

The status of weed-associated populations of the brown planthopper, *Nilaparvata lugens* (Stål) – host race or biological species?

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Populations of the brown planthopper, *Nilaparvata lugens* (Stål), from the Philippines were collected from and reared on the grass weed, *Leersia hexandra* Swartz. Six different populations from five localities were studied and compared with a sympatric rice-feeding population.

Experiments on survival, virulence and oviposition preferences demonstrated that populations from one host plant survived poorly on the other and showed a strong preference for the species from which they derived. Crosses between the two populations showed some barriers to hybridization, but viable and fertile hybrids were obtained. Mate choice experiments demonstrated that, when a choice was available, no heterogametic matings occurred.

Pulse repetition frequencies of female and male calls differed consistently and significantly between rice- and *Leersia*-associated populations. Hybrid calls were intermediate between the parental calls. Playback experiments showed that the call differences were primarily responsible for maintaining the identities of the host-associated populations.

It was concluded that the populations from rice and from *L. hexandra* represent two distinct, but very closely allied, sympatric species in the Philippines.

KEY WORDS: – Brown planthopper – *Nilaparvata lugens* – rice – *Leersia hexandra* – biological race – biotype – species – acoustic signals – courtship – hybridization – isolating mechanism – mate recognition.

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INTRODUCTION

The brown planthopper, *Nilaparvata lugens* (Stål), is generally thought to be specific to wild and cultivated rices (*Oryza* species). Despite reports of possible alternative hosts and the collection of adults from a wide variety of plants, it is usually said to repeat generations only on rice (Mochida & Okada, 1971, 1979). However, insects which feed on rice have been shown to adapt readily to a wide array of previously resistant cultivars (Cheng, 1977; Pathak & Heinrichs, 1982; Claridge & Den Hollander, 1982) and this has led to speculation that *N. lugens* may form host-specific races as a step leading to sympatric species formation (Pathak & Heinrichs, 1982). Despite shifts in virulence of *N. lugens* on resistant rice varieties, no evidence for any sexual isolation leading to possible species formation is apparent to support this contention (Claridge & Den Hollander, 1980; Claridge, Den Hollander & Morgan, 1985).

The recent discovery in the Philippines (Luzon and Mindanao) of populations of *N. lugens* feeding on *Leersia hexandra* Swartz, a weed grass often found growing in ditches and irrigation channels near rice paddies, has again raised the possibility of a sympatric host race or biotype, and a reservoir of *N. lugens* which is able to attack rice (Medrano & Heinrichs, 1982; Domingo, Heinrichs & Saxena, 1983). Heinrichs & Medrano (1984) reported no survival of the populations from *Leersia* on the rice varieties TN1, Mudgo and ASD7. The insects were crossed with *N. lugens* from rice and the F₁ hybrids were found to survive on rice. Because of this the *Leersia*-associated population was considered as a potential source of new variants. Further, it was suggested that the *Leersia*-feeding population was a primitive, non-virulent 'biotype' of *N. lugens* (Saxena & Barrion, 1984; Saxena, Velasco & Barrion, 1983a). In a morphometric study, no significant differences were found between the two host-associated populations (Saxena *et al.*, 1983a), but some differences in chromosomes have been reported (Saxena & Barrion, 1983).

Nilaparvata lugens is a distinct morphological species differing from its closest relatives in SE Asia particularly in the structure of the male genitalia (Mochida & Okada, 1979). A further morphological species, *N. bakeri* (Muir), frequently feeds on *Leersia* in the Philippines and co-exists with the *Leersia*-feeding *N. lugens*. It has been reported from the International Rice Research Institute (IRRI) farm (Saxena, Velasco & Barrion, 1983b) and we collected it from Zaragosa in Luzon.

At Cardiff we have studied populations of *N. lugens* from *Leersia* collected in the Philippines. In order to establish the relationship between populations from rice and those from *Leersia*, we have made investigations of two types: (1) insect/host plant relations in terms of host preference, and survival and virulence on each host, and (2) genetic differentiation in terms of ability and readiness to hybridize, mate choice and differentiation of mate recognition signals produced during courtship, and responses to such signals. Our aim was to assess whether the populations associated with the two hosts represent one polyphagous species, two host races, or two separate biological species.

For simplicity in the following account the populations of *N. lugens* derived from rice will be termed 'rice populations' and those derived from *L. hexandra* 'Leersia populations'.

POPULATIONS STUDIED

The rice population was collected from the field at Liliw, Laguna, Luzon, Philippines, and cultured in Cardiff on the rice cultivar TN1. The general methods of rearing and maintaining *N. lugens* have been reported in detail previously (Claridge *et al.*, 1985).

A *Leersia* population was collected from the farm of the IRRI, Los Baños, Laguna, Luzon, February 1982. A further sample population from the same locality, together with three from other sites in Luzon, was collected in April 1983, and another from Mindanao in 1984 (Fig. 1). The populations were cultured on rooted cuttings of *Leersia* in Cardiff. The population from Zaragoza was used for most of the experiments reported here, unless otherwise stated.

HOST PLANT RELATIONS

Host plant relations of the two populations were studied by measurements of survival, virulence and oviposition preference on the two hosts.

Survival

The methods used were outlined in Claridge & Den Hollander (1982). Briefly, 25 first instar nymphs were placed on a plant, and the following were recorded: (1) the percentage of insects to reach the adult stage, (2) the mean weight of either the first ten females to emerge or of the total numbers if less than ten, and (3) the time until 50% of the survivors reached the adult stage. The rice population was tested on rice (TN1) and *Leersia*, and the *Leersia* populations on rice (varieties TN1 and Delta) and *Leersia*. The results show that the rice population does not survive on *Leersia*, and the *Leersia* population does not survive on TN1 (Table 1). However, a few of the *Leersia* population survived on Delta, but the survivors were small and weak, and all attempts to produce a F₁ generation on rice have so far failed.

Virulence

Nilaparvata lugens feeds from the phloem sap of its host during which large quantities of honeydew are produced. Amounts of honeydew produced and weight changes of individual insects when confined on test plants may be used as good measures of feeding virulence. The methods used have been described in Claridge & Den Hollander (1982). The amount of honeydew produced and the weight change of individual adult female insects from each population over a 24 h period were measured on both rice and *Leersia*. The results (Figs 2 & 3) reflect those of the survival experiment. Both measures are high for each population when on their own host plant, but low when on the other.

Oviposition preferences

Nilaparvata lugens has been reported to oviposit indiscriminately with respect to different rice varieties and even also to oviposit on non-host plants (Saxena & Pathak, 1979). To determine if the two populations exhibited any preference,

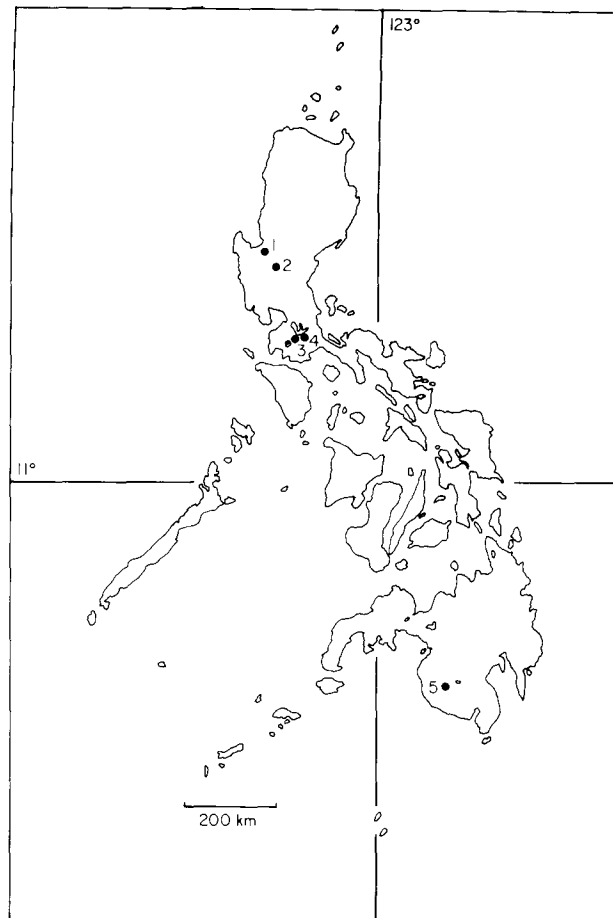


Figure 1. Sketch map of Philippines to show localities from which *Leersia* populations of *N. lugens* were collected by us: 1, Rosalis, Pangasinan, 15°53'N, 120°38'E; 2, Zaragoza, Nueva Ecija, 15°29'N, 120°46'E; 3, IRRI, Los Baños, Laguna, 14°11'N, 121°12'E; 4, Victoria, Laguna, 14°14'N, 121°19'E; 5, Koronadal, South Cotabato, 6°30'N, 124°51'E.

Table 1. Percentage survival to adult stage, mean weight of adult females and time for 50% of survivors to reach adult stage for first instar nymphs of rice and *Leersia* populations of *N. lugens* tested on *Leersia hexandra* and rice (varieties TN1 and Delta)

Population of <i>N. lugens</i>	Host plant	No. of individuals and replicates	Percentage survival	Mean weight of females (mg)	Time to adult (days)
Rice	TN1	100 (4 × 25)	78	2.45	14
Rice	<i>Leersia</i>	100 (4 × 25)	0	—	—
<i>Leersia</i>	TN1	100 (4 × 25)	2	—	19
<i>Leersia</i>	TN1	66 (2 × 18, 1 × 30)	0	—	—
<i>Leersia</i>	Delta	400 (4 × 100)	7	1.53	20
<i>Leersia</i>	Delta	100 (4 × 25)	2	—	19
<i>Leersia</i>	<i>Leersia</i>	100 (4 × 25)	60	2.02	15

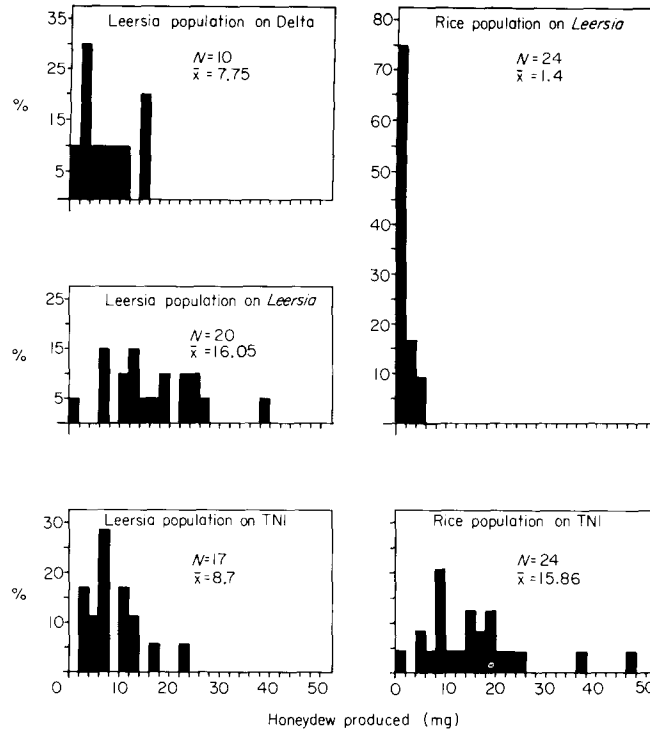


Figure 2. Honeydew produced in 24 h by individual adult females from rice and Leersia populations of *N. lugens* on rice (varieties TN1 and Delta) and *Leersia hexandra*.

mated, gravid females of each were given a choice between rice and *Leersia* for oviposition. Twelve females of each type were placed singly in 8" x 1" glass tubes, each containing a rice seedling (TN1) and a *Leersia* cutting. After 48 h the plants were removed and examined for the presence of eggs. Each population demonstrated a strong preference for ovipositing on the host plant from which it derived (Table 2).

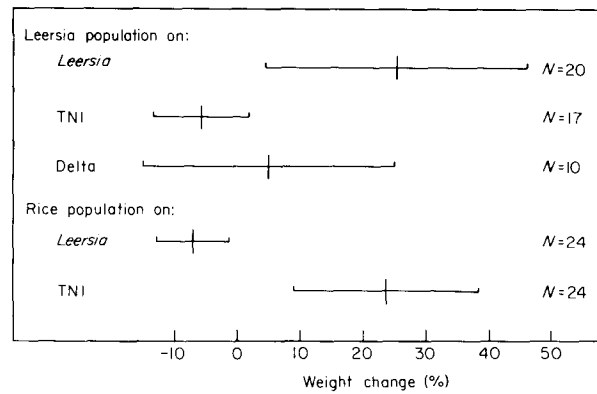


Figure 3. Means and standard deviations for percentage weight change of individual adult females from rice and Leersia populations of *N. lugens* on rice (varieties TN1 and Delta) and *Leersia hexandra* over 24 h.

Table 2. Numbers of eggs laid in oviposition preference tests by individual mated females of rice and *Leersia* populations of *N. lugens* on *Leersia hexandra* and TN1 rice plants

Experiment	Rice population: no. of eggs laid on		Leersia population: no. of eggs laid on	
	rice	<i>Leersia</i>	rice	<i>Leersia</i>
1	0	0	0	45
2	28	17	0	70
3	9	21	0	42
4	10	0	0	0
5	21	0	0	69
6	0	0	0	46
7	8	14	0	41
8	15	0	0	58
9	21	0	0	81
10	38	0	0	96
11	0	0	0	10
12	18	0	0	76
Total	168	52	0	634

GENETIC STATUS

Studies to determine the genetic status of the two host-plant-associated populations consisted of interpopulation crosses and tests on viability of hybrids, mate choice experiments, and analyses of acoustic signals in courtship together with playback experiments.

Interpopulation crosses and viability of hybrids

Crosses were attempted between the two populations in the way described previously by Claridge *et al.* (1985). Each pair consisted of a 4–5 day old virgin male and a similar female. They were placed together in an 8" × 1" glass tube containing a rice seedling and a *Leersia* cutting. After 24 h the female was removed and the spermatheca dissected and examined for the presence of sperm. The results for reciprocal crosses and controls (Table 3) reveal that some barrier to mating exists between the populations, as heterogeneous combinations had a low rate of successful insemination.

Table 3. Percentage of successful inseminations in crosses between rice and *Leersia* populations of *N. lugens*

Population crosses	N	Percentage successful insemination
<i>Leersia</i> ♂ × <i>Leersia</i> ♀	25	80
<i>Leersia</i> ♂ × rice ♀	22	18
Rice ♂ × rice ♀	24	88
Rice ♂ × <i>Leersia</i> ♀	19	21

To investigate the fertility of population crosses and F_1 hybrids, single pairs of 4–5 day old virgin males and females were set up in cages containing a rice plant (TN1) for the rice \times rice crosses and a *Leersia* plant for the *Leersia* \times *Leersia* crosses. Interpopulation crosses and F_1 hybrid crosses from these were set up in cages containing plants of both host types. Ten replicates were made of each cross.

The insects were left in the cages for 1 week and then removed. The number of nymphs subsequently emerging from each experiment were counted. When no more nymphs emerged the plants were examined and the numbers of unhatched eggs were counted. Any crosses for which either no eggs or only unembryonated eggs were found were discarded from the analysis, since it was assumed that either one of the parents had died or fertilization had not taken place.

The results revealed no obvious genetic incompatibility between the two populations (Table 4). The crosses produced viable and fertile F_1 hybrids with no evidence of any hybrid breakdown.

To test the survival of F_1 hybrids, 50 first instars from F_1 crosses of the rice and *Leersia* populations were set up on either rice (TN1) or *Leersia* plants. The numbers surviving adult ecdysis on each host were noted (Table 5). The insects survived poorly on *Leersia*. Similar results were reported by Medrano & Heinrichs (1982) and Heinrichs & Medrano (1984).

Mate choice

In the above hybridization experiments males and females were confined with no choice of mate. In mate choice experiments, females from each host population were presented with a choice of two males, one from their own population and one from the other. Mating combinations were confirmed as successful by the presence of sperm in the female spermatheca after dissection. If mating had not occurred within 30 min, the experiment was terminated. The method is described by Claridge *et al.* (1985). In a total of 59 choices, no heterogametic matings were recorded (Table 6).

Table 4. Means and standard deviations for total egg production and percentage egg hatch resulting from crosses between rice and *Leersia* populations of *N. lugens* and F_1 hybrids between them

Cross	N	Egg production		Percentage egg hatch	
		Mean	s.d.	Mean	s.d.
Parental					
Rice \times rice	6	120	23	73	18
<i>Leersia</i> \times <i>Leersia</i>	8	209	53	77	14
Rice ♀ \times <i>Leersia</i> ♂	7	131	61	86	17
Rice ♂ \times <i>Leersia</i> ♀	7	180	90	84	18
F_1 hybrids					
Rice ♀ \times <i>Leersia</i> ♂	10	275	60	84	13
Rice ♂ \times <i>Leersia</i> ♀	7	112	69	66	16

Table 5. Percentage survival of F_1 hybrids between rice and *Leersia* populations of *N. lugens* on TN1 rice and *Leersia hexandra*

Hybrid population	Host plant	No. of individuals	Percentage survival
Rice ♀ × <i>Leersia</i> ♂	TN1	50	66
Rice ♀ × <i>Leersia</i> ♂	<i>Leersia</i>	50	0
<i>Leersia</i> ♀ × rice ♂	TN1	50	46
<i>Leersia</i> ♀ × rice ♂	<i>Leersia</i>	50	10

Mate recognition signals

Previous work (Ichikawa & Ishii, 1974; Ichikawa, 1979; Claridge *et al.*, 1985) has shown that *N. lugens* males and females communicate through substrate-borne vibrations. These acoustic signals are species specific and are the means by which conspecifics recognize one another for mating purposes (Claridge, 1983).

In rice *N. lugens* these signals have been demonstrated in the male to vary geographically in pulse repetition frequency (PRF). Success in experimental crosses between populations differing widely in PRF proved difficult (Claridge *et al.*, 1985). Female calls showed little variation between populations.

Signals of rice and *Leersia* populations were recorded and compared. The methods were as outlined in Claridge *et al.* (1984). The calls were similar in overall pattern (Fig. 4), but both sexes differed in PRF. The difference in PRF between the male calls of rice and *Leersia* populations was significant (Fig 5, $P < 0.001$). This difference is of the same order of magnitude as the extremes of the range of geographical variation within rice populations (Claridge *et al.*, 1985). The female calls differed even more strikingly in PRF between the two populations, with no overlap in the ranges of variation (Fig. 6). Females from all *Leersia* populations tested had very similar PRFs.

It might be argued that the differences in call were in some way direct responses to the different host plants. However, two females of the *Leersia* populations which were reared on rice (Delta) were recorded and found to have PRFs of 4.3 and 5.3 per second. These figures are well within the normal range of PRF for the *Leersia* population.

The PRFs of calls of both male (Fig. 5) and female (Fig. 6) F_1 and F_2 hybrids were intermediate between the two parental calls and differed significantly from each parent ($P < 0.001$). This strongly suggests a polygenic system of inheritance for the calls.

Table 6. Results of mate choice experiments between rice and *Leersia* populations of *N. lugens*

Females	Males	<i>N</i>	Homogametic matings	Heterogametic matings
<i>Leersia</i>	<i>Leersia</i> and rice	21	17	0
Rice	<i>Leersia</i> and rice	38	19	0

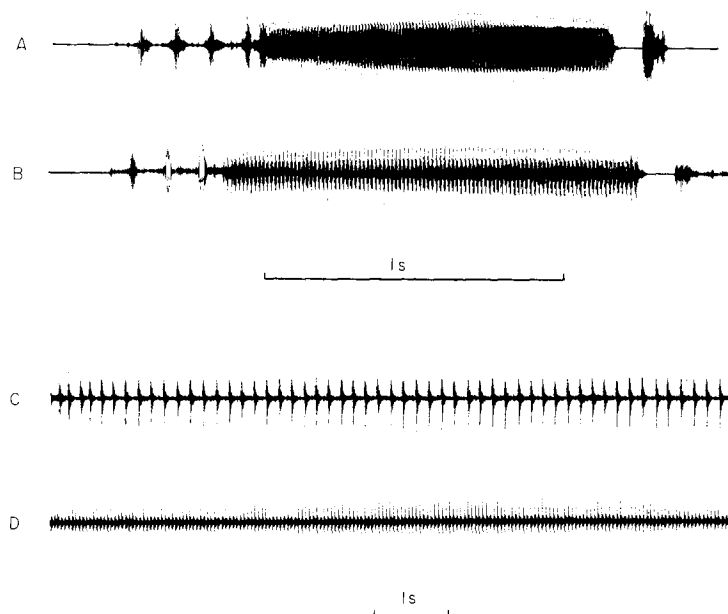


Figure 4. Oscillograms of sections of individual male and female calls from rice and *Leersia* populations of *N. lugens*. A, male *Leersia* population; B, male rice population; C, female *Leersia* population; D, female rice population. A and B to different scales from C and D.

Playback experiments

During mate choice experiments, acoustic monitoring showed that both males and females tended to respond to the other by answering, and males then moved towards the females. However, it was noted that insects seemed only to respond to calls from the opposite sex of their own population. To confirm the importance of these recognition signals, prerecorded songs of both populations were played back to individual insects and their responses noted. The apparatus used in the playback experiments has been described previously (Claridge *et al.*, 1985). A single 4–5 day old virgin female was placed on a rice seedling, allowed to

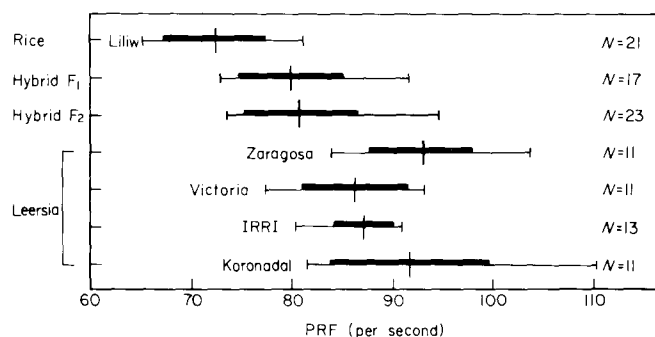


Figure 5. Pulse repetition frequencies (PRFs) of male calls from rice and *Leersia* populations and F₁ and F₂ hybrids between them. Vertical line represents mean for each population, thick bar one standard deviation on either side of mean, thin bar total range.

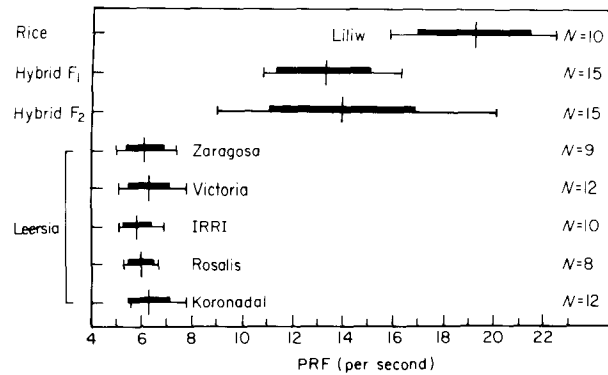


Figure 6. Pulse repetition frequencies (PRFs) of female calls from rice and *Leersia* populations and F₁ and F₂ hybrids between them. Conventions as in Fig. 5.

settle, and was then played 20 s bursts of male signals derived alternately from each population with 20 s gaps of no calling between each burst. Ten such bursts were played to each female, alternating the first call of the series between the rice and *Leersia* populations. The signals to which the females answered were scored and the percentage responding to each call was tabulated (Table 7).

For the male playback a slightly different scheme was used. It was essentially the same as the mate choice experiments (Claridge *et al.*, 1985), but instead of a female on the central plant, the prerecorded calls were played back into it. Again, 20 s bursts of female signals were used, alternating between the two populations and with 20 s pauses between calls. Ten such sequences were played to each male. By monitoring with the recording apparatus, it was possible to establish which male responded to each call. The percentages of males answering each call are summarized in Table 7.

Both males and females differentiated between calls from the two populations, but even these results mask the extent of the differentiation. Where individuals responded to calls from the other population, the responses were different in

Table 7. Percentages of males and females of rice and *Leersia* populations of *N. lugens* responding to playback of prerecorded calls of female and male calls respectively. Actual numbers of insects responding and total numbers given in parentheses

	Percentage responding to	
	Rice male call	<i>Leersia</i> male call
Female response		
Rice females	93 (14/15)	13 (2/15)
<i>Leersia</i> females	27 (4/15)	87 (13/15)
Percentage responding to		
	Rice female call	<i>Leersia</i> female call
Male response		
Rice males	77 (23/30)	30 (6/20)
<i>Leersia</i> males	17 (5/30)	90 (18/20)

degree from those of their own population. They responded much sooner and more vigorously and called for longer periods in response to calls from their own population. In addition, males began active searching behaviour in response to calls of their own females, something they rarely did to calls from the other population.

POPULATION CAGE EXPERIMENT

In order to test the efficiency of the isolating value of the call differences between the two populations, a mixed population cage experiment was established containing both *L. hexandra* and rice (TN1) plants. Fifty first instar nymphs of each of the rice and *Leersia* populations were placed in a small cage (40 × 10 cm) and allowed to develop to adults and to reproduce. Fifth instar female nymphs of the F₁ generation were removed from the cage and isolated. Their calls were recorded 4–5 days after adult ecdysis. Of 50 individual females recorded, only one had a PRF (14.1 per second) within the previously established range of F₁ hybrids (Fig. 6). The PRF of this individual also fell just inside the known range of the rice population and it could not therefore unequivocally be placed as a hybrid. Thus, even under the crowded conditions of a small cage, there is little evidence of natural hybridization between the two populations.

DISCUSSION AND CONCLUSIONS

The two sympatric plant-associated populations of brown planthopper described here must be very closely related. We have been unable to find any consistent morphological differences between them. In addition, our own crossing experiments and those of Medrano & Heinrichs (1982) and Heinrichs & Medrano (1984) showed that F₁ and F₂ hybrids may be produced, with little indication of hybrid inviability. Also, our preliminary studies on fertility suggest no obvious reduction in egg production and egg hatch in F₁ and F₂ hybrids.

Our data on feeding and food preferences of the two populations confirm the findings of Heinrichs & Medrano (1984), and Domingo *et al.* (1983), that the two host-associated populations show strong preferences for the plants from which they are derived and very poor survival on the other plant. The survival of a few individuals of the *Leersia* population on the rice variety Delta suggests that it might be possible to select a population which would be capable of living on it, in the same way that it has been possible to select rice populations to feed on previously resistant rice cultivars (Claridge & Den Hollander, 1982).

Mate choice experiments show that there is a behavioural barrier to interbreeding between the two populations and that when choice is available no heterogametic matings occur. Thus, though successful hybridization was frequently achieved if individual virgin males and females from the two populations were confined together, when given a choice insects from the two populations always mated with their own types. The barrier to mating is due to the differences in pulse repetition frequencies of both male and female calls described above. These barriers ensure that interpopulation crosses in the field are either very rare or non-existent.

Clearly, if field hybridization between these populations were common, the

differences between them would break down. No individuals from the four field populations which we have so far been able to record from the Philippines show any indication of hybrid influences and little evidence of hybridization was obtained from our population cage experiment.

Thus, the evidence from our studies of these populations, which are widely sympatric in the Philippines, suggests that they represent distinct biological species. There is conclusive evidence that they do not interbreed in the field and therefore are able to maintain their behavioural differences (see discussion in Claridge & Den Hollander, 1983). Since they do not interbreed they cannot be regarded as biological races or biotypes as suggested by Saxena *et al.* (1983a).

It would be especially interesting to search for similar *Leersia*-associated populations in other geographical regions. Recently, we obtained *Leersia*-feeding populations from northern Australia, but we have not yet completed studies on them. Clearly, the *Leersia* species in the Philippines should be given a specific name different to the rice species. However, we should prefer to await the results of investigations on similar populations in other regions before either proposing a new name or resurrecting an old one.

The discovery of closely related populations of phytophagous insects with different host plant preferences has interested evolutionists for many years. Thorpe (1930) gave one of the first general reviews of the subject and popularized the use of the term biological race for such populations. More recent authors (e.g. Bush, 1975; White, 1978) have advocated theories of the sympatric origin of species in 'parasitic' animals through the evolution of partially isolated host races as intermediate stages in speciation. Many ecologists have accepted that such evolutionary processes are common in animals with specialized food habits (e.g. Price, 1980; Southwood, 1978).

Despite the widespread acceptance of host races as important stages in the speciation process amongst phytophagous insects, few adequately studied examples are available. Indeed, as emphasized both by Futuyma & Mayer (1980) and Jaenike (1981), most examples which have been investigated in sufficient detail have been shown to be groups of distinct but morphologically similar species. The significance of sympatric speciation in the evolution of insect herbivores in our view has yet to be established.

No undisputed examples of host races amongst insect herbivores are known to us. Data on mate choice and species recognition signals have rarely been collected. Planthoppers and leafhoppers are extremely good animals on which to make such studies. They show varying degrees of host plant specificity. Also, they communicate primarily by acoustic signals which are especially suitable for detailed analysis and investigation (Claridge, 1983).

It is not possible to say how the rice and *Leersia* species discussed here arose, but there can be no doubt of their very close relationship. In such species host differences are the most obvious features and it is often tempting to conclude that host plant differentiation played an important role in speciation. However, the described differences in courtship signals function in species isolation and may have arisen when ancestral populations were geographically isolated. Indeed, our studies on geographical variation in calls of allopatric populations of the rice species throughout its range in Asia and Australasia (Claridge *et al.*, 1985) show similar differences for male calls to those we have described here for the two host-specific sympatric species. Thus, it is at least possible that the two

species evolved differences in courtship signals in allopatry and that the host plant differences should be regarded as secondary specializations.

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REFERENCES

- BUSH, G. L., 1975. Modes of animal speciation. *Annual Review of Ecology and Systematics*, 6: 339-364.
- CHENG, C. H., 1977. The possible role of resistant rice varieties in rice brown planthopper control. In *Rice Brown Planthopper*. Taiwan: Food and Technology Centre for the Asian and Pacific Region.
- CLARIDGE, M. F., 1983. Acoustic signals and species problems in the Auchenorrhyncha. In W. J. Knight, N. C. Pant, T. S. Robertson & M. R. Wilson (Eds), *Leafhoppers and Planthoppers of Economic Importance*. London: Commonwealth Institute of Entomology.
- CLARIDGE, M. F. & DEN HOLLANDER, J., 1980. The "biotypes" of the rice brown planthopper *Nilaparvata lugens*. *Entomologia experimentalis et applicata*, 27: 23-30.
- CLARIDGE, M. F. & DEN HOLLANDER, J., 1982. Virulence to rice cultivars and selection for virulence in populations of the brown planthopper *Nilaparvata lugens*. *Entomologia experimentalis et applicata*, 32: 213-221.
- CLARIDGE, M. F. & DEN HOLLANDER, J., 1983. The biotype concept and its application to insect pests of agriculture. *Crop Protection*, 2: 85-95.
- CLARIDGE, M. F., DEN HOLLANDER, J. & MORGAN, J. C., 1985. Variation in courtship signals and hybridization between geographically definable populations of the rice brown planthopper, *Nilaparvata lugens* (Stål). *Biological Journal of the Linnean Society*, 24: 35-49.
- DOMINGO, I. T., HEINRICHS, E. A. & SAXENA, R. C., 1983. Occurrence of brown planthopper on *Leersia hexandra* in the Philippines. *International Rice Research Newsletter*, 8: 17.
- FUTUYMA, D. J. & MAYER, G. C., 1980. Non-allopatric speciation in animals. *Systematic Zoology*, 29: 254-271.
- HEINRICHS, E. A. & MEDRANO, F. G., 1984. *Leersia hexandra*, a weed host of the brown planthopper, *Nilaparvata lugens* (Stål). *Crop Protection*, 3: 77-85.
- ICHIKAWA, T., 1979. Studies on the mating behaviour of four species of auchenorrhynchous Homoptera which attack the rice plant. *Memoirs of the Faculty of Agriculture, Kagawa University*, 34: 1-60.
- ICHIKAWA, T. & ISHII, S., 1974. Mating signal of the brown planthopper *Nilaparvata lugens* Stål (Homoptera: Delphacidae): vibration of the substrate. *Applied Entomology and Zoology*, 9: 196-198.
- JEANIKE, J., 1981. Criteria for ascertaining the existence of host races. *American Naturalist*, 117: 830-834.
- MEDRANO, F. G. & HEINRICHS, E. A., 1982. *Leersia hexandra* as weed host for the brown planthopper. *International Rice Research Newsletter*, 7: 15-16.
- MOCHIDA, O. & OKADA, T., 1971. A list of the Delphacidae (Homoptera) in Japan with special reference to host plants, transmission of plant diseases, and natural enemies. *Bulletin of the Kyushu Agricultural Station*, 15: 737-843.
- MOCHIDA, O. & OKADA, T., 1979. Taxonomy and biology of *Nilaparvata lugens* (Hom., Delphacidae). In *Brown Planthopper; Threat to Rice Production in Asia*. Los Baños, Philippines: IRRI.
- PATHAK, P. K. & HEINRICHS, E. A., 1982. Selection of biotype populations 2 and 3 of *Nilaparvata lugens* by exposure to resistant rice varieties. *Environmental Entomology*, 11: 85-90.
- PRICE, P. W., 1980. *Evolutionary Biology of Parasites*. New Jersey: Princeton University.
- SAXENA, R. C. & BARRION, A. A., 1983. Cytogenetic variation between *Nilaparvata bakeri* (Muir) and *Nilaparvata lugens* (Stål) planthoppers. *International Rice Research Newsletter*, 8: 12-13.

- SAXENA, R. C. & BARRION, A. A., 1984. Comparative cytology of brown planthopper populations infesting *Leersia hexandra* Swartz and rice in the Philippines. *International Rice Research Newsletter*, 9: 23-24.
- SAXENA, R. C. & PATHAK, M. D., 1979. Factors governing susceptibility and resistance of certain rice varieties to the brown planthopper. In *Brown Planthopper: Threat to Rice Production in Asia*. Los Baños, Philippines: IRRI.
- SAXENA, R. C. VELASCO, M. V. & BARRION, A. A., 1983a. Morphological variations between brown planthopper biotypes on *Leersia hexandra* and rice in the Philippines. *International Rice Research Newsletter*, 8: 3.
- SAXENA, R. C., VELASCO, M. V. & BARRION, A. A., 1983b. Interspecific hybridization between *Nilaparvata lugens* (Stål) and *Nilaparvata bakeri* (Muir) collected from *Leersia hexandra* Swartz. *International Rice Research Newsletter*, 8: 13-14.
- SOUTHWOOD, T. R. E., 1978. The components of diversity. In Mound, L. A., Waloff, N. (Eds), *The Diversity of Insect Faunas, Symposium of the Royal Entomological Society of London*, 9: 19-40.
- THORPE, W. H., 1930. Biological races in insects and allied groups. *Biological Review*, 5: 177-212.
- WHITE, M. J. D., 1978. *Modes of Speciation*. San Francisco: W. H. Freeman.