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Variable Resistance to Homopterans in Rice Cultivars

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Rice-breeding programs in Asia have successfully provided farmers with cultivars that have genetic resistance to the major insect pests, including the leafhoppers and planthoppers. The widespread planting of resistant cultivars has resulted in the selection of hopper populations that have overcome the resistance factor(s) in the plant. Procedures to measure the degree and rate of selection for virulence on resistant cultivars have been developed, and rice-breeding strategies to increase the stability of hopper-resistant cultivars have been implemented.

BACKGROUND

Rice, an annual grass of the genes *Oryza*, is the major food crop in developing countries and serves as the primary or secondary food of 90% of the world's poor. Per capita consumption of rice in most Asian countries is 100 kg per year, and demand continues to grow, especially in Africa and Latin America. Among the major constraints to rice production are the pests: diseases, insects, and weeds. Although there are approximately 100 important insect pests for rice throughout the world, the number in any given locale is only 5 to 10. Among the major insect pests are those that belong to the order Homoptera consisting of the Cicadellidae (leafhopper) and Delphacidae (planthopper) families. The rice leafhoppers and planthoppers listed in Table 1 were formerly of minor importance but are now among the most important insects attacking rice. Hoppers damage plants by removal of the phloem sap with their sucking mouthparts and as vectors of rice viruses [except *Sogatella furcifera* (Horváth)].

Cultivated rice, *Oryza sativa* L., evolved from wild perennial rices to a domesticated annual following geographic dispersal, climatic changes, ecogeographic diversity, and human selection (1). Human selection has resulted in cultivated rice that has been selected primarily for grain quality and yield but not for insect resistance. Consequently, cultivated varieties generally have less resistance to insect pests than wild rices (2). Insect control on the traditional cultivars involved primarily cultural practices and insecticides. With a shift to the cultivation of the high-yielding "miracle" rices and improved cultural practices (fertilizer, double cropping, staggered planting, and increased irrigation facilities) that accompanied the "Green Revolution," leaf- and planthopper problems increased. The first miracle rice, IR8, was released by the International Rice Research Institute (IRRI) in 1965. In order to maximize the yield potential of IR8 and modern varieties released later, increased fertilizer and insecticide use became a major thrust of national production programs. However, because of the cost, the danger of poisoning applicators, and concern for the environment, a breeding program for the development of insect-resistant rice cultivars was established at IRRI. Screening of the world rice collection to identify donors for resistance to the brown planthopper, *Nilaparvata lugens* (Stål), and the green leafhopper, *Nephotettix virescens* (Distant), was begun in 1967 and for the whitebacked planthopper, *S. furcifera* (Horváth), in 1973 (3). In the 1970s the Centro International Agricultura Tropicale in Colombia established a breeding program for the planthopper *Sogatodes oryzicola* (Muir).

CURRENT STATUS

There are currently national breeding programs for leaf- and planthoppers in many Central and South American countries and throughout most of South and Southeast Asia. Cultivars with resistance to one or more of the following insects have been released for commercial cultivation and are extensively grown: *Laodelphax striatellus* (Fallen), *N. virescens*, *N. lugens*, *S. furcifera*, and *S. oryzicola*. A major concern and constraint to scientists in rice-breeding programs is variability in the levels of resistance that occur through the selection of virulent insect populations that are capable of damaging these cultivars. Insect populations that develop virulence and damage rice cultivars previously resistant to them are termed "biotypes." (See references 4 and 5 for discussion regarding the concept of insect biotypes in agriculture.)

Variability in *N. lugens* Populations

Of the major rice leaf- and planthoppers, variability in levels of virulence has been a most severe problem in the breeding and commercial utilization of *N. lugens*-resistant rice cultivars. This insect is monophagous and

Table 1 Major leafhoppers and planthoppers of rice

Insect	Distribution	Virus vectored
	Leafhoppers	
Nephotettix cincticeps (Uhler)	China, Japan, Korea	Yellow dwarf, transitory yellowing, dwarf
Nephotettix nigropictus (Stål)	Asia, North Australia	Tungro, yellow dwarf, transitory yellowing, dwarf
Nephotettix virescens (Distant)	South and Southeast Asia	Tungro, yellow dwarf, transitory yellowing
Recilia dorsalis (Motschulsky)	Asia, North Australia	Dwarf, tungro, orange leaf
	Planthoppers	
Nilaparvata lugens (Stål)	Asia, Pacific, North Australia	Grassy stunt, ragged stunt, wilted stunt
Sogatella furcifera (Horváth)	Asia, Pacific, North Australia, North Africa, Middle East	None
Sogatodes oryzicola (Muir)	Central and South America	Hoja blanca
Laodelphax striatellus (Fallen)	China, Japan, Korea, Europe	Black-streaked dwarf, and stripe in China, Japan, and Korea

restricted to feeding on rice. Although occasional outbreaks have been recorded in Japan and Korea over the last two millenia, *N. lugens* only became a major pest in the tropics during the 1960s (6).

A systematic evaluation of the world collection of *O. sativa* began in 1967 at IRRI, and by 1986, 334 accessions had been identified as having resistance to *N. lugens* (3). Most of the resistant accessions are from India and Sri Lanka. In addition, 132 wild *Oryza* spp. accessions were identified as resistant. Genetic analyses of a selected number of the *O. sativa* accessions has resulted in the identification of six resistance genes (Table 2).

IR26 with the *Bph* 1 gene from Mudgo, an Indian cultivar, was the first *N. lugens*-resistant cultivar released from the IRRI breeding program in 1974. Although it was resistant in the Philippines, it was susceptible to the Indian *N. lugens* population when first evaluated. This was the first evidence of variable levels of virulence in allopatric populations of *N. lugens*. Later, international collaborative studies provided further evidence of the variability of reactions of resistant rice cultivars between South and Southeast Asia (7) (see Table 3). With the release of IR26 there was an immediate suppression of *N. lugens* in the Philippines, and similar results occurred in Indonesia and other Southeast Asian countries. Within 2 to 3 years (approximately six crops), outbreaks of *N. lugens* were observed on IR26. The increase of *N. lugens* virulence on IR26 was not completely unexpected. By selection of an *N. lugens* culture from Luzon Island, IRRI entomologists had established three populations that were distinct for their virulence on differential cultivars. The original field population that could only be reared on cultivars with no gene for resistance (e.g., TN1, IR8, IR20, IR22, IR24) was designated biotype 1; the population selected for virulence on cultivars with the *Bph* 1 gene (IR26, IR28, IR29, IR30) was designated biotype 2; and the population selected for virulence on cultivars with the *bph* 2 gene (IR32, IR36, IR38, IR42) was designated biotype 3 (Fig. 1).

In 1976, cultivar IR36 was released to control populations that had developed virulence to IR26 in the Philippines. The Philippine release was followed by the release of

Table 2 Genes for resistance to rice homopterans

Insect species		
Nilaparvata lugens	*Sogatella furcifera*	*Nephotettix virescens*
Bph 1	*Wbph* 1	*Glh* 1
bph 2	*Wbph* 2	*Glh* 2
Bph 3	*Wbph* 3	*Glh* 3
bph 4	*wbph* 4	*glh* 4
bph 5	*Wbph* 5	*Glh* 5
Bph 6		*Glh* 6
		Glh 7

IR36 and IR42 (both with the *bph* 2 gene) in most of Southeast Asia. Because of its insect and disease resistance, tolerance to adverse soils, and high yields, IR36 soon became the most popular rice cultivar in Asia and was planted on more than 13 million hectares. By 1982, there were reports of *N. lugens* outbreaks on IR36 and IR42 (8). Subsequent investigations have not substantiated the reports of *N. lugens* outbreaks on IR36, and attempts to select a virulent strain on 30-day-old plants of IR36 have met with a minimum of success (E. A. Heinrichs and F. G. Medrano, personal observation). It appears that even though biotype 3 (reared on ASD7 with the *bph* 2 gene) can kill small IR36 seedlings (Fig. 1), older plants maintain resistance. In contrast to IR42, IR36 apparently has, in addition to the *bph* 2 gene, some genetic component that provides a higher level of stability to *N. lugens* biotype selection. IR56, with the *Bph* 3 gene, was released for commercial cultivation in 1982, and in 1988, IR66, with the *bph* 4 gene was released. Reports from Sumatra, Indonesia, indicate that *N. lugens* field populations have been selected for virulence on the *Bph* 3 gene cultivar, and recently there have been reports of high populations on IR66.

As indicated in the selection of biotypes 2 and 3 from inbred *N. lugens* populations at IRRI, there is a high level of variability in virulence within the species. This is evident from studies in which distinct patterns of virulence were selected in 7 to 10 generations (9–11) (Fig. 2). Confirmation of the extreme variability of virulence patterns in the field was shown by Claridge et al. (12) in

Table 3 Grouping of brown planthopper biotypes based on the response of differential cultivars

Biotype	Response of cultivar
Philippines biotype 1, China, Japan, Korea, Malaysia, Taiwan (field)	—Resistant: IR26, ASD7, Rathu Heenati, Babawee, Ptb 33 —Susceptible: TN1
Philippine biotype 2, Solomon Islands	—Resistant: ASD7, Rathu Heenati, Babawee, Ptb 33 —Susceptible: IR26, TN1
Philippine biotype 3 and Taiwan biotype 3	—Resistant: IR26, Rathu Heenati, Babawee, Ptb 33 —Susceptible: ASD7, TN1
Bangladesh and Hyderabad, India	—Resistant: Rathu Heenati, Babawee, Ptb 33, —Susceptible: IR26, ASD7, TN1
Coimbatore, India	—Resistant: Babawee, Ptb 33 —Susceptible: Rathu Heenati, IR26, ASD7, TN1
Pantnagar, India	—Susceptible: IR26, ASD7, Rathu Heenati, Babawee, Ptb 33, TN1

* Genes for resistance in the test cultivars: IR26 = *Bph* 1; ASD7 = *bph* 2; Rathu Heenati = *Bph* 3; Babawee = *bph* 4; TN1 = none.

their study of six Sri Lankan populations collected from a wild rice species, traditional cultivars, and modern improved cultivars. When *N. lugens* populations were tested for virulence, they were shown to be most closely adapted to the cultivar from which they were collected despite the fact that populations were all collected within 200 km of one another. Differences in levels of virulence of *N. lugens* from different geographical regions were also reported within Andhra Pradesh state in India (13) and within Korea (14). There is evidence that virulence is inherited in a polygenic manner rather than by a gene-for-gene relationship between the insect and plant (15–17).

Variability in *N. virescens* Populations

Allopatric populations of *N. virescens* with variable levels of virulence to differential cultivars were first reported in 1979 (18). Distinct differences were found when comparing the reactions of seedlings of differential cultivars to a Philippine *N. virescens* population maintained in culture at IRRI and a Bangladesh population maintained at the Bangladesh Rice Research Institute (BRRI). Cultivars with the *Glh* 1, *Glh* 2, *Glh* 3, or *Glh* 5 gene were resistant at IRRI but susceptible at BRRI. Of 473 cultivars that were resistant to the Philippine *N. virescens* population, only 10 were resistant in Bangladesh.

A few years later, an international collaborative study was conducted to determine the variability of *N. virescens* populations in India, Indonesia, Malaysia, Philippines, Thailand, and Vietnam (19). Pankhari 203, which has the *Glh* 1 gene and was reported as susceptible in the previously mentioned Bangladesh study, was also susceptible in India and Malaysia but was resistant throughout the other Southeast Asian countries. The

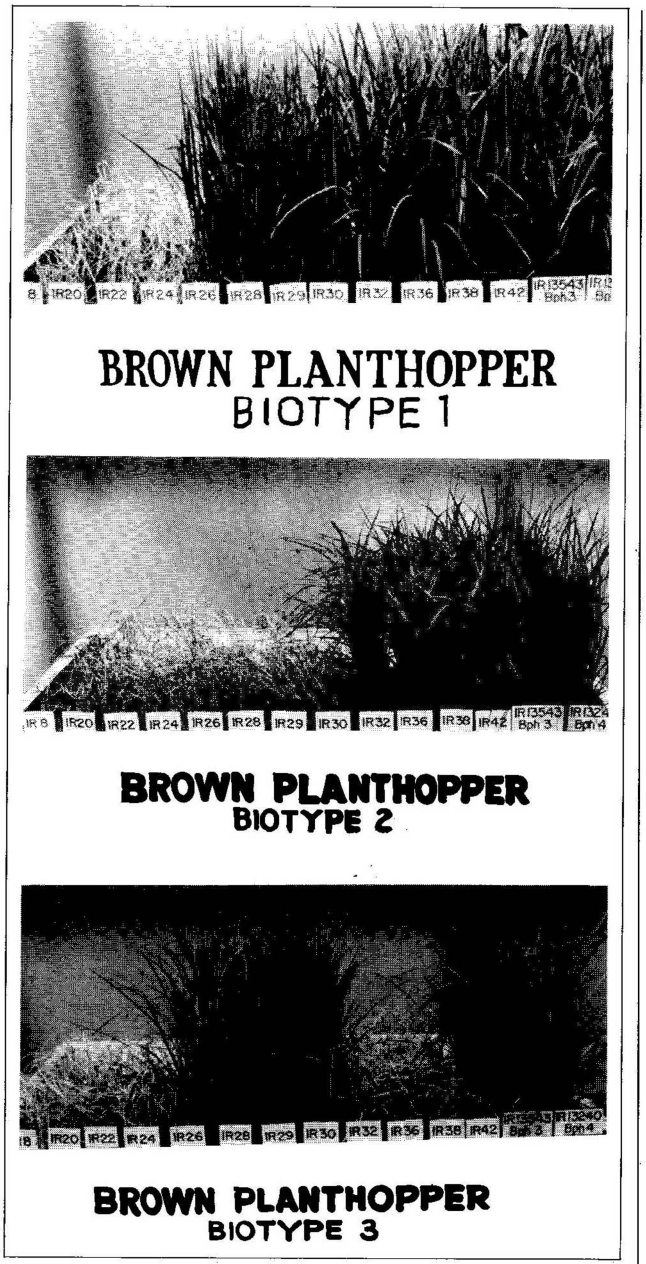

Figure 1 Reactions of differential rice cultivars to *N. lugens* biotypes 1, 2, and 3 at the International Rice Research Institute in the Philippines. Biotype 1 kills only cultivars with no genes for resistance; biotype 2 is virulent on cultivars with the *Bph* 1 gene for resistance; and biotype 3 is virulent on cultivars with the *bph* 2 gene for resistance.

other differential cultivars evaluated for resistance to *N. virescens* populations had generally the same reactions in all of the countries tested.

Although IR8 (released in 1965), IR20, and IR26 (all with the *Glh* 3 gene) were sequentially grown throughout the Philippines over a 20-year period, evidence of a possible increase in virulence of the *N. virescens* population was not documented until 1982 (20). Following IR26, IR36 was released in the Philippines in 1976 and subsequently became the most widely grown rice cultivar. In a survey conducted in the Philippines in 1979, there was no distinct evidence of an increase of *N. virescens* virulence on this cultivar (20). However, in a repeat of the survey

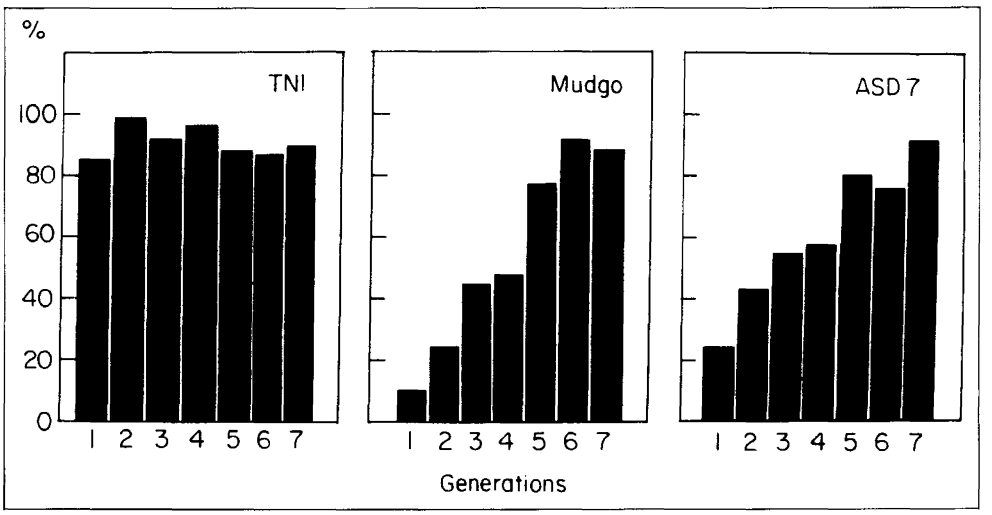

Figure 2 Percent survival of *N. lugens* biotype 1 nymphs from the first to the seventh generation of selection on susceptible (TN1) and resistant (Mudgo and ASD7) rice cultivars.

in 1984, *N. virescens* populations on IR36 in Luzon Island, the "rice bowl" of the Philippines, had levels of virulence significantly greater than those of the greenhouse colony that had not been exposed to selection pressure (21).

Although reasons for the apparent greater level of stability of *N. virescens*-resistant cultivars (e.g., IR8 and IR26) as compared with *N. lugens*-resistant cultivars (e.g., IR26) have not been determined, some possible explanations have been suggested. First, IR8 and IR36 have only moderate levels of resistance to *N. virescens*, in contrast to IR26, which has a high level of resistance to *N. lugens*. Second, *N. virescens* is polyphagous and feeds on a number of grasses and weeds in addition to rice, whereas *N. lugens* is monophagous and is restricted to feeding on rice. Thus, there is probably less selection pressure on the *N. virescens* population.

Controlled, laboratory/greenhouse studies have been conducted to determine the effect of selection for virulence on *N. virescens* feeding, development, and tungro virus transmission. After selection on resistant cultivars for 19 generations, survival increased and duration of nymphal period decreased. On two cultivars, Pankhari 203 (*Glh* 1 gene) and IR8 (*Glh* 3 gene), there was a shift from xylem feeding to increased feeding in the phloem (22). Phloem feeding is necessary for tungro virus transmission.

Rate of selection for virulence on five cultivars with varying levels of *N. virescens* resistance was determined in a follow-up study by Heinrichs and Rapusas (unpublished). Survival on the test cultivars increased to a level equal that on a susceptible cultivar after one to five generations of selection. The ability of *N. virescens* to vector tungro virus differed on the various test cultivars. On highly resistant Pankhari 203, there was no tungro virus infection after 20 generations of selection. On moderately resistant IR8, tungro infection increased from 35% infected plants before selection to 85% (not significantly different from the susceptible cultivar) after only four generations of selection (Fig. 3).

In another study, laboratory selection on cultivars with the same major genes for *N. virescens* resistance resulted in varying levels of cross-virulence to other cultivars with the same major gene for resistance (23). The authors concluded that minor genes play an important role in determining the degree of cross-virulence of *N. virescens* on different cultivars.

Variability in *S. furcifera* and *S. oryzicola* Populations

Commercial cultivars bred for resistance to *S. furcifera* have not been released. However, there is evidence of variability in the virulence of allopatric populations of *S. furcifera*. Of the 118 rice cultivars evaluated for resistance in the seedling stage at IRRI in the Philippines and at the All India Coordinated Rice Improvement Project in Hyderabad, India, 49 had different reactions (24). Cultivar N22 with the *Wbph* 1 gene for resistance to the Philippines population is susceptible in India.

Laboratory studies at IRRI have shown that selection for *S. furcifera* virulence to resistant cultivars occurs the same as with *N. lugens* and *N. virescens* (25). Populations reared on a resistant cultivar for only two generations increased in virulence to a level equal to that of *S. furcifera* on a susceptible cultivar.

Although cultivars with resistance to *S. oryzicola* have been commercially grown in Latin America for two decades, problems due to biotypes with increased levels of virulence and subsequent increases in the *S. oryzicola*-vectored hoja blanca virus have not been reported. This level of stability in resistance to *S. oryzicola* is assumed to be due to the fact that the major component imparting resistance to *S. oryzicola* is tolerance, rather than antibiosis. Because tolerance in cultivars such as IR8 exerts no selection pressure on the *S. oryzicola* population, these cultivars have had an apparent high level of stability in contrast to the *N. lugens* resistant cultivars in Asia, which have high levels of antibiosis.

Genetic Nature of Variability in *N. lugens*

Breeding for *N. lugens* resistance has involved the transfer of major genes for *N. lugens* resistance from donor sources into agronomically superior genotypes. Because of the major genes for resistance in the rice cultivars, it was assumed that there was a gene-for-gene relationship on behalf of resistance in the plant and virulence in *N. lugens*. However, studies on the genetics of virulence of biotypes 1, 2, and 3 conducted at IRRI using insect

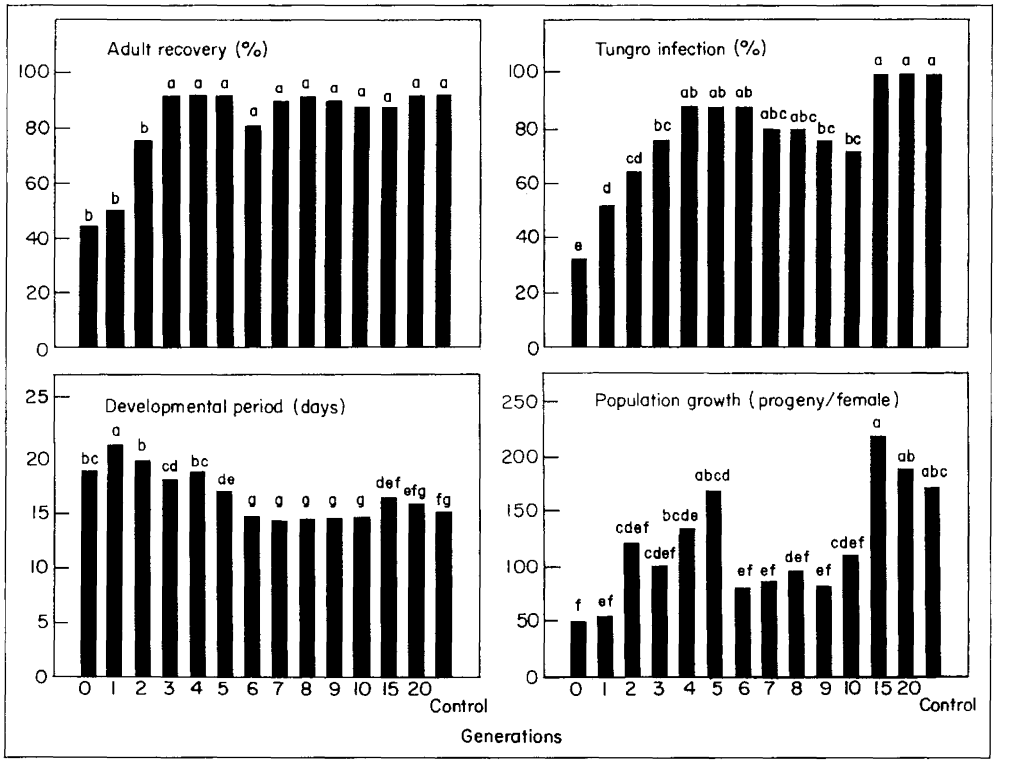

Figure 3 Percent of adult recovery (nymphs surviving to the adult stage), developmental period, population growth, and tungro virus infection when an *N. virescens* population was selected for virulence on resistant rice cultivar IR8 for 20 generations. The control refers to *N. virescens* reared on susceptible cultivar TN1. Bars within each parameter with the same letter are not significantly different at $P = 0.05$ of Duncan's multiple range test.

survival (15), feeding activity (15,16), nymphal development, and fecundity (16) as criteria for virulence indicated that virulence is inherited as a polygenic or quantitative trait. The evidence suggests that many genotypes are represented in the populations that have been designated as biotypes 1, 2, and 3. It is thus assumed that field populations of the various biotypes, as based on virulence, develop by an accumulation and recombination of various effective minor genes through the elimination of off-types, inbreeding among individuals selected, and reproductive competition among different genotypes under the continuous selection pressure of exposure to resistant cultivars (16). Thus, beginning with any specific biotype other biotypes may be selected by rearing *N. lugens* on other rice cultivars (15).

Criteria for Measuring Variability in Virulence

Plant damage The most common test to determine the level of virulence of a given homopteran population on a particular rice cultivar is the greenhouse evaluation of seedlings in seed boxes (Fig. 1, Table 3). Seeds of differential cultivars are sown in seed boxes, and 7 days later seedlings are infested with first- and second-instar nymphs. When the susceptible plants are killed, the differential cultivars are graded for plant damage and rated as susceptible or resistant. Biotypes are determined in relation to their reaction on the differential cultivars. Field tests can also be utilized to determine the reaction of differential cultivars to natural populations of hoppers.

Insect growth and development Survival (Fig. 2), population growth, duration of nymphal stages, adult longevity, body weight, and fecundity have been used by various authors to measure the level of virulence on specific *cultivars* (9,10,26). It is significant to note that in selection experiments the rate of selection varies depending on the criterion of measurement used, as indicated in Fig. 3 where adult recovery (survival) of *N. virescens* on a resistant cultivar in succeeding generations increased at a different rate than that of population growth. Survival on the resistant cultivar was equal to survival on the susceptible cultivar in generation three of selection. Population growth on the resistant cultivar, however, equaled that on the susceptible cultivar only after 15 generations of selection.

Host preference Sogawa (26) used host preference as a means to determine whether a given *N. lugens* population was adapted to a particular resistant cultivar. One-month-old plants of a susceptible and a resistant cultivar were transplanted next to each other in a clay pot. About 20 to 30 female adults were placed on the resistant cultivar, and migration from the resistant to the susceptible cultivar was measured periodically up to 48 h.

Feeding Feeding activity, behavior, and location are used to measure virulence of rice homopterans (3,9,10,26–29). Visual estimates, gravimetric measurements, volumetric measurements, and color intensity of honeydew produced are tools for determining the amount and rate of feeding (27). A video camera was used as an aid to observe the feeding behavior of *N. lugens* on rice cultivars (28). This method allows the recording of frequency and duration of probing and the rate at which honeydew droplets are released. Different waveforms produced by a device for electronic measurement of insect feeding indicate whether an insect is resting or involved in the various feeding activities (i.e., probing, salivation, or ingestion) (29). The types of inges-

tion waveforms indicate whether the insect is sucking xylem or phloem sap. This is important in determining the virus transmission efficiency of a rice homopteran population. *N. virescens* populations selected for virulence on resistant cultivars have increased feeding in the phloem, which apparently is necessary for virus transmission (Fig. 3). Histological sectioning of rice plant tissue fed upon by homopterans can be used to determine the feeding site within rice tissue. Stylet sheaths left by the insect in the xylem, phloem, and other tissues are clearly evident after staining (Heinrichs and Rapusas, in preparation).

Criteria for Measuring Characteristics of Homopteran Populations

Morphometry A controversy exists regarding the use of morphometric data to separate *N. lugens* biotype populations. Saxena and Rueda (30), in studies of biotypes 1, 2, and 3 in culture at IRRI, measured more than 100 morphological characters of the rostrum, legs, and antennae. Multiple discriminant analysis (using Wilk's Lambda method) of the three biotypes based on morphological data indicated distinct morphological segregation of the three biotypes. Claridge et al. (31) confirmed Saxena and Rueda's results in that they were able to separate the three IRRI biotypes by multivariate techniques when the insects were reared on their normal host cultivars. However, after rearing the three biotypes on the same susceptible cultivar for only one generation, no significant differences were found among them. Claridge et al. concluded that the differences are predominantly environmentally induced and do not represent major genetic differentiation and, thus, that there is no evidence that morphometric data can be used to identify field populations with distinct patterns of virulence.

Cytology Cytological variations have been reported for *N. lugens* biotypes 1, 2, and 3 at IRRI (32). Variations in the number and kinds of metaphase I cells, distance of the sex chromosomes from autosomal grouping, number of combined autosomes and sex chromosomes, and length and width of sex chromosomes were used as criteria to distinguish among the biotypes.

Enzyme polymorphism A comparison of esterase variation of *N. lugens* populations in 23 localities in Taiwan using polyacrylamide slab gel electrophoresis indicated geographical variation in the frequency of esterase alleles. Greater genetic distinctiveness of the northeast Taiwan population was reported (33).

Using horizontal starch gel electrophoresis to examine IRRI *N. lugens* biotypes 1 and 3, protein polymorphisms were observed in 6 of 11 enzymes (34). Biotype 1 exhibited greater genetic variation than biotype 3.

Acoustics Pulse repetition frequencies of male courtship signals have been shown to be distinctive for *N. lugens* populations (34). Frequencies of populations from Australia and the Solomon Islands were the most distinct from each other. In contrast to the differences in allopatric populations, sympatric populations consisting of biotypes 1, 2, and 3 from IRRI had similar pulse repetition frequencies, indicating that acoustics were independent from the virulence of the three biotypes against differential rice cultivars. Hybridization experiments indicated that pulse repetition frequencies are under genetic control involving a polygenic system of inheritance.

FUTURE DIRECTIONS

The successful management of homopteran populations attacking rice requires an integrated approach in which host plant resistance is combined with cultural controls, biological agents, and the judicious use of insecticides. Insect-resistant cultivars will be a key tactic in the integrated approach, but its success will depend on the rice-breeding strategies employed.

There is a great deal of genetic diversity in the world collection of rice, including differences in resistance to homopterans. Proper utilization of the diverse genes will be necessary to cope with the problem of virulent insect populations that overcome plant resistance. A vast pool of *O. sativa* cultivars is available that provides diverse sources of genetic resistance for utilization in rice-breeding programs. In addition, wild rices (*Oryza* spp.) provide an additional source of genetic diversity. Although some of these wild rice sources cannot be utilized in conventional breeding programs, because they are distantly related to *O. sativa* and genetically incompatible, they will serve as sources of new genes in genetic-engineering approaches.

Rice-breeding strategies to cope with biotype problems involve a number of approaches, including major gene deployment. Examples of major gene deployment approaches currently being used in various countries in Asia are the *sequential release* of cultivars with a new major resistance (R) gene when the previous resistance gene is overcome, *pyramiding* genes by incorporation of two or more R genes into a cultivar, *gene rotation* in which cultivars with different R genes are used in different cropping seasons, and *geographical deployment* in which different genes are used in adjacent cropping areas.

Selection for virulence is most severe on cultivars having the major R genes that provide primarily the antibiosis type of resistance. Thus, a horizontal type of resistance that provides resistance to all biotypes must be pursued in rice-breeding efforts because it is of a polygenic nature (several minor genes) and durable. In contrast to antibiosis, tolerance is of a polygenic nature and is a durable type of resistance because it exerts no selection pressure on the insect population (35). Combining tolerance to homopterans with tolerance/resistance to homopteran-vectored viruses will provide a type of resistance that is expected to be stable and provide an effective means of managing rice homopteran populations that is compatible with biological and cultural controls.

In the meantime, homopteran biotypes are expected to continue to be a problem on resistant rice cultivars. Thus, early detection of shifts in virulence is necessary so that gene deployment strategies can be most effective. Numerous procedures are available to measure the degree of virulence of homopteran populations, but it has not been determined which of the laboratory tests best reflect the virulence of field populations.

Resistant cultivars have been widely and successfully used in Asia and Central and South America in the management of certain rice homopterans. Rice-breeding lines with resistance to additional homopteran species are in the pipeline. To most successfully utilize the diversity of insect-resistant germplasm requires novel rice-breeding techniques and the integration of the resistant cultivars into rice insect management programs so as to provide an increased level of stability.

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GLOSSARY

accession: Seed of a cultivar or strain registered at a natural center and worth conservation.

allopatric: Distribution in which ranges do not overlap.

antibiosis: A component of host plant resistance that causes insects not to grow, survive, or reproduce well because of a toxic or other direct detrimental effect of the host plant.

antixenosis: A component of host plant resistance that causes a plant not to be preferred for oviposition or feeding by an insect.

biotype: A population of insects that is capable of damaging plant cultivars that are resistant to other populations of the same insect species. It is distinguished from other populations of the same species by parasite ability.

breakdown of resistance: The inability of a plant cultivar to maintain resistance when attacked by a newly selected insect population.

cross-virulence: The situation in which selection for virulence on one cultivar results in virulence to one or more other cultivars.

cultivar: A cultivated variety of a plant.

differential cultivars: Plant cultivars with different genes for insect resistance that are used to identify biotypes.

gene-for-gene resistance: See vertical resistance.

horizontal resistance: A type of resistance expressed equally against all biotypes of a pest species. It does not involve a gene-for-gene relationship as does vertical resistance.

major gene resistance: Resistance in which the effect of a gene is great. Synonymous with monogenic or oligogenic resistance, i.e., resistance governed by one or a few genes, respectively.

minor gene resistance: Resistance in which the effect of any one gene is small and may be strongly influenced by the environment. Used synonymously with polygenic resistance.

monogenic resistance: Resistance governed by one major gene.

plant resistance to insects: The consequence of hereditary plant qualities resulting in a plant being relatively less infected or damaged by insects than a susceptible plant lacking these qualities.

polygenic resistance: Resistance governed by several or many genes, each of which has a minor effect.

selection pressure: Exposure to stresses, such as insects, that tend to induce natural selection in the exposed population.

susceptible: Lacking resistance.

sympatric: Distribution in which ranges overlap.

tolerance: Ability of a plant to withstand infestation and to support insect populations that severely damage susceptible plants.

traditional cultivars: Cultivars commonly grown by farmers before the advent of the modern varieties (cultivars).

vertical resistance: A type of resistance that is expressed only against some biotypes of an insect species and is governed by one or more major genes in the host plant each of which corresponds to a matching gene for virulence in the pest species; also called gene-for-gene resistance.

virulence: Presence of a gene or genes in an insect that allows it to overcome (break down) the gene for insect resistance in a plant, thus making the insect able to utilize the plant as a host (susceptible).

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