Prevalence of whitebacked planthoppers in Chinese hybrid rice and whitebacked planthopper resistance in Chinese japonica rice

Kazushige Sogawa, Guangjie Liu, and Qiang Qiang

The whitebacked planthopper (WBPH), *Sogatella furcifera*, was only a secondary insect pest of rice before the 1970s in China. However, WBPH increased significantly and became the most predominant insect pest, replacing the brown planthopper (BPH), *Nilaparvata lugens*, in rice areas planted with indica hybrid rice in China in the 1980s. WBPH also became an important economic insect pest of japonica rice in Central China because of its massive displacements from the hybrid rice areas in South China. Eventually, devastating outbreaks of WBPH, as well as BPH, broke out over the entire rice area of China in 1987 and 1991, when hybrid rice had extended to almost half of the total rice area in China. Chinese hybrid rice introduced to Vietnam caused a historical outbreak of WBPH in the Red River Delta in 2000. High susceptibility to WBPH in a Chinese hybrid rice, Shunyou 63 (SY-63), is primarily inherited from the WA-CMS line, which is extremely vulnerable to WBPH infestation. In addition, greater tolerance of WBPH infestations in SY-63 due to vigorous growth is further attributed to the unusual upsurge of WBPH populations.

A Chinese japonica rice, Chenjiang 06 (CJ-06), was found to be highly resistant to WBPH. The WBPH resistance in CJ-06 is mediated by both the sucking inhibition and ovicidal reaction of the host plant. The sucking inhibitory and ovicidal traits are independently conferred by monogenic dominant genes, which are located on chromosomes 4 and 6, respectively. The sucking inhibitory trait exerts a distinct antixenosis, which disrupts host-plant selection by the macropterous females of WBPH immigrated into the paddy fields. The ovicidal trait causes a high mortality of WBPH eggs deposited onto CJ-06. By means of both antixenotic and antibiotic resistance, WBPH populations are constantly suppressed below the economic threshold level in CJ-06. These dual mechanisms could provide this Chinese japonica rice with durable resistance to WBPH. Field trials in WBPH epidemic areas in China demonstrated that the insecticide-free or reduced cultivation of WBPH-resistant japonica rice was more profitable than the insecticide-dependent cultivation of hybrid rice SY-63.

Keywords: Whitebacked planthopper, outbreak, Chinese hybrid rice, Chinese japonica rice, varietal resistance, sucking inhibitory resistance, ovicidal resistance

The brown planthopper (BPH), *Nilaparvata lugens*, and the whitebacked planthopper (WBPH), *Sogatella furcifera*, are herbivores restricted to the rice plant, *Oryza sativa* (Sogawa 1982). Because of their rice-monophagy and *r*-strategic ecology, rice varieties as major food resources and the environment of the paddy ecosystem as a breeding habitat directly influence the pest status of BPH and WBPH. Technical innovations through the introduction of high-yielding varieties (HYVs) and synthetic fertilizers and pesticides caused dynamic changes in the pest status of these rice planthoppers. From 1979 and into the 1980s, BPH and WBPH became epidemic in South and Southeast Asia, where traditional rice varieties were markedly replaced by modern HYVs to bring about the Green Revolution in rice agriculture (Dyck and Thomas 1979, Heinrichs and Mochida 1984, Dhaliwal et al 1985, Gallagher et al 1994, Rombach and Gallagher 1994). It has also been well documented that the simultaneous introduction of broad-spectrum insecticides induced a serious resurgence of planthopper populations (Ressing et al 1982a, Kenmore et al 1984). Resistant HYVs were promptly defeated by the adaptive genetic makeup of planthopper populations, the so-called biotypes. The uncontrollable outbreaks of rice planthoppers led to the crisis of paddy ecosystems, and brought about a paradigm shift in the management of rice insect pests in tropical rice areas (Heong and Sogawa 1994). In this regard, it is possible to say that BPH and WBPH are the sensitive barometers of mismanagement of tritrophic interactions among rice plants, planthoppers, and natural enemies in paddy ecosystems.

Rice agriculture in China is characterized by the wide adoption of high-yielding F_1 hybrids of rice. Since its introduction in 1976, hybrid rice spread rapidly to about half of the total rice area in China by 1990. Reportedly, a significant increase in rice production in the 1980s largely depended upon hybrid rice. However, it is also pointed out that the frequency of outbreaks of BPH and WBPH increased correspondingly with the spread of hybrid rice area in the 1980-90s in South China (Hu et al 1992, Tang et al 1998). Particularly, WBPH increased unusually and became the most predominant insect pest of hybrid rice (Liu et al 2002, Sogawa et al 2003b). The BPH biotype shift also possibly became accelerated in Chinese hybrid rice when hybrid rice with the *Bph1* gene for BPH resistance from IR varieties spread over the insect migration zone in South and Central China. After 1990, previously BPH-resistant hybrid rice became highly susceptible to BPH. WBPH generated in hybrid rice areas migrated massively to the japonica rice areas in Central China, and caused economic damage to japonica rice. Intensive insecticide applications to rice plants at the early tillering stage became inevitable to protect the plants from WBPH infestations. Eventually, devastating outbreaks of WBPH and BPH occured over the entire rice area in China in 1987 and 1991. Simultaneously, overseas invasions of these rice planthoppers into Japan increased significantly since the mid-1980s. Similar evidence was also recorded in Taiwan (Cheng and Huang 2004). As a result of intensive insecticide applications for controlling WBPH on hybrid rice and japonica rice in China, pesticide-resistant WBPH populations immigrated to Japan (Endo et al 1988).

An upsurge of rice planthopper infestations and the subsequent increase in insecticide investment in paddy ecosystems heighten the risk of pest resurgence due to

the destruction of natural enemies, the development of insecticide resistance in insect pests, and toxic pollution of environments and agro-products (Heong and Schoenly 1998). Particularly, the insecticide pollution of agro-products is a serious social problem in China. Therefore, pesticide-dependent high-yielding hybrid rice technologies are not friendly to paddy ecosystems and the environment for sustainable and safe rice production. Growing pest and pesticide problems in rice agriculture in China turned our attention to using the varietal resistance to rice planthoppers inherent in japonica rice germplasm in China. Insect pest resistance in rice plants is an alternative approach to reduce pesticide dependence in the management of insect pests in paddy fields.

This report deals with the field evidence and possible mechanism of WBPH resistance prevalent in Chinese hybrid rice in the earlier chapters and the WBPH resistance in Chinese japonica rice in the latter chapters of this publication.

Prevalence of whitebacked planthopper in Chinese hybrid rice

WBPH was only a secondary insect pest of rice before the 1970s in China. However, immediately after the release of hybrid rice in 1976, the first WBPH outbreak occurred on a hybrid rice, Nanyou 2, in Hunan Province in 1977 (Tan 1987). In 1982, about 1,600 ha of Shanyou 6 fields were severely infested with WBPH, and 80 ha were completely destroyed in hybrid rice pilot areas in Guangdong Province, South China, where Shanyou 2, Shanyou 6, and Weiyou 6 were introduced deliberately (Feng and Huang 1983). The field density of WBPH in Fujiang Province increased significantly from 1978 to 1988. Before 1980, the average field density was below 5 insects per hill, but this increased to 40 insects per hill in 1987 (Lin 1989) (Fig. 1). The frequency of WBPH outbreaks was positively correlated with the expansion of hybrid rice area from 1980 to 1990 in Guangdong Province and similarly in Hunan and Guangxi provinces. Light-trap catches of WBPH exceeded those of BPH at Shantou, Guangdong Province, by 1985, and WBPH became the most predominat insect pest (Lin 1994).

In Central China, an unusually high density of WBPH was first found in hybrid rice Shanyou 6 in Zhejiang Province in 1979. Observations in farmers' fields for 3 years from 1980 to 1982 showed that the population density of WBPH was 8 to 38 times higher than that in inbred rice (Ruan 1983). After that, it was demonstrated that the rate of WBPH reproduction in Shanyou-6 was 2.6–3.9 times higher than that in three inbred rice varieties (Huang et al 1985). Higher fecundity of WBPH on hybrid rice such as Shanyou 6, Shanyou 63, and Weiyou 35 was also recorded (Yu et al 1991, Shi and Lei 1992). This field evidence and these observations showed that WBPH is much more reproductive in Chinese hybrid rice than in inbred rice.

WBPH has been only a minor insect pest of monsoon rice in the Red River Delta (RRD) in Vietnam. However, WBPH had a historical outbreak on about 153,000 ha of winter-spring rice planted with Chinese hybrid rice in the RRD in 2000 (Thanh et al 2001). Since then, WBPH has steadily increased as a new important economic insect pest of rice in the rice granary (Thanh et al 2007). Chinese hybrid rice was first introduced to Vietnam in the early 1990s, and it quickly extended to cover 70–80% of
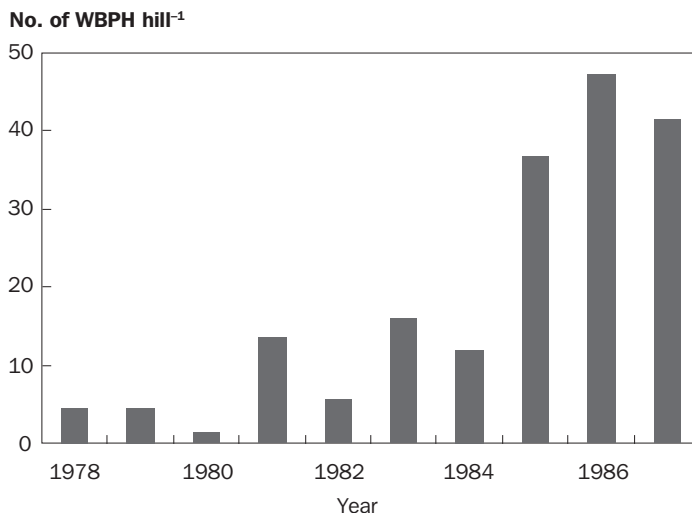
No. of WBPH hill^{-1}

Fig. 1. Significant increase in average density of WBPH per hill of rice plants in Ningde District, Fujian Province, China (from Lin 1989).

the rice area in the RRD. Subsequent intensive investment in insecticides is spoiling the previous great efforts for integrated pest management (IPM), and inducing a paddy ecosystem crisis.

Population trends of WBPH in hybrid rice SY-63 and its parents

Shanyou 63 (SY-63) was one of the most popular Chinese indica hybrid rice varieties in the 1990s, when about 40% of the total hybrid rice area was covered only by SY-63. SY-63 is an F_1 hybrid between CMS line Zhenshan 97A (ZS-97A) carrying the wild abortive-CMS trait and restorer line Minghui 63 (MH-63) carrying the *Bph1* gene for BPH resistance from IR30. SY-63 and its parental lines are all susceptible to WBPH. WBPH can establish populations on them. However, there are considerable differences in the reproductive performance of WBPH among them.

The population trends of WBPH in SY-63 and its parental lines, ZS-97A and MH-63, were examined comparatively in field experiments. The density of macropterous immigrants was apparently higher in SY-63 and ZS-97A than in MH-63. The highest nymphal population developed on ZS-97A, and caused complete hopper burn (Sogawa et al 2003e) (Fig. 2). WBPH also established a high density of nymphal population on SY-63. Because of greater tolerance of WBPH infestations, WBPH continuously reproduced progenies in SY-63 even after ZS-97A plants collapsed completely because of hopper burn. In a separate field trial, maintenance line Zhenshan 97B (ZS-97B) and CMS line ZS-97A were found to be equally susceptible to WBPH, and suffered hopper-burn damage by the first-generation progeny. On the other hand, the WBPH population density was the lowest in the MH-63 field, where no visible damage appeared. Dry weights of newly emerged WBPH adults sampled by a sweeping method in ZS-97A,
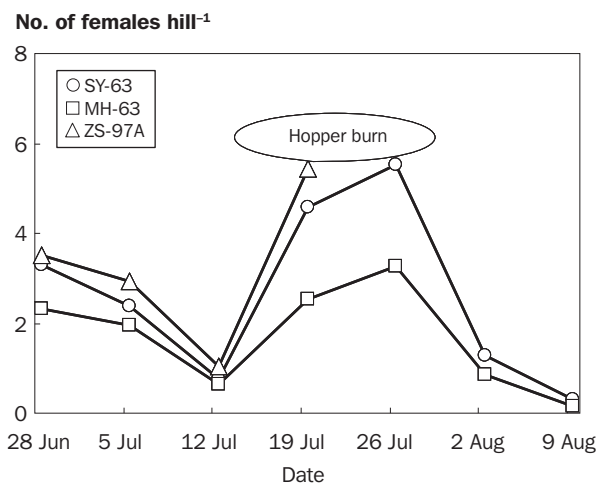
No. of females hill^{-1}

Fig. 2. Density fluctuations of WBPH adult females in SY-63 and its parental lines (CNRRI 1999).

SY-63, and MH-63 fields were 68.1 ± 18.4 mg, 50.1 ± 9.0 mg, and 28.8 ± 13.7 mg, respectively.

Biomass interactions between WBPH and hybrid rice

Average amounts of honeydew excreted by a single female adult of WBPH were 14.8, 11.8, and 6.9 mg per day on ZS-97A, SY-63, and MH-63, respectively (Sogawa et al 2003e). Different amounts of honeydew excretion show that ZS-97A and SY-63 are apparently more susceptible than MH-63. The sucking rate of WBPH is influenced by the quality of the phloem sap of host plants. Total free amino acid concentrations were 9.2%, 2.7%, and 2.4% in the phloem saps collected from ZS-97A, SY-63, and MH-63 plants, respectively. The highest sucking rate in ZS-97A may be related to the highest concentration of free amino acids in its phloem sap.

Average dry weight of the progeny reproduced by six WBPH females per plant was about 250 mg and 243 mg on SY-63 and ZS-97A, respectively, which is significantly higher than the 74 mg on MH-63. When eight females were introduced to each plant, WBPH dry biomass production increased significantly up to 321 mg on SY-63, but it was only 249 mg on ZS-97A. This different WBPH biomass productivity indicates that SY-63 has a much larger carrying capacity for the WBPH progeny load than ZS-97A. WBPH biomass production on MH-63 was suppressed to less than half that on SY-63 and ZS-97A.

The plant biomass of SY-63 and ZS-97A was more efficiently converted to WBPH biomass than was MH-63 biomass. Functional biomass losses (mg of dry plant biomass lost per mg of dry WBPH biomass produced) were about 10 mg and 12 mg in SY-63 and ZS-97A, respectively, whereas the loss was 32 mg in MH-63 (Fig. 3A). Likewise, daily plant biomass production by SY-63, ZS-97A, and MH-63
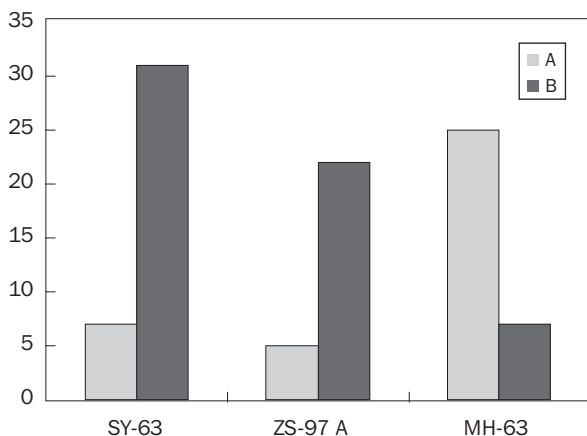
Fig. 3. Biomass interactions between WBPH and host plants, SY-63 and its parental lines. (A) Plant biomass loss (mg, dry weight) equivalent to 1 mg WBPH biomass production. (B) Potential daily WBPH biomass productivity (mg, dry weight per day), where average daily biomass production of host plants is converted to WBPH biomass.

was estimated to be equivalent to about 32 mg, 23 mg, and 9 mg WBPH biomass production, respectively (Fig. 3B). Based on these biomass interactions between WBPH and host rice plants, SY-63 and ZS-97A are found to be highly susceptible to WBPH, and equally suitable as food sources (Sogawa et al 2003e). On the other hand, SY-63 has a greater carrying capacity for WBPH load due to its greater rates of daily biomass productivity than ZS-97A. Greater ability of biomass production by SY-63 could be responsible for F_1 hybrid vigor.

Susceptibility to and tolerance of WBPH in hybrid rice

It is apparent by field performance that ZS-97A is unusually vulnerable to WBPH infestations, probably because of the complete lack of field resistance and tolerance of WBPH during the process of breeding. However, WBPH susceptibility is not related to the CMS trait in ZS-97A because ZS-97A and its maintainer line, ZS-97B, are equally susceptible to WBPH. Therefore, karyoplasmic genes confer susceptibility to WBPH in ZS-97A. The high WBPH susceptibility in ZS-97A is inherited by SY-63. However, greater tolerance of WBPH infestation conceals the susceptibility to WBPH in SY-63 in the field. Because of the greater tolerance due to a greater ability of biomass production in SY-63, SY-63 can persist under such a heavy WBPH infestation that could collapse ZS-97A plants completely. F_1 hybrid vigor provides SY-63 with a greater carrying capacity for WBPH load due to its greater daily biomass productivity than ZS-97A. It is also evident, however, that susceptibility to WBPH in SY-63 does not exceed the level in ZS-97A. Thus, neither heterosis nor heterobeltiosis are involved in the high susceptibility to WBPH in the F_1 hybrid SY-63.

Both ZS-97A and MH-63, the parents of SY-63, are susceptible to WBPH. However, there is a significant difference in the level of susceptibility to WBPH in terms of population growth, honeydew excretion, and biomass response to WBPH infestation between them. MH-63 is apparently less susceptible than ZS-97A. Less susceptibility to WBPH in MH-63 could be inherited from IR30, the precursor of MH-63, which is susceptible to WBPH in the standardized seedbox screening test (SSST), but moderately resistant in the modified seedbox screening test (MSST).

In addition to the susceptibility, WBPH abundance in SY-63 is also attributed to its greater tolerance due to a possible F_1 heterosis for vigorous vegetative growth, which gives a greater carrying capacity for a heavier WBPH population load. In the case of SY-63, tolerance does not work as a mechanism of varietal resistance. Basically susceptible but tolerant hybrid rice such as SY-63 will offer more favorable and durable breeding habitats to WBPH than simply susceptible inbred rice. Therefore, WBPH reproduces many more progeny on SY-63 than on the equally susceptible inbred rice. Tolerance because of F_1 hybrid vigor in susceptible hybrid rice only magnifies the host-plant capacity for planthopper load, and contributes to heighten pest density. Improvement of field resistance in CMS lines will be a practical approach to prevent WBPH prevalence on hybrid rice, as well as the introduction of dominant WBPH resistance genes to the restorer lines. If combined with field resistance in hybrid rice, tolerance will exert itself as an efficient trait to reduce plant damage.

Resistance to the whitebacked planthopper in Chinese japonica rice

WBPH resistance in a Chinese japonica rice, Chenjiang 06

We discovered a distinct resistance to WBPH in a Chinese japonica rice, Chenjiang 06 (CJ-06). Mechanisms of varietal resistance to WBPH in CJ-06 were investigated in comparison with a susceptible hybrid rice, SY-63. Field experiments revealed that WBPH immigrants exhibited nonpreference for CJ-06 and failed to establish a population on it, whereas the immigrants preferred to settle and reproduce on SY-63. Also, significantly less honeydew excretion by WBPH females on CJ-06 than on SY-63 indicated suppressed sucking on CJ-06 (Sogawa et al 2003c). A single WBPH female usually excretes more than 10 mg of honeydew per day on susceptible rice varieties, but less than 5 mg on CJ-06. This type of WBPH resistance in CJ-06 is described as "sucking inhibitory resistance."

WBPH eggs suffered high mortality in induced watery lesions at oviposition sites of CJ-06 plants (Fig. 4). The watery lesions rapidly led to the formation of conspicuous necrotic ovicidal symptoms before the eggs hatched. Egg mortality in the watery lesions occurred within 1–2 days after oviposition. WBPH resistance due to ovicidal response is called "ovicidal resistance" (Sogawa et al 2003c). Such watery lesions seldom occurred in SY-63, in which egg hatchability was very high.

Both fecundity and egg hatchability were markedly reduced on CJ-06 compared with those on SY-63 when newly emerged females were fed on CJ-06. The fertility of WBPH on CJ-6 was only about one-tenth of that on SY-63 (Fig. 5). Based on this finding, we concluded that sucking suppression and ovicidal reaction are the
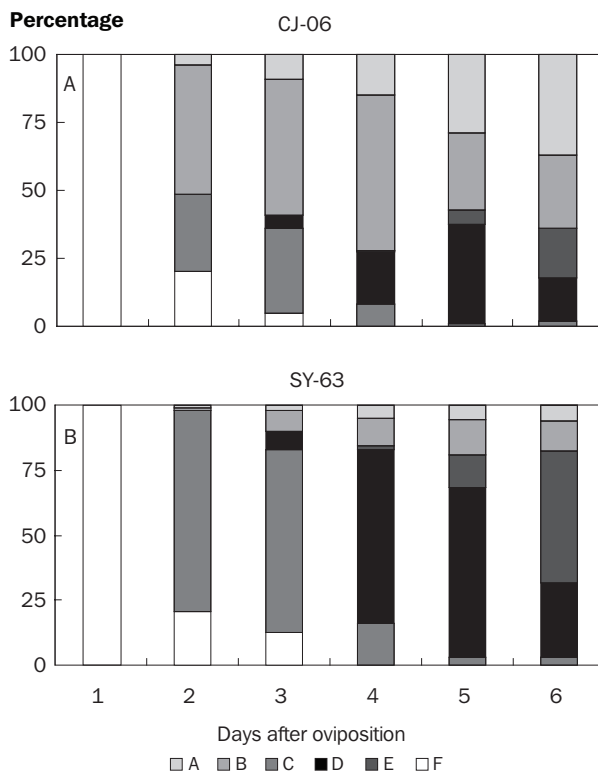
Fig. 4. Comparison of embryonic development of WBPH eggs deposited to CJ-11 (A) and SY-63 (B). A = dead eggs (brown), B = dead eggs (white), C = hatched eggs, D = eggs with eye-spots, E = eggs with yellow spot, F = fresh eggs.

major components for WBPH resistance in CJ-06, which is expressed not only as an antixenosis against WBPH immigrants but also as an antibiosis to reduce fecundity and egg hatchability against WBPH inhabitants, respectively. Such dual mechanisms of varietal resistance, namely, the sucking inhibitory and ovicidal resistance, could confer a stable and durable resistance to WBPH in CJ-06 in paddy fields (Sogawa et al 2003c).

Performance of ovicidal and sucking inhibitory resistance

Field expression of sucking inhibitory and ovicidal resistance in CJ-06 and its family varieties was evaluated by exposing them to natural infestations with WBPH under field conditions. It was found that there were significant differences in population performance of WBPH in varieties with a different genetic background for WBPH resistance (Sogawa et al 2003a). WBPH could not establish populations in CJ-06, Nonghu 6 (NH-6), and Dan 209 (D-209) that had both sucking inhibitory and ovicidal resistance because of distinct antixenosis against the immigrant females. Ovicidal resistance in
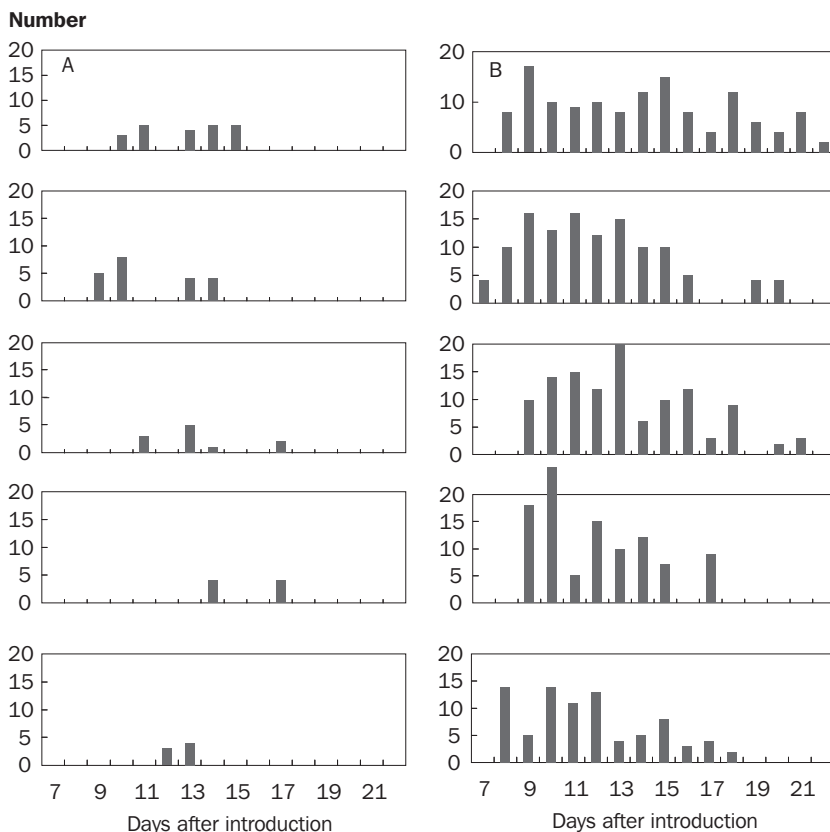
Fig. 5. Daily emergence of WBPH nymphs on five plants of CJ-11 (A) and SY-63 (B) at early tillering stage, on which a pair of newly emerged WBPH adults was introduced.

these varieties had almost no opportunity to act as a resistance mechanism against WBPH. Likewise, WBPH populations could not develop in varieties that had only sucking inhibitory resistance such as Funong 709 (FN-709) and Xiushui 04 (XS-04) due to antixenosis to the immigrant females. WBPH density declined as generations progressed on these varieties.

On the other hand, host selection response and oviposition by WBPH females and development of nymphs were not prevented in varieties Nongken 58 (NK-58), Ce 21 (C-21), Xianhu 24 (XH-24), and Belila (BLL). These varieties have ovicidal resistance but no sucking inhibitory resistance. These ovicidal varieties did not disrupt the settlement of WBPH immigrants, and allowed them to lay eggs. However, subsequent progeny density was kept low due to high mortality of the eggs deposited on these varieties. Early vegetative growth was deterred slightly in the ovicidal varieties because of necrotic symptoms due to the intensive oviposition and ovicidal response as well as sucking by a small number of nymphs that emerged escaping ovicidal

response. However, such early slight infestations were completely compensated for by later vegetative growth. On the contrary, WBPH reproduced exponentially for two consecutive generations, causing serious damage to Laohudao (LHD), a Chinese japonica landrace, which has no traits of resistance to WBPH.

Distribution of ovicidal and sucking inhibitory resistance in rice germplasm

Ovicidal and sucking inhibitory resistance to WBPH in japonica, indica, F_1 hybrid, and tropical japonica rice varieties were evaluated. The ovicidal phenomenon was originally discovered in japonica rice varieties in Japan (Sogawa 1991, Seino et al 1996, Suzuki et al 1996). It was confirmed that ovicidal varieties were found only among japonica rice (Sogawa et al 2003g). No ovicidal varieties were involved in indica, hybrid, and tropical japonica varieties. In addition, 42 japonica and 43 indica varieties from different provinces in China were reevaluated for WBPH resistance. Ten japonica varieties (about 24%) had ovicidal resistance, causing 53% to 100% egg mortality. In more than 95% of the indica varieties, WBPH egg mortality was below 30%. Only four japonica varieties from Zhejiang Province significantly suppressed honeydew excretion by WBPH, indicating sucking inhibitory resistance. Moreover, among 21 japonica landraces in Zhejiang Province, ovicidal and sucking inhibitory response of WBPH showed independent and continuous variations (Sogawa et al 2003g). Sanqianhuang (SQH), Changhongdao (CHD), and Aigandao (AGD) had ovicidal resistance. Jijiaofuang (JJH) and Maqueqing (MQQ) inhibited WBPH sucking. No landrace was found to carry both resistance traits together. These findings indicated that WBPH resistance traits have been retained in the japonica landraces in China (Sogawa et al 2003g).

It was found that a perennial Chinese wild rice (*O. rufipogon*, Dongxiang wild rice), a possible ancestor of japonica rice, shows ovicidal response against WBPH eggs, but a strain of annual tropical wild rice, *O. nivara*, a possible ancestor of indica rice, did not have the ovicidal trait. It is therefore considered that the ovicidal trait in japonica rice has originated in its possible ancestral wild rice.

Inheritance of ovicidal and sucking inhibitory resistance

Modes of inheritance of both sucking inhibitory and ovicidal resistance to WBPH in CJ-06 were analyzed by preparing F_1, F_2, and F_3 progenies from reciprocal crosses between CJ-06 and a susceptible indica variety, TN1. All the F_1 progeny were resistant, having both resistance traits. The sucking inhibitory and ovicidal resistance in F_2 segregated independently at a ratio of 3 (resistant):1 (susceptible). Four phenotypes with different combinations of sucking inhibitory and ovicidal traits segregated into a ratio of 9:3:3:1. The F_3 progenies that were established from individual F_2 plants showed very complicated expressions of WBPH resistance, mixing up the homozygotes and heterozygotes of sucking inhibitory and ovicidal traits. It was too difficult to discriminate homozygous and heterozygous groups for each resistance trait; F_3 batches that include resistant individual plants were all recorded as the progeny from resistant F_2 plants. Segregation ratios for each resistance trait in F_3 plants were 3 (homozygotes
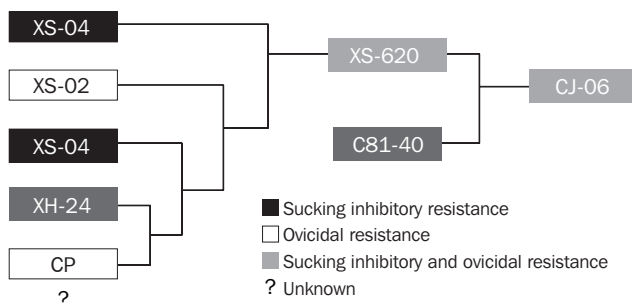
Fig. 6. WBPH resistance in the intermediate maternal varieties of CJ-11.

and heterozygous-resistant):1 (homozygous-susceptible). Segregation ratios for the combined resistance traits were 9:3:3:1. These results proved that two dominant genes independently conferred sucking inhibitory and ovicidal resistance to WBPH in CJ-06 (Sogawa et al 2003d). Preliminary crossings showed that the sucking inhibitory trait in CJ-06 is easily introduced into Japanese japonica rice.

Genealogical analysis of WBPH resistance in CJ-06
Genealogical analysis indicated that both the sucking inhibitory and ovicidal resistance to WBPH in CJ-06 were inherited together from Xiushui 620 (XS-620) (Fig. 6). Ovicidal resistance is a characteristic defense mechanism against WBPH infestations common in japonica rice. Thus, the japonica varieties involved in the pedigree of CJ-06 commonly retained ovicidal resistance. NK-58, a japonica rice introduced from Japan in the 1960s, was apparently one of the original donors of the ovicidal resistance trait (Sogawa et al 2003a). A distinct ovicidal response was also detected in XH-24 (Fig. 7).

Among the intermediate parental varieties of XS-620, only XS-04 had a strong sucking inhibitory resistance, but it had no ovicidal resistance. Of three parental lines of XS-04, only D-209 and FN-709 were sucking inhibitory. NH-6, a common parent of D-209 and FN-709, also inhibited WBPH sucking. It was confirmed that NH-6, D-209, FN-709, and XS-04 expressed distinct sucking inhibitory resistance (Sogawa et al 2003a) (Fig. 8). However, the parents of NH-6, NK-58, and LHD had no sucking inhibitory resistance, and were susceptible to WBPH. Thus, the real origin of sucking inhibitory resistance in NH-6 remained obscure. Two indica varieties, IR26 and IR28, which were used to introduce the *Bph1* gene for BPH resistance to CJ-06, were highly susceptible to WBPH, and had neither sucking inhibitory nor ovicidal resistance.

QTLs for ovicidal resistance
Quantitative trait loci (QTLs) associated with ovicidal resistance to WBPH in Zaiyeqing 8 (ZYQ-8, indica)/Jingxi 17 (JX-17, japonica) doubled-haploid (DH) lines were analyzed. The japonica parent JX-17 had ovicidal resistance to WBPH. The ovicidal trait in the DH lines was phenotyped based on the necrotic symptoms on the
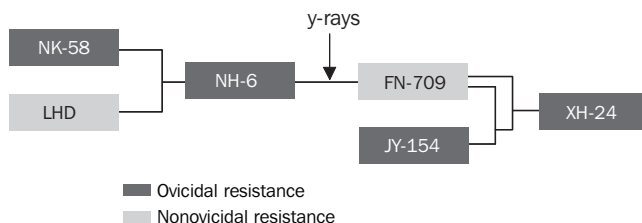
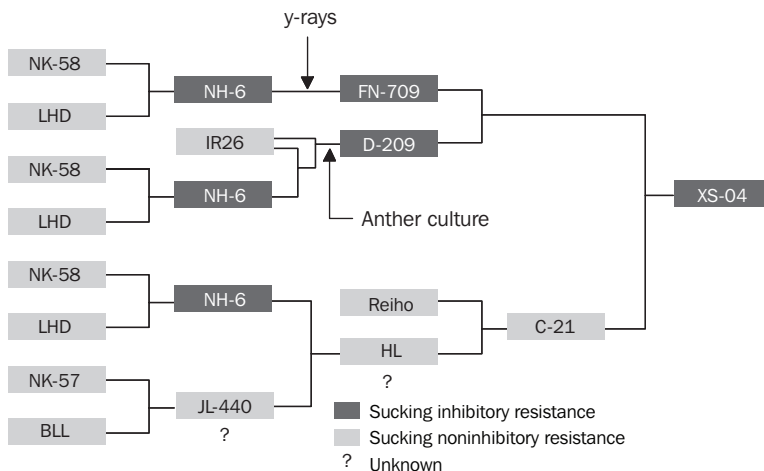Fig. 7. Ovicidal resistance in the pedigree of XH-24.

Fig. 8. Sucking inhibitory resistance in the pedigree of XS-04.

leaf sheaths due to ovicidal response at three different growth stages. Four ovicidal QTLs were detected on japonica segments of chromosomes 1, 2, 6, and 8 in the DH lines at early and mid-tillering stages. One more QTL appeared at the mid-tillering stage, which was located on an indica segment of chromosome 9. The ovicidal loci decreased to two at the maximum tillering to booting stages. The QTL (qOVC-6b) flanked by RFLP markers CT115 and CT506 on chromosome 6 explained 27.2% of the phenotypic variance, with an LOD score of 6.63 (Table 1). The analysis was based on the maximum score of ovicidal symptoms for each DH line throughout the experimental period, which revealed three QTLs on chromosomes 6 and 9. Two major QTLs (qOVC-6a and qOVC-6b) were located on the two closely adjacent segments of CT201-RZ450 and CT115-CT506 on the short arm of chromosome 6, which account for 25.7% and 29.6% of the phenotypic variance, with an LOD score of 7.00 and 7.31, respectively (Sogawa et al 2003f) (Table 1, Fig. 9). It is interesting that one of the minor QTLs (qOVC-9) on chromosome 9 comes from indica parent ZYQ-8, which has no ovicidal response. Detailed QTL-based analysis for the ovicidal response in

Table 1. QTLs associated with ovicidal symptoms due to WBPH oviposition.

Growth stage[a]	QTL	Chromosome	Marker interval	Peak LOD	Variance explained	Additivity
Early tillering (22)	qOVC-1b	1	GA594–CT380A	2.32	10.0	0.52
	qOVC-2b	2	G357–GA120	2.09	9.5	0.51
	qOVC-6c	6	G200–C235	2.29	9.2	0.52
	qOVC-8	8	BP127A–RZ617	2.60	9.5	0.52
Mid-tillering (32)	qOVC-1a	1	CT158–CT550	2.27	11.7	0.71
	qOVC-2c	2	GA120–GA43	2.29	8.8	0.61
	qOVC-6b	6	CT115–CT506	3.38	12.1	0.72
	qOVC-8	8	BP127A–RZ617	2.54	9.3	0.65
	qOVC-9	9	G103–G93F	2.52	13.4	−0.75
Max. tillering (54)	qOVC-2a	2	G1327–C132	2.38	9.6	0.81
	qOVC-2c	2	GA120–GA43	2.22	8.7	0.71
	qOVC-6b	6	CT115–CT506	6.63	27.3	1.39
Tillering (22–54)	qOVC-6a	6	CT201–RZ450	7.00	25.7	1.24
	qOVC-6b	6	CT115–CT506	7.31	29.6	1.33
	qOVC-9	9	G103–G93F	2.30	12.4	−0.84

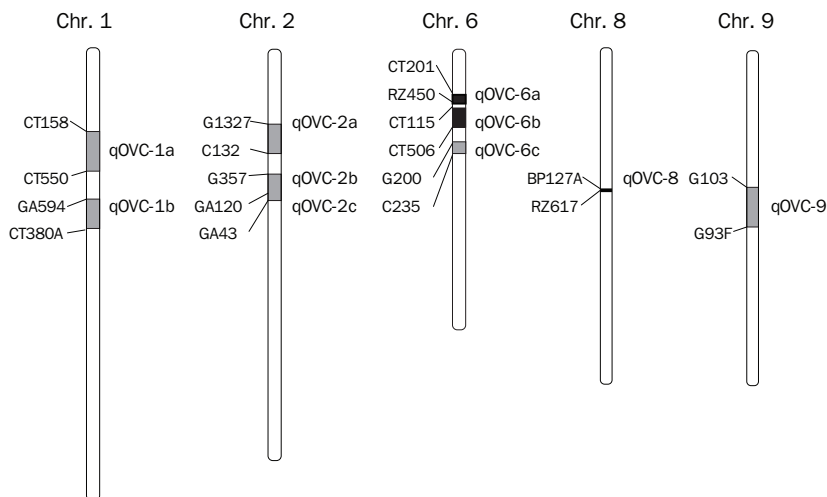[a]Numbers in parentheses indicate days after transplanting.

Fig. 9. Location of ovicidal QTLs on rice chromosomes. The markers flanking each QTL are shown to the left of each chromosome.

Japanese japonica rice Asominori has also demonstrated that a dominant ovicidal gene, *OVC*, is located on the short arm of chromosome 6, and R1954 is a target marker for marker-assisted selection (MAS) of the ovicidal gene (Yamasaki et al 1999, 2003).

QTLs for sucking inhibitory resistance

In order to analyze QTLs for sucking inhibitory resistance to WBPH, a new DH population consisting of about 180 lines was established from a cross between the WBPH-resistant japonica CJ-06 and susceptible indica TN1 by the anther culture method (Sogawa et al 2004). Both the sucking inhibitory and ovicidal resistance traits showed approximately 1 (resistant):1 (susceptible) segregations in the DH population.

Sucking inhibitory resistance was evaluated by the amount of honeydew excreted by the female adults of WBPH. Sucking inhibitory resistance is also evaluated by the density of macropterous females of WBPH immigrated and number of eggs deposited by them on each DH line in the paddy fields. WBPH females excreted only 1.7 mg of honeydew per day on J-06 on average, whereas 24.8 mg of honeydew was excreted on TN1. The amount of honeydew excretion varied from 0 to 34.4 mg per day among 109 DH lines tested beyond the parental range. On 53 DH lines (48.6%), WBPH females excreted less than 5 mg of honeydew per day. Those DH lines have sucking inhibitory resistance. There was a close positive correlation (r = 0.80**) between the amount of honeydew excretion by WBPH females and field density of WBPH immigrant females in each DH line. Also, a significant positive correlation (r = 0.72**) was found between honeydew excretion and egg density (Sogawa et al 2005a).

The most effective QTLs for honeydew excretion (qHND-4), immigrant density (qIMG-4), and number of eggs deposited (qEGN-4) were mapped on the identical CJ-06 segment flanked by the SSR markers RM401 and RM335 on chromosome 4 (Sogawa 2007) (Table 2, Fig. 10). These QTLs accounted for 71.7%, 78.4%, and 58.7% of the respective phenotypic variances, with LOD scores of 15.6, 21.8, and 15.3. This finding indicated that a single gene for sucking inhibition was located at the above QTL region. In addition, four minor QTLs related to sucking inhibitory resistance were mapped on chromosomes 2, 3, and 11.

QTLs for nymphal density and plant damage

Relative density of the first-generation progeny varied widely among the DH lines. The progeny density in the sucking inhibitory lines was significantly lower than in the nonsucking inhibitory lines (Tables 3 and 4). Also, among the nonsucking inhibitory lines, the density was significantly lower in the ovicidal lines than in the nonovicidal ones (Tables 3 and 4). Reproduction of progeny was suppressed primarily by the sucking inhibitory trait, and also by the ovicidal resistance to a lesser extent (Sogawa et al 2005a). Three QTLs related to progeny density were located on chromosomes 4 and 6. The most effective QTL was mapped at the same position of chromosome 4, where the sucking inhibitory gene is localized (Sogawa 2007) (Fig. 10). Another

Table 2. QTLs associated with sucking inhibitory resistance.

| Data	QTL	Chromosome	Marker interval	Peak LOD	Variance explained	Additivity
Immigrant density	qIMG-2	2	RM341–RM263	3.07	14.6	−21.4
	qIMG-3	3	RM426–RM520	2.63	16.4	24.5
	qIMG-4	**4**	**RM401–RM335**	**21.76**	**78.4**	**56.1**
	qIMG-11	11	RM209–RM202	3.87	21.5	28.1
Amount of honeydew excreted	qHND-2a	2	RM341–RM263	2.84	30.4	−6.8
	qHND-2b	2	RM318–RM240	2.91	21.3	−8.2
	qHND-3a	3	RM251–RM16	2.61	28.6	6.3
	qHND-3b	3	RM426–RM520	2.40	16.5	7.8
	qHND-4	**4**	**RM401–RM335**	**15.56**	**71.7**	**15.0**
No. of eggs deposited	qEGN-2	2	RM341–RM263	2.53	45.1	−51.5
	qEGN-3a	3	RM251–RM16	2.81	26.4	35.5
	qEGN-3b	3	RM426–RM520	3.42	18.4	34.9
	qEGN-4	**4**	**RM401–RM335**	**15.34**	**58.7**	**66.8**
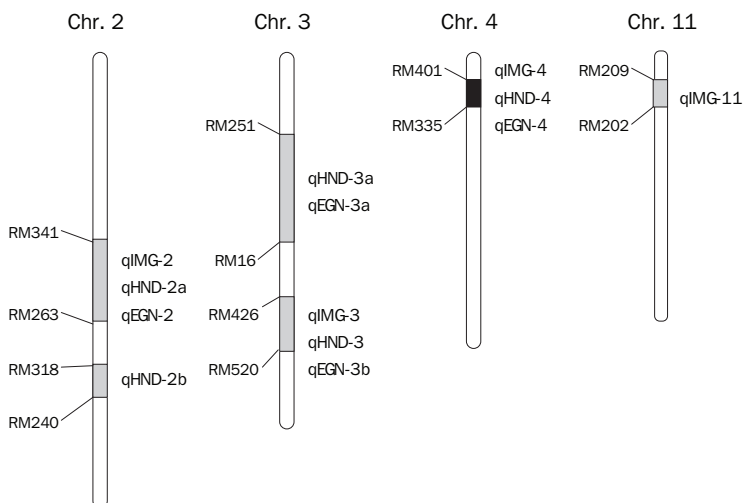
Fig. 10. Location of sucking inhibitory QTLs on rice chromosomes. The markers flanking each QTL are shown to the left of each chromosome.

QTL was found at the region near the ovicidal QTL on chromosome 6 (Fig. 9). These QTLs indicate that low nymphal density is strongly attributed to sucking inhibitory and ovicidal resistance to WBPH.

Of 151 DH lines tested, 65 lines (43.0%) did not suffer any visible damage by WBPH infestation, which all belonged to the sucking inhibitory lines. Five DH lines (3.3%) were completely killed by the heavy density of WBPH populations, which were all nonsucking inhibitory DH lines. This evidence indicated that final plant damage is also primarily influenced by the sucking inhibitory trait (Table 5). Two QTLs for

Table 3. Relative densities of immigrants and progeny in CJ-11/TN1 DH lines with different phenotypes of WBPH resistance in 2003.

Phenotype[a]	No. of lines	Immigrant	G1 progeny
R/R	36	1.2 ± 0.7 a	66 ± 87 a
R/S	43	1.1 ± 0.1 a	126 ± 55 a
S/R	41	6.5 ± 0.3 b	408 ± 45 b
S/S	31	6.7 ± 0.4 b	827 ± 95 c
CJ-11		0.3	7
TN1		5.6	681

[a]Phenotype: R/R = sucking inhibitory/ovicidal; R/S = sucking inhibitory/nonovicidal; S/R = nonsucking inhibitory/ovicidal; S/S = nonsucking inhibitory/nonovicidal. Immigrant: density of macropterous females per hill. G1 progeny: number of first-generation progeny (nymphs and adults) tapped down into a tray (29 cm × 41 cm) from 2 hills. In each column, means followed by the same letter are not significantly different in the Kruskal-Wallis test.

Table 4. Relative densities of immigrants and progeny in CJ-11/TN1 DH lines with different phenotypes of WBPH resistance in 2004.

Phenotype	No. of lines	Immigrant	G1 progeny	B female	G2 progeny
R/R	19	0.5 ± 0.4 a	17 ± 13 a	0.2 ± 0.2 a	8 ± 8 a
R/S	42	0.7 ± 0.5 a	21 ± 15 a	0.2 ± 0.2 a	11 ± 12 a
S/R	18	1.7 ± 0.6 b	31 ± 15 a	0.7 ± 0.6 b	16 ± 21 a
S/S	20	1.8 ± 0.8 b	69 ± 31 b	0.7 ± 0.6 b	33 ± 19 b
CJ-11		0.2	21	0	2
TN1		0.2	165	1.4	124

Phenotype: same as Table 3. Immigrant: same as Table 3. B female: density of brachypterous adult females per hill, which emerged from the G1 progeny. G1 and G2 progeny: number of first- and second-generation progeny sampled by tapping method. In each column, means followed by the same letter are not significantly different in the Kruskal-Wallis test.

Table 5. Scores of plant damage caused by WBPH infestation in CJ-11/TN1 DH lines with different resistance phenotypes.

Phenotype[a]	No. of lines	Damage score					Mean ± SD
		0	1	2	3	4	
R/R	31	22	9	0	0	0	0.29 ± 0.45 a
R/S	49	33	15	1	0	0	0.35 ± 0.51 a
S/R	35	8	14	8	4	1	1.31 ± 1.04 b
S/S	36	2	11	15	4	4	1.92 ± 1.04 b
Total	151	65	49	24	8	5	

[a]Phenotype: same as Table 3. Damage score: 0 = no damage; 1 = only lower leaves died; 2 = lower half of plant died; 3 = three-fourths of plant died; 4 = whole plant died. In each column, means followed by the same letter are not significantly different in the Kruskal-Wallis test.

plant damage were found on chromosomes 3 and 4. These loci were also involved in the QTLs associated with the sucking inhibitory trait. This QTL analysis showed that the major QTLs for nymphal density and damage intensity were all mapped at the identical locus where the putative sucking inhibitory gene is located. This indicates that the sucking inhibitory trait plays a major role in WBPH resistance in the CJ0-06/TN1 DH population.

Differential expressions of WBPH resistance in the field and SSST

Sucking inhibitory resistance to WBPH in CJ-06/TN1 DH lines was evaluated comparatively through a field experiment based on WBPH immigrant density and the SSST (Sogawa et al 2005b). All the susceptible lines in the field evaluation were susceptible in the SSST as well. However, 35 of the resistant 66 lines (53%) in the field were categorized in the susceptible groups in the SSST. Likewise, there were no significant differences in WBPH immigrant density between the DH lines that were highly resistant and susceptible in the SSST. These results revealed that the SSST could not properly evaluate WBPH resistance in the DH lines. Four QTLs for WBPH resistance phenotyped by immigrant density were detected on chromosomes 2, 3, 4, and 11. Of these, the QTL on chromosome 4 was the most effective as mentioned in the previous section. On the other hand, five QTLs associated with seedling mortality were mapped on chromosomes 2, 3, 4, 5, and 6. In addition to a major QTL on chromosome 4 (LOD 10.5, variance 68%), there was another major QTL located on chromosome 5 (LOD 12.1, variance 78%), which was an SSST-specific artifact, and entirely independent of the WBPH ecology and rice plant interactions in the field. Needless to say, the ovicidal resistance to WBPH in the DH lines cannot be evaluated by the SSST.

Molecular markers and QTL mapping offer more efficient approaches to analyze and use complex genetic traits for insect resistance in crop plants (Yencho et al 2000, Tao et al 2003). The QTL-based approach requires not only a well-saturated molecular marker map and appropriate recombinant inbred host-plant populations but also ecologically significant phenotyping procedures. The QTLs for each ecological trait would improve our understanding about the genetic basis and ecological mechanisms for insect resistance in crop plants. For this purpose, phenotyping is a prerequisite for meaningful QTL analysis for varietal resistance to insect pests in crop plants.

The SSST is a widely accepted procedure to evaluate genetic resistance to rice planthoppers in rice germplasm. However, in the SSST, the actual ecological and agricultural interactions between planthoppers and rice plants are virtually neglected. The SSST is based only on the immediate sucking damage to young rice seedlings infested artificially with newly hatched planthopper nymphs in the seedbox. Such a rice plant and planthopper interaction do not exist in paddy fields. Therefore, the QTLs detected by the SSST do not give any information about mechanisms for WBPH resistance and host-plant traits associated.

QTL-based analyses of host-plant traits for WBPH resistance should be performed based on the ecological interactions between planthopper populations and rice plants in a given agricultural context. In order to set up meaningful phenotyping tests, proper combinations among the morph and stage of WBPH, growth stage of rice plants, and trait or response to be measured are crucial. QTL mapping for critical planthopper and host-plant performance at each key stage in the insect and host-plant interactions in the field gave us very practical information about the mechanism of field resistance in rice plants. Successful gene-tagging for major resistance QTLs will promote MAS approaches to breed more IPM-compatible rice varieties with WBPH resistance (Yencho et al 2000).

Performance of WBPH resistance in CJ-06 in paddy ecosystems

The sucking inhibitory resistance in CJ-06 disrupts population establishment by WBPH in paddy fields at the first step of host-plant selection by macropterous WBPH immigrants (Tables 3 and 4). Low density of the initial immigrants is strongly attributed to the subsequent low density of the WBPH population and limited infestation to CJ-06. In addition, WBPH population growth is further suppressed in CJ-06 by ovicidal resistance, by which WBPH eggs suffer high mortality at the oviposition sites. These dual mechanisms of varietal resistance in CJ-06 could give this Chinese japonica rice a durable resistance to WBPH.

Japonica rice in East Asia has been exposed to massive migrations of rice planthoppers by Asian monsoon every year. Particularly, newly transplanted rice plants are directly infested with WBPH immigrants, whose density is much higher than that of BPH. The ovicidal resistance in japonica rice is not so distinct as sucking inhibitory resistance, but it is efficient enough to suppress the population densities of WBPH progeny within the ranges that the host plants have for coping with insect infestations by their compensatory vegetative growth. The ovicidal response in japonica rice is a necessary alternative defense mechanism against WBPH in newly transplanted
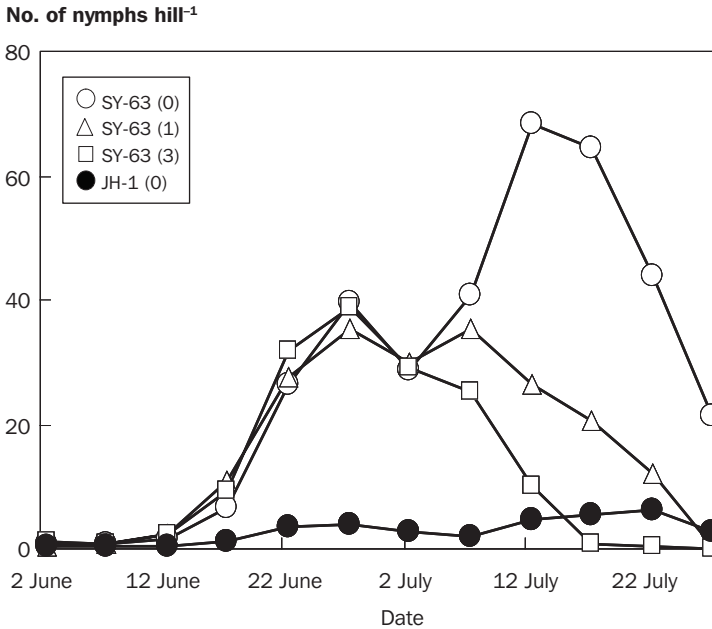
No. of nymphs hill⁻¹

Fig. 11. Population trends of WBPH on JH-1 and SY-63 in Xiushan (2002). Values in parentheses indicate times of insecticide (imidacloprid) spray. Imidacloprid was sprayed on 2 July (single-spray plots), 11 July, and 2 August (3-spray plots). Imidacloprid is usually sprayed mixed with orga-nophosphorus insecticides such as triazophos.

paddy fields, where the natural enemy fauna are not yet recruited enough to control WBPH immigrants. It is also known that the ovicidal trait in japonica rice affects BPH eggs, and possibly newly hatched stem borers as well. Such moderate and horizontal resistance due to the ovicidal trait in CJ-06 could be an efficient insurance to prevent the breakdown of species-specific monogenic sucking inhibitory resistance to WBPH by preventing the occurrence of WBPH biotypes. In exploring genetic considerations in the use of insect-resistant germplasm, we should focus on the problem of maximizing the durability of insect resistance by minimizing selection for virulent biotypes (Kennedy et al 1987). There has been no evidence of a breakdown in ovicidal resistance to WBPH in japonica rice so far. However, selection experiments indicated that WBPH has abilities to defeat possible sucking inhibitory resistance in indica rice, which is conferred by *Wbph 2* and *Wbph 5* genes (IRRI 1980, Shen et al 2003a,b). Also, it has been known that most of the rice varieties with *Wbph 1* genes for WBPH resistance are not resistant to the WBPH populations in India (IRRI 1978).

Our on-farm experiments demonstrated that the WBPH-resistant improved japonica rice Jinhua-1 (JH-1), which has the same genetic background for WBPH resistance as CJ-06, could stop the use of insecticides for controlling WBPH in a WBPH epidemic hybrid rice area (Fig. 11). In addition, the insecticide-free cultivation
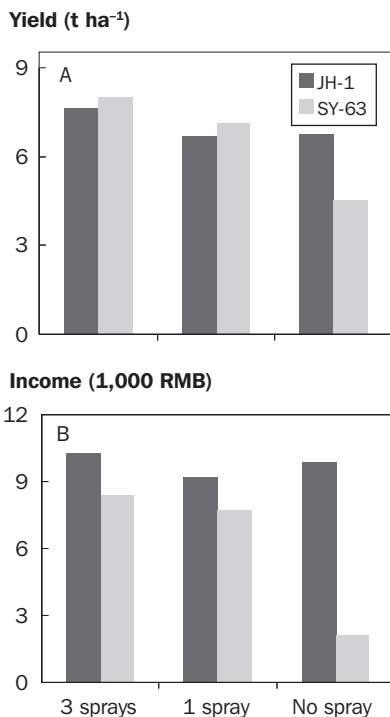
Yield (t ha^{-1})

Income (1,000 RMB)

Fig. 12. Average rice yield (A) and income (B) from JH-1 and SY-63 planted under different numbers of insecticide (imidacloprid) sprays in Xiushan in 2003.

of the WBPH-resistant JH-1 was more profitable than the insecticide-dependent high-yielding cultivation of hybrid rice SY-63 (Liu et al 2003, 2006) (Fig. 12). Thus, WBPH-resistant japonica rice is an ecologically sound and economically profitable IPM component in WBPH epidemic japonica rice areas.

Conclusions

Because of rice monophagy, the pest status of WBPH is directly influenced by the quality of rice varieties and environmental conditions of paddy fields. Because of *r*-strategic biology, mismanagement of paddy ecosystems appears in the form of epidemics of WBPH. Highly susceptible and tolerant Chinese hybrid rice has offered WBPH more favorable nutrient resources and breeding habitats than inbred rice, which has led to an unusual upsurge of WBPH population density. Insecticide applications to protect insect-susceptible hybrid rice could further encourage WBPH epidemics by the destruction of bio-control agents in paddy ecosystems. We should not forget

the history of the BPH menace induced by insecticides, which were disseminated to rice farmers with high-yielding rice seeds as a packaged technology for the rice Green Revolution. A case study with a leading Chinese hybrid rice, Shanyou 63, shows that the improvement of hypersusceptibility to WBPH in the WA-CMS line is more necessary than the incorporation of a WBPH resistance gene to the restorer line.

Genetic resistance to WBPH in japonica rice germplasm was first discovered in a Chinese japonica rice, Chunjiang 06 (CJ-06). The WBPH resistance in CJ-06 is conferred by the dual modalities of resistance, namely, antixenosis due to sucking inhibition and antibiosis due to ovicidal response. Of these, ovicidal response, which is induced by WBPH oviposition, is restricted to japonica rice. The ovicidal trait cannot be evaluated by such a mechanistic evaluation method as the standardized seedbox screening test (SSST), which has exclusively been used to breed the rice planthopper-resistant HYVs. The occurrence of SSST-susceptible ovicidal resistance suggests the practical importance of evaluating insect resistance in rice based on the actual ecological interactions between the insect and rice plant in paddy ecosystems. QTL-based analyses based on ecological host-plant interactions will provide useful information about efficient genetic traits, which render ecologically appropriate resistance or defense mechanisms to host plants, and the recent development of molecular marker technology enables us to use such field resistance to insect pests through MAS approaches.

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Notes

Authors' addresses: Kazushige Sogawa, Crop and Environmental Sciences Division, International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippines; Guangjie Liu and Qiang Qiang, China National Rice Research Institute, Hangzhou 310006, China.