926R	7.0 \pm 0.7	88.9 \pm 2.4	0.44 \pm 0.01	0.69 \pm 0.01	12.8 \pm 0.11	13.5 \pm 0.09b
	IR68899A	7.7 \pm 1.8	90.6 \pm 4.3	0.43 \pm 0.01	0.71 \pm 0.01	12.8 \pm 0.11	13.4 \pm 0.10b
	IR68899B	5.7 \pm 0.0	93.3 \pm 2.3	0.45 \pm 0.01	0.69 \pm 0.01	12.6 \pm 0.11	13.4 \pm 0.09b
	IR75221H	7.7 \pm 0.7	90.6 \pm 3.4	0.45 \pm 0.01	0.71 \pm 0.01	12.7 \pm 0.11	13.1 \pm 0.11a

Means within a column and group sharing the same letter are not significantly different (LSD test, $P > 0.05$). Where means are not followed by letters, the main effect of rice line is not significant ($P > 0.05$).

creased resistance of a hybrid in comparison with its more resistant or more susceptible parent (Table 1). Adult weight of female *M. patnalis* reared on the hybrid IR64616H was significantly lower than that of females reared on the parental lines of this hybrid. All the other measures of *M. patnalis* performance (survival, male weight, and male and female rate of development) were also lower on IR64616H than on its parental lines, but not significantly so. Thus, IR64616H may have heterobeltiosis (improvement over the better parent) for resistance to *M. patnalis*. Two other hybrids were more resistant to *M. patnalis* than their better parent in a single test of resistance. Female developmental time was significantly longer on the hybrid in group A2 and survival was significantly lower on the hybrid in group B2, in comparison with their respective parental lines. In only one test, that for male weight in group C1, did a hybrid show significantly greater susceptibility than its more susceptible parent.

Heterosis is sometimes defined as the amount by which a hybrid exceeds its midparent value. Hybrid scores were not consistently higher or lower than the midparent values of the restorer and A lines within groups, with the exception of group D1 as described above.

Resistance to *N. lugens*. Parental lines did not differ significantly in resistance to *N. lugens* in most tests within eight of the 11 groups (A1, A3, A4, A5, B2, B3, C1, and E1) (Table 2). Within these eight groups, hybrid scores were not consistently higher or lower than the more extreme parent or the midparent values. There was only one test in which a hybrid had significantly greater resistance or susceptibility than its more extreme parent: in group E1 female developmental time was lowest on the hybrid.

In the three remaining groups (A2, B1, and D1), there was a trend of higher *N. lugens* resistance in the restorer and hybrid lines than in the A and B parental

lines, although the differences were not always statistically significant (Table 2). There was no indication of heterobeltiosis in these three groups, i.e., the hybrids were not more resistant than the resistant restorer lines. Differences in resistance among lines within groups A2, B1, and D1 were most strongly evident in the damage ratings from the seedbox screening test. The restorer lines in groups A2, B1, and D1 apparently have a dominant major gene for resistance or have quantitative resistance that is largely dominant.

If the restorers in A2, B1, and D1 have a major resistance gene, then the *N. lugens* colony we used was partially adapted to this gene, because differences between the restorer line and A line were not consistently high across the various tests. The *N. lugens* population in Laguna Province is almost completely adapted to the *Bph1* and *bph2* genes, and partially adapted to the *Bph3* gene (Alam and Cohen 1998; M.B.C. and L. Sunio, unpublished data).

Comparison of A and B Lines. There were few differences in insect resistance between A and B lines (Tables 1 and 2), which have the same nuclear genomes but different cytoplasmic (mitochondrial and chloroplast) genomes. In group A2, there was a small but significant difference in *N. lugens* male developmental time between IR68897A and IR68897B, and in group E1 *M. patnalis* survival was significantly higher on IR68899A than on IR68899B. However, the A and B lines within A2 and E1 did not differ in any of the other tests of resistance. The cytoplasmic genomes used as sources for male sterility in the A lines apparently do not carry dominant genes for resistance or susceptibility to *N. lugens* and *M. patnalis*, in relation to the nuclear genomes of the A and B lines.

Discussion

Our results do not provide support for the hypotheses that F₁ hybrids generally have heterosis or heterobeltiosis for antibiosis-based resistance or susceptibility to insect herbivores. Out of 11 groups in which hybrids were compared with their parental lines for resistance to two insect species, there was only one case (group D1 for resistance to *M. patnalis*) in which a hybrid might have heterosis or heterobeltiosis for resistance or susceptibility. However, further investigation of this topic is of interest because there are plausible mechanisms that could result in increased resistance or susceptibility in hybrids.

Insect performance is sometimes enhanced on plants with higher nitrogen content (Awmack and Leather 2002). Thus, one reason that hybrids might be more susceptible than inbred cultivars to insects is that hybrids have greater nitrogen uptake and nitrogen use efficiency (defined as grain yield per unit nitrogen fertilizer applied) (Virmani 1994, Yang et al. 1999). Yang et al. (1999) propose that this greater efficiency is due to "greater root N absorption potential, greater shoot N-use capacity (N demanded by the shoot, i.e., how much and how fast the shoot can use N), and greater N remobilization efficiency (N translocated to

the grain)." These nitrogen uptake and use characteristics could result in more available nitrogen to insect herbivores.

In contrast, it could be hypothesized that hybrids would tend to be more resistant than their parental lines, due to a possible increase in production of defensive secondary metabolites or of structural compounds that reduce insect feeding efficiency, such as lignin. The ability to test this hypothesis may have been limited in our study because most of the parental lines that we used were relatively susceptible to *N. lugens* and *M. patnalis*. F₁ hybrids of susceptible parents might be less likely to show heterosis or heterobeltiosis for resistance than those of parents with quantitative resistance. Three groups (A2, B1, and D1) included a parent with moderate and dominant resistance to *N. lugens*, whereas none of the parental lines seemed to have resistance to *M. patnalis*. We did not detect heterobeltiosis for resistance to *N. lugens* in groups A2, B1, or D1. We do not know whether the resistant parents in these groups have a major gene or quantitative resistance. Heterosis or heterobeltiosis might be more likely to occur when one or both parental lines have quantitative resistance, the expression of which can be strongly influenced by interaction with other genes and the environment.

The lack of resistance to *M. patnalis* in parental lines was expected. Although screening of rice germplasm collections has identified cultivars and wild species with resistance to pyralid leafrollers, no rice varieties with high levels of resistance to these insects have been released (Pathak and Khan 1994). Among the traits that have been found to contribute to resistance to leafrollers in rice are leaf morphology (Islam and Karim 1997) and silica content (Ramachandran and Khan 1991). Varieties with narrow leaves are apparently more resistant because it is more difficult for leafrollers to fold the leaves and form the protective compartment in which they feed (Islam and Karim 1997). In group D1, in which the hybrid IR64616H was more resistant than its parental lines, leaf width did not differ significantly among the four lines at 1, 8, or 15 d after infestation (C.C.B., unpublished data). At 22 d after infestation, leaf width of the hybrid and restorer lines in D1 were significantly greater than that of the A and B lines (C.C.B., unpublished data). Thus, it does not seem that differences in leaf width account for the increased resistance in IR64616H.

There are several reports in other crops of heterosis for insect resistance, when heterosis is defined as increased resistance relative to the midparent value (Pathak 1991, Kumar 1993, Sharma et al. 1996, Kumar and Mihm 1996). Increased resistance relative to the midparent value can result from dominance and other nonadditive gene action, e.g., epistasis. Quantitative resistance in sorghum to the sorghum midge, *Contarinia sorghicola* Coq. (Diptera: Cecidomyiidae) is dominant in some crosses and additive in others (Sharma et al. 1996). Pathak (1991) found additive and dominant and epistatic inheritance of quantitative resistance in maize to the spotted stem borer, *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae). Resis-

tance was dominant to *C. partellus* and the African maize stalk borer, *Busseola fusca* Fuller (Lepidoptera: Noctuidae), in crosses analyzed by Kumar (1993); and to the southwestern corn borer, *Diatraea grandiosella* (Dyar) (Lepidoptera: Pyralidae) and sugarcane borer, *Diatraea saccharalis* F., in crosses analyzed by Kumar and Mihm (1996). Kumar (1993) did not detect heterobeltiosis for resistance or susceptibility. The data presentation in the other studies does not allow conclusions to be drawn concerning heterobeltiosis.

Studies of the inheritance of insect resistance in rice hybrids have focused on qualitative resistance. Major genes conferring resistance to *N. lugens* or *Nephotettix virescens* (Distant) (Hemiptera: Cicadellidae) have been used extensively in rice breeding. These genes are inherited in hybrids as expected: hybrids are resistant if an inbred parent contains a dominant resistant gene but not if the major gene is recessive (Virmani 1994).

Concerns have been raised about the susceptibility of rice hybrids compared with inbred cultivars in China, where there have been reports of a higher frequency of insect outbreaks on hybrids (Mew et al. 1988, Sogawa et al. 2003). Some studies have found that hemipteran and lepidopteran pests have enhanced development or higher survival on hybrids compared with inbred cultivars (Huang et al. 1985, Tan 1987). We did not observe similar results in our experiments, which compared hybrids directly with their parental lines. Because the mechanisms for heterosis include epistatic and gene \times environment effects, its occurrence depends on experimental conditions and the specific parents used. Thus, our study does not show that heterotic susceptibility to *N. lugens* or *M. patnalis* cannot occur. Although future studies may identify hybrids that have decreased antibiosis-based resistance to insects, other factors may explain the pest problems observed on rice hybrids in China. Hybrids may be more attractive to migrating or dispersing insects, due to the dense canopy resulting from more vigorous vegetative growth. Higher pest populations or more frequent outbreaks on hybrids in producers' fields might also be caused by differences in agronomic practices applied to hybrids, e.g., earlier planting dates (Mew et al. 1988) or higher fertilizer application rates.

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