VARIATION WITHIN AND BETWEEN POPULATIONS OF THE BROWN PLANTHOPPER, NILAPARVATA LUGENS (STÅL)

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ABSTRACT

N. lugens is a widely distributed and effectively specific pest of rice in Asia. Populations, often termed "biotypes", have rapidly evolved in virulence to rice varieties which incorporate genes for resistance. Field populations in one area normally show great individual variability for virulence characteristics. The term biotype may be misleading, as it implies a common genetic basis for such characteristics.

Spatially isolated populations of *N. lugens* often show variation in virulence characters. Also, such populations have developed various degrees of genetic divergence, as measured by hybridisation experiments and electrophoretic differences. Differences in acoustic courtship signals may be important in the establishment of barriers to hybridisation.

INTRODUCTION

The Brown Planthopper, *Nilaparvata lugens* (Stål) has become a major pest of rice in Asia since the early 1970s following the widespread introduction of high-yielding varieties. Modification of the habitat associated with growing the new varieties, rather than a greater genetic vulnerability, probably contributed to the development of this pest. The new agricultural practices included extensive monoculture of genetically uniform varieties, continuous cropping, staggered planting, irrigation and the use of high levels of nitrogenous fertilizers and insecticides (Dyck and Thomas, 1979; Dyck *et al*, 1979).

N. lugens is widely distributed in the tropical and temperate regions of Asia, in northern Australia and western Oceania (Figure 1). In tropical regions it is resident throughout the year, but it cannot overwinter in more temperate regions such as Japan and Korea, and must reinvade from warmer areas each summer (Kisimoto, 1979; Kuno, 1979).

Although many alternative hosts have been suggested, *N. lugens* appears to repeat generations continuously only on cultivated and wild rices (*Oryza* species) (Mochida and Okada, 1979). It damages the plant directly through feeding on it and also by transmitting the virus diseases "grassy stunt" (Ling, 1967) and "ragged stunt" (IRRI, 1978). Heavy infestations cause desiccation of the plant, a condition known as "hopperburn", and may result in the total loss of the crop (Dyck and Thomas, 1979).

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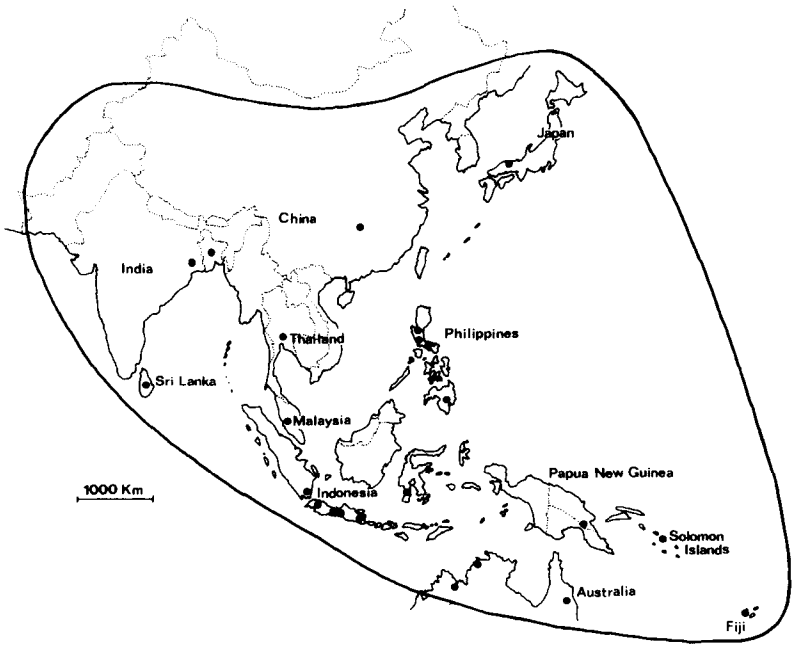


Figure 1. Map showing distribution of N. lugens. The localities from which culture populations are at present held in Cardiff are marked by •

Control was initially based on the use of insecticides. However, because of the problems of chemical control, such as pollution of the environment, nonspecificity of most insecticides and high costs, in addition to the development of resistance and the threat of resurgence, alternative control methods were sought. Plant resistance was an attractive alternative, having none of the disadvantages associated with chemical control (Pathak, 1975). Although in many instances resistance may be short-lived because of the ability of pests to adapt and overcome the resistance (Ou, 1977; Day, 1974; Russell, 1978), resistance in rice as a means of combating N. lugens has been pursued with great success (Khush, 1979).

Methods of mass rearing of N. lugens and screening of rice varieties have been developed at the International Rice Research Institute, Los Banos, Philippines (IRRI, 1967). For mass screening, test lines are sown in rows 5 cm apart in 60 x 45 x 10 cm seedboxes. One row each of a susceptible and resistant check are interspersed at random per seedbox. The outside rows are planted with the susceptible check in order to contain the insects. After 7 days the seedlings are thinned if necessary to give 20-30 seedlings per row and then infested with second- and third-instar nymphs from the insect colonies at a density of 5-10 insects per seedling. The plants are scored for resistance when the susceptible check is killed, usually after 7-10 days.

Using these methods, resistance to N. lugens was discovered at IRRI in the varieties Mudgo (Pathak et al., 1969) and ASD7 (Athwal et al., 1971). The resistance in Mudgo is based on a single dominant gene, termed Bph 1, and in ASD7 on a single recessive, termed bph 2. These genes are different but closely linked (Athwal & Pathak, 1972) and each has been incorporated into high-yielding varieties. IR26, incorporating Bph 1, was released in the Philippines in 1973, but by 1975 field populations were able to overcome the resistance (Feuer, 1976). Following this, IR32, incorporating bph 2, was released. A similar sequence of releases was made in Indonesia and Vietnam (Seshu & Kauffman, 1980). IR32 was succeeded by IR36: a superior plant type which also incorporates bph 2. At present IR36 is widely planted in South-East Asia. Although this variety is still proving resistant in the field, forced rearing on ASD7 in the Laboratory has produced populations able to overcome the resistance of bph 2.

Two further genes for resistance have been recognised, Bph 3 in Rathu Heenati and bph 4 in Babawee (Lakshiminarayana & Khush, 1977). These are currently also being incorporated into high-yielding varieties at IRRI for future field release (Khush, 1979). The variety PTB 33 has two genes for resistance, but their allelic relationships are not known (Khush, 1979).

Populations of N. lugens able to overcome the resistance of rice have been termed biotypes and designated numbers depending on which genes they can overcome (IRRI, 1976). Biotype 1 can only infest varieties thought to have no resistance genes (such as TN1). Biotype 2 can infest varieties having either no resistance gene or Bph 1 (Mudgo), but not those with bph 2 (ASD7). Biotype 3 can infest those having either no resistance gene or bph 2, but not those with Bph 1.

Several attempts have been made to demonstrate differences between the biotype populations in morphology and other characteristics, such as fecundity, electrophoretic variation, karyotype and sexual isolation. The only differences that have been published are a statistically significant difference in the distribution of the hind basitarsus spine number and the frequency of esterase electromorphs (Sogawa, 1978, a,b) and very recently morphometric differences involving characters of the head and tarsi (IRRI, 1981). However, no evidence has been produced to demonstrate that these differences

are linked to virulence. They may simply reflect founder effects or random drift within each colony.

The biotypes are recognisable only by their different abilities to infest particular resistant rice varieties. It has been assumed that these differences are clear-cut and that the biotypes represent another example of a gene-for-gene relationship between virulence and resistance.

As a result of our experimental work in Cardiff we have questioned some of the assumptions about the nature of the biotypes and the variation in N. lugens. This paper will discuss our interpretation of the variation in N. lugens, first within populations at one location and then between populations from different geographic areas. The variation considered will be in virulence, courtship and electrophoretic differences.

VARIATION IN VIRULENCE

a. Within populations

The reactions of some populations of N. lugens to some varieties are not consistent and often difficult to duplicate (Seshu & Kauffman, 1980; Kabir & Alam, 1981; Fernando et al., 1979). Similar variability was even demonstrated within the inbred biotype cultures maintained at IRRI (Claridge & Den Hollander, 1980).

The methods used for assessing virulence of N. lugens populations have all been based previously on mass screening, either by the seedbox method or the percentage survival of a population placed on a rice variety, or the amount of honeydew produced by a number of insects on a rice variety. None of these methods reveal individual variation within a population.

By enclosing an individual insect in a parafilm envelope attached to a living rice plant and measuring the weight of the insect before and after 24 h and the weight of honeydew produced during this period, an estimate of the virulence of individuals may be obtained. Results of such studies have revealed wide variation within the biotypes and large overlap between them on all the varieties tested (Figure 2) (Claridge and Den Hollander, 1980). Even populations from a susceptible variety, when tested on a resistant one, revealed a gradation in virulence and a few individuals performed as well as those from a virulent population. Field populations also showed a broad range of virulence (Claridge and Den Hollander, 1980).

The continuous variation in virulence within populations argued against a single-gene determination of virulence. Crosses were made between the biotypes and the parental populations, and the F_1 and F_2 generations were tested for virulence on resistant varieties. The variation in virulence of the F_1 generation tended to be distributed

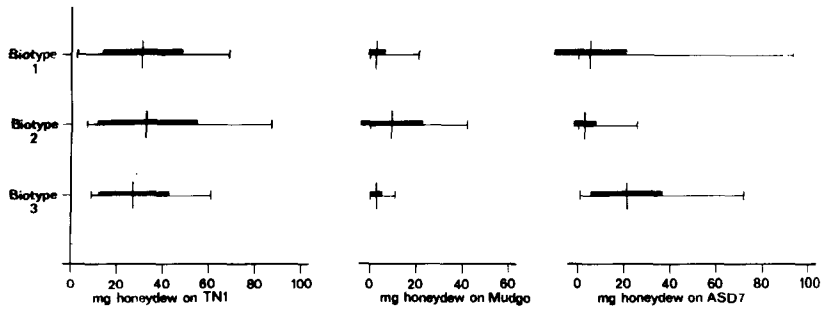


Figure 2. Mean, standard deviation and range of honeydew produced by individuals of Philippine biotypes 1, 2 and 3 on rice cultivars TN1, Mudgo and ASD7.

between that of the parentals. The F_2 was similarly distributed, but with a larger range of variation than the F_1 in two experiments and a smaller range in the other two (Table 1). No segregation indicative of simple mendelian inheritance was apparent.

Table 1. Weight of honeydew produced by the Philippine biotypes and F_1 and F_2 generations of crosses between them, on resistant varieties of rice.

CROSS	RICE VARIETY	mg HONEYDEW PRODUCED IN 24 HOURS PARENTAL	F_1	F_2
BIOTYPE 1 X BIOTYPE 2	MUDGO	2.8 ± 3.2 9.4 ±13.0	4.3 ± 7.9	3.8 ± 7.2
BIOTYPE 1 X BIOTYPE 3	ASD7	5.5 ±15.4 18.6 ±10.7	4.9 ± 4.7	3.7 ± 6.4
BIOTYPE 2 X BIOTYPE 3	MUDGO	2.6 ± 5.4 9.4 ±13.0	4.7 ± 5.4	5.2 ±10.2
BIOTYPE 2 X BIOTYPE 3	ASD7	2.7 ± 4.5 18.6 ±10.7	7.8 ±11.2	7.0 ±10.3

This pattern of inheritance is typical of characters controlled by polygenes.

Polygenic inheritance allows a large range of genetic variation to exist within a population, since similar phenotypic properties may be acquired by a variety of combinations of genes. Because of the inherent variation in virulence, populations of N. lugens respond rapidly to selection exerted by resistant varieties. Initial low virulence of a population on a new variety is quickly enhanced by recombination and selection. When restricted to a resistant variety, virulence (estimated by an index determined from the percentage survival, average weight of female adults and the time taken for 50% of the survivors to reach the adult stage) improves markedly in only a few generations (Claridge and Den Hollander, 1982). Populations may be considered virulent on the new resistant variety in about 10 generations. Effectively they have been transformed into a new biotype (Figure 3).

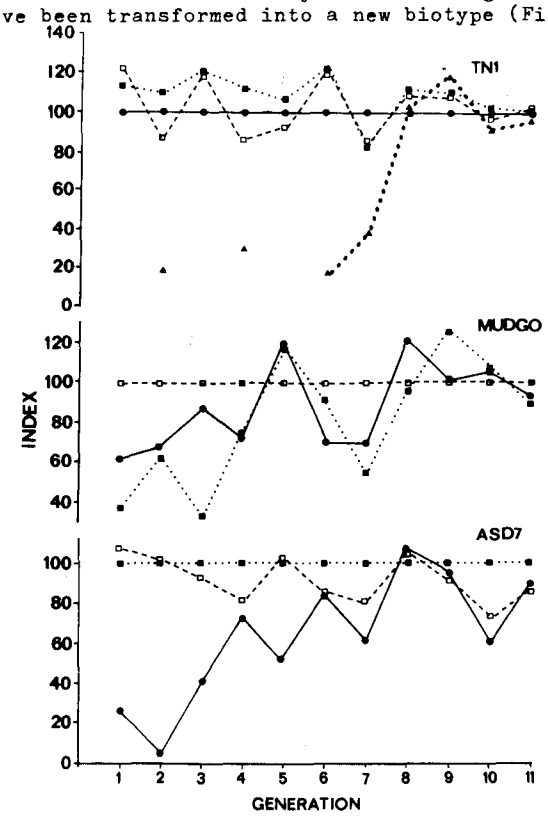


Figure 3. Index calculated from % survival, weight of first 10 females to emerge and time taken for 50% of the survivors to emerge of Philippine biotypes 1, 2 and 3 for 11 generations of selection on TN1, Mudgo and ASD7. An Australian population is also included on TN1. ● biotype 1, ▫ biotype 2, ▪ biotype 3, ◦ Australian population.

This selection by the rice has also been demonstrated in the field by the close adaptation of local populations of N. lugens to host varieties in Sri Lanka (Table 2) (Claridge, Den Hollander and Furet, 1982).

Table 2. Means for mg honeydew produced and percentage weight change in 24 hours of newly emerged adult females from local populations of N. lugens in Sri Lanka from five different cultivars and wild rice tested on all the rice varieties.

		Yakadawee	Demas	H-8	BG-379-2	BG-90-2	Wild Rice
Yakadawee	%	33.7	3.6	12.1	13.0	15.9	24.8
	mg	20.3	13.8	11.6	9.7	19.0	13.0
Demas	%	13.1	8.6	-8.8	-2.1	7.1	14.9
	mg	12.52	9.1	3.7	5.6	6.0	11.4
H-8	%	19.7	-5.9	13.3	6.5	16.1	15.9
	mg	16.7	6.6	20.6	15.3	20.4	13.5
BG-379-2	%	-0.7	-5.9	3.2	15.2	8.2	2.2
	mg	4.0	5.3	9.28	16.4	10.4	4.9
BG-90-2	%	16.4	6.8	18.6	4.6	23.5	19.5
	mg	15.7	8.5	18.8	10.3	22.3	14.0
Wild Rice	%	23.9	12.6	14.2	10.7	18.1	12.1
	mg	14.6	10.0	9.6	13.3	15.9	14.2

b. Between geographic areas

In addition to variation in virulence within populations, variation is also found between populations from different geographic areas. For example, Mudgo and IR26, both with Bph 1 gene for resistance, were initially resistant in the Philippines, but not in India or Sri Lanka (Seshu & Kauffman, 1980). This was the first indication of geographic variation in the virulence of N. lugens.

The International Rice Brown Planthopper Nursery (IRBPHN) was set up in 1975 to monitor geographic variation in N. lugens and to identify new resistant rice varieties. Their latest report (Seshu & Kauffman, 1980) summarised the findings. Briefly, Mudgo was resistant at all sites in East and South-East Asia, but not to biotype 2 in the Philippines, Taiwan or Indonesia. It was also susceptible at all sites in South Asia (India) and in the Solomon Islands. ASD7 was resistant at all sites in East and South-East Asia and Solomon Islands, but not to biotype 3 in the Philippines, biotype 2 and 3 in Taiwan or in South Asia. PTB33 was resistant at all sites except Pantnagar (India) and Gannoruwa (Sri Lanka) (Verma et al., 1979). TN1 was found to be susceptible at all sites. The varieties Rathu Heenati and Babawee with Bph 3 and bph 4 resistance genes respectively, were resistant to all "biotypes" in the Philippines and Taiwan, and at all sites in South and South-East Asia, Solomon Islands and South Asia, except at Pantnagar. The population at Pantnagar is virulent on all known varieties of rice (Verma et al., 1979).

Besides the variation between sites, reactions often varied from year to year. Different results were often obtained from laboratory screening and field trials. Sometimes also a traditional variety, the source of a particular resistance gene, was resistant, but the improved variety incorporating the same resistance gene was susceptible (Seshu & Kauffman, 1980).

In addition to the geographical variation reported by IRBPHN, we have found that the susceptible check variety TN1 is highly resistant to N. lugens from Australia (Figure 3) (Claridge & Den Hollander, 1982). This directly challenges the assumption that TN1 possesses no genes for resistance.

VARIATION IN COURTSHIP

Courtship in N. lugens is by acoustic signals transmitted through the substrate (Ichikawa & Ishii, 1974, Claridge et al, 1982). The female call consists of regularly repeated simple pulses. The male call is more complex consisting of repeated sequences, each of three phases (see Claridge, this volume). The second phase of each sequence in the male call is the most consistent and the pulse repetition frequency (PRF) of this has been counted and compared within and between populations. Individuals appear quite consistent for PRF, but considerable variation occurs within a population (Table 3). The distributions of PRF for populations from different geographic areas were generally not significantly different (Table 3). The exceptions were the populations from Australia, all of which had a significantly higher frequency, and the populations from the Solomon Islands which had a significantly lower frequency, when compared with a population from the Philippines.

The differences in PRF of male calls were reflected in the level of successful crosses between the Australian, Philippines and Solomon Islands populations. Individual virgin females were placed in test tubes containing a rice seedling and a male either from the same or a

Table 3. Mean, standard deviation and range of Pulse Repetition Frequency (PRF) of N. lugens populations from Australia (Mareeba), Philippines (Liliw) and Solomon Islands (Honiara).

	Mean	S.D.	Range
AUSTRALIA	86.3	3.3	76.8 - 96.0
PHILIPPINES	72.4	5.0	57.6 - 86.4
SOLOMON ISLANDS	65.1	3.4	52.8 - 76.8

different population. They were left together for 24 hours, the female was then removed and the spermatheca dissected out and examined for the presence of sperm. Crosses within populations had a high success rate for insemination, while crosses between localities had a lower success rate.

Although the level of crossing between populations was low, those individual crosses which were successful showed no signs of hybrid inviability, sterility or an unbalanced sex ratio. This implies that while differences exist between the populations, the genetic differences may be relatively small.

ELECTROPHORETIC VARIATION

The apparent lack of morphological differences between N. lugens populations suggested the use of biochemical methods to examine variation. Gel electrophoresis has been widely used to reveal both intra- and inter-population variation. Its advantages are that it is relatively free from environmental effects, sensitive and quick. It was decided to examine electrophoretic variation in esterases as Sogawa (1978) had reported differences between the biotypes at IRRI in the frequency of certain electrophoretic phenotypes. Because of the difficulties in establishing the allelic relationships of some of the esterase bands, the results will be presented here in the form of electrophoretic phenotypes only.

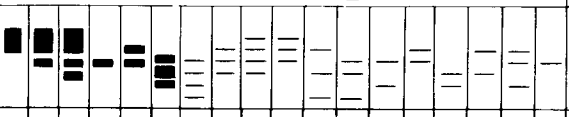
a. Intrapopulation Variation

Subcultures of the biotypes from IRRI maintained at Cardiff were examined and found to be polymorphic for esterases. The frequencies of the different phenotypes varied between the biotypes. Biotype 1 was significantly different from biotypes 2 and 3, but these were not significantly different from each other. The pattern of differences is due to the higher frequency of the rarer phenotype in biotype 1. No absolute differences were found between the biotypes which might explain virulence differences.

b. Inter-population Variation

The examination of esterases was extended to include populations from several localities within the Philippines and throughout Asia. Some care must be taken in interpreting these results as they are based largely on laboratory cultures derived from initially small field samples.

Table 4. Frequencies of different esterase phenotypes in populations of N. lugens.

LOCALITY	PHENOTYPE																		N
																			
Philippines Biotype 1		·83	·17																77
" Biotype 2		·98	·02																54
" Biotype 3		·98	·02																50
" Los Baños	·02	·98																	133
" Naga	·04	·96																	24
" Iloilo	·15	·65	·20																40
Japan		·78	·07	·10	·05														82
China		1·00																	28
India	·08	·92																	12
Sri Lanka	·02	·79	·06	·07															160
Malaya		·50	·25	·25															32
Indonesia		·93	·07																60
Papua New Guinea		·92			·08														14
Fiji	·02	·04	·04	·04	·04	·82													57
Solomon Islands						1·00													87
Australia Mareeba				·02	·27	·20	·04	·17	·02	·11	·01	·04		·09	·01				89
" Darwin				·11	·39	·07		·11					·04	·18		·04	·07	·04	28
" Kununurra					·33			33	·06				·13					·13	15

Differences are apparent between some geographic areas (Table 4). The phenotypes in column 4 and 5 are not present in the Philippines, but occur in Sri Lanka, Japan and Malaysia, while the phenotype in column 1 occurs only in the Philippines and Sri Lanka. However, these phenotypes are relatively rare in all of the populations where the phenotype in column 3 predominates. The most striking differences occurred in the Australian and Solomon Islands populations. The phenotype from the Solomon Islands showed no variation and the bands differed in mobility from those of all other populations. The band of maximum activity also did not correspond to that in any other population (Table 4). The Australian population was different again, it was variable and extremely difficult to score reliably as the esterase

activity was very low (Table 4). It was not possible to determine whether the bands of activity corresponded to those of any other populations.

The differences between the Australian, Philippines and Solomon Islands populations have been confirmed by electrophoresis of field frozen material, in addition to laboratory culture populations.

DISCUSSION

Populations of N. lugens, often termed biotypes, have evolved virulence to rice varieties which incorporate different genes for resistance. The use of the term biotype of insect pests has generated much controversy (Claridge & Den Hollander, in press). It has often been used either in the sense of all members of a population sharing a physiological adaptation, or all members being genetically identical with respect of genes for virulence.

Studies of the variation within the "biotypes" of N. lugens revealed a wide distribution in the virulent ability of individuals and no clear demarcation between the biotypes on resistant varieties (Claridge & Den Hollander, 1980). Crosses between the biotypes indicate polygenic inheritance of virulence, which means that all members of a biotype are unlikely to be genetically identical (Den Hollander & Pathak, 1981). In both senses therefore the use of the term biotype for this insect is inappropriate. The naming or numbering of biotypes also implies a fixed characteristic, but selection experiments have demonstrated that this is not so, and that a population may adapt rapidly to the challenge of a new resistant rice variety (Claridge & Den Hollander, 1982; Pathak & Heinrichs, 1982). This versatility is probably due to the wide variation in, and polygenic determination of, virulence in most populations. To give biotypes the same number implies that they have identical virulence, but this is often not the case. For example, biotype 2 in the Philippines is only able to infest varieties with either no resistance genes or Bph 1, but biotype 2 in Taiwan can infest varieties with no resistance gene, Bph 1 and bph 2 (Seshu & Kauffman, 1980).

Variation within populations of N. lugens still needs further examination. For example, the population at Pantnagar is virulent on all resistant varieties. This may be due to each individual in the population being able to infest all varieties, but equally the population may consist of a mixture of individuals each able to infest only one variety.

Geographic variation in virulence divides N. lugens into the three broad regions of: South Asia, East and South-East Asia and Australia. However, where populations apparently share virulence characteristics, it has not been established whether the virulence has a common genetic basis. Virulence has been shown to vary considerably over even quite short distances in Sri Lanka as a result of adaptation to locally grown varieties. To divide N. lugens into regions based on virulence may be too coarse and prove only of temporary value.

Geographic variation in other characters, such as PRF of courtship song, ability to hybridize and electrophoretic phenotypes, occurs between populations, often those which have similar virulent abilities. These differences certainly show that genetic differences do indeed occur between spatially isolated populations.

N. lugens cannot overwinter in temperate regions, yet each summer it re-establishes in Japan and Korea. It has been confirmed that this occurs through long-distance migration from mainland China, across the South China Sea and into Japan and Korea (Kisimoto, 1979). An initial low density of migrants rapidly multiplies to form the summer population. To what extent long-distance migration occurs in the tropics has not been established. Studies have confirmed that N. lugens is capable of long-distance wind-assisted migration in the tropics (Rosenberg, 1981). Regular large-scale migrations should prevent the development of regional differences through intermixing. The demonstration of geographic variation tends to argue against long-distance migration as a normal occurrence in the tropics. Clearly further studies on geographical variation are urgently needed.

Cultivated rice probably originated in northern India and subsequently spread to southern India and Sri Lanka (Chang, 1976; Nakagahra et al., 1975). The presence of wild rice, the wide diversity of traditional varieties and the fact that all resistance genes to N. lugens identified so far originate from this area, all support this conclusion. Not only is this region the gene centre for resistance, it is also the gene centre for virulence in N. lugens. The most virulent populations with the ability to feed on and damage the broadest range of rice varieties also occur in this region. These virulent populations cannot have evolved under the same conditions as the host resistance breaking populations in the Philippines and other parts of Asia after the introduction of high-yielding varieties. The genetically uniform high-yielding varieties result in strong selection for one overriding virulent ability. The wide flexibility of N. lugens populations in South Asia is probably due to selection over a long period of time to combat the high diversity of rice present in this area. It would be interesting to determine whether wild rice in this area is polymorphic for resistance genes.

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