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VIRULENCE TO RICE CULTIVARS AND SELECTION FOR VIRULENCE IN POPULATIONS OF THE BROWN PLANTHOPPER *NILAPARVATA LUGENS*

M. F. CLARIDGE and J. DEN HOLLANDER

Department of Zoology, University College, Cardiff, CF1 1XL, Wales U.K.

Biotype 1, 2 and 3 populations from the Philippines were selected for 11 generations on 3 standard rice cultivars, TN1 (no gene for resistance), Mudgo (Bph 1), and ASD7 (bph 2). Percentage survival, weight of newly emerged ♀♀ and time taken for 50% of survivors to become adults were scored for each line at each generation and combined into a single index. Virulence was assessed before and after 10 generations of selection by measuring weight change and weight of honeydew produced by ♀♀ in 24 hr. Performance and virulence of all lines changed markedly towards the normal "biotype" on each variety. Thus biotypes were labile and effectively converted one to another.

A population from Australia first responded to TN1 as resistant. After selection it resembled Philippine biotype 1 in virulence to TN1.

It is concluded that individual *N. lugens* are variable in feeding performance and populations are capable of rapid response to selection. The use of the term biotype is therefore misleading.

KEY WORDS: Biotype — Brown Planthopper — *Nilaparvata lugens* — Honeydew — Population — Rice — Resistant plant varieties — Selection — Variation — Virulence.

Resistant varieties have been widely used to combat pests and diseases of agricultural crops. Four genes conferring resistance to the Brown Planthopper, *Nilaparvata lugens* (Stål), have been identified in rice and incorporated into high yielding varieties (Khush, 1979). However, populations of the insect have developed in parts of Asia (I.R.R.I., 1975; 1976; 1979a; 1979b) which can overcome the resistance of some of the varieties which incorporate some of these genes. These populations have been termed biotypes and numbered with respect to the genes which cause resistance in the varieties which they are able to destroy (Table I).

Considerable effort is being devoted to developing strategies such as the sequential release of resistance genes, the pyramiding of resistance genes in one variety, the use of multilines and moderately resistant varieties in an attempt to control the Brown Planthopper and avoid the development of virulent populations of the pest (Khush, 1979).

Most of the studies on the properties and development of the biotypes of *N. lugens* have been made at the International Rice Research Institute (I.R.R.I.), Philippines, using insects derived from local field populations in Luzon (summarised by Pathak & Khush, 1979). Thus biotypes 1, 2 and 3 refer to populations or parts of populations which are sympatric and differ only in their ability to damage rice varieties which incorporate no gene for resistance, Bph 1 gene and bph 2 gene, respectively. Similar and additional biotypes have been identified in many other parts of Asia including India, Indonesia, Japan, Korea, Solomon Islands, Sri Lanka, Taiwan and Thailand (I.R.R.I., 1979b).

Previously, we demonstrated considerable individual variation within the Philippine biotypes and an overlap between them in virulence on the varieties used to separate them

TABLE I

Possible biotypes of N. lugens *showing rice variety susceptible to each and associated nomenclature and dominance status of resistance genes of host plant. TN1 said to be susceptible to all biotypes. After Lakshiminarayana & Khush (1977) and Khush (1979)*

Biotype	Rice variety	Resistance gene
1	TN1	None identified
2	Mudgo	Bph 1 (dominant)
3	ASD7	bph 2 (recessive)
4	Rathuheenati	Bph 3 (dominant)
5	Babawee	bph 4 (recessive)

(Claridge & Den Hollander, 1980). Similar results have since been obtained independently by Sogawa (1981). Crosses between the biotypes yielded F_1 and F_2 generations with virulence intermediate to the parentals and gave no simple segregation ratio in the F_2 (Den Hollander & Pathak, 1981). These results suggested that virulence in the Brown Planthopper is continuously distributed and determined by a system of polygenes. The biotypes then represent different segments of the continuous distribution selected by particular rice varieties. The polygenic nature of virulence ensures the presence of considerable genetic variation in each biotype since a particular level of virulence to a particular rice variety may be achieved by various combinations of genes. We thus concluded that the use of the term biotype in this species was misleading and concealed the true nature of variation in virulence in field populations and that such terminology might be even more misleading when applied to geographically separate or allopatric populations (Claridge & Den Hollander, 1980).

In this paper we present the results of further studies on the virulence of *N. lugens* populations and the ways in which they respond to selection on standard rice cultivars. We include here data on Philippine biotypes 1, 2 and 3 and also on a previously unstudied allopatric population from Queensland, Australia.

MATERIALS AND METHODS

The Philippine biotype populations studied here were subcultures from cultures maintained at I.R.R.I. In addition, a population from the Burdekin River region, Queensland, Australia, imported to Britain by Mr. E. Harris, Centre of Overseas Pests Research, was used. All cultures were maintained in a temperature-controlled glasshouse at Cardiff on rice varieties TN1 (for biotype 1), Mudgo (biotype 2), ASD7 (biotype 3) and Towada (Australian population).

Selection experiments were made using a scheme slightly modified from Den Hollander & Pathak (1981). For the biotype populations, ♀♀ from each were allowed to oviposit on the usual host (control) variety and the resulting offspring separated into lines on 35-day-old TN1, Mudgo and ASD7. Within each line 4 replicates of 25 first-instar nymphs were placed on separate plants each in a mylar cage and left to develop. After each generation the first 10 adult ♂♂ and ten adult ♀♀ to emerge in each line were placed on a new plant of the variety being used for selection in order to produce nymphs for the next generation. Each selection experiment was continued for 11 generations.

Three measures of success in development for each generation were scored:

(A) % survival of original 25 nymphs to adult stage, (B) weights of the first 10 ♀♀ to emerge (taken within 12 hr of emergence), (C) time taken for 50% of the survivors to reach adult ecdysis. This involved daily monitoring until all nymphs had either died or became adult. These 3 measures of success were also combined into a single index in an attempt to give a realistic appraisal of the performance of the selected lines compared to the controls (i.e., biotype 1 on TN1, biotype 2 on Mudgo, and biotype 3 on ASD7). The combined index was given by:

$$100/1 \times \frac{a/b \times c/d}{e/f}$$

where for each variety % survival on selected variety = a, on control = b (*e.g.* biotype 1 on TN1); mean weight on selected variety = c, on control = d; and time taken for 50% survivors to reach adult stage on selected variety = e, on the control = f. This combined index has the advantage of relating the performances on selected lines to that of the control line standardised at 100.

In addition to scoring each generation for the 3 above-described measures of success in development, the virulence of each line after 10 generations of selection was assessed by measuring weight change and honeydew production of individual insects. In order to do this newly emerged adult ♀♀, from 0—12 hr post-ecdysis, were starved for 4 hr by enclosing them in a clear perspex box with moist filter-paper and kept in a heated glasshouse. They were then weighed and placed in a parafilm envelope, which was attached to the culm of a living 35—40-day-old rice plant. After 24 hr in a constant temperature room (25° and 12 hr light), the insect was removed and weighed again. Any honeydew produced during the 24-hr-period collected in the envelope. This was cut off, weighed, blotted dry and weighed again to give the weight of honeydew (Claridge & Den Hollander, 1980). The controls (those kept for 10 generations of the selection procedure on their normal host variety) were tested for virulence on all 3 varieties while the other lines were tested on the variety on which they

had been selected and also again on the original variety from which they derived before selection.

The Australian population was treated in essentially the same way as the Philippine biotype populations, except that it was selected only on TN1 and after 10 generations tested for virulence on TN1 and Towada, the variety on which it is normally cultured in Cardiff. In addition, virulence tests of the population were also made using the weight change and honeydew production techniques on the 5 rice varieties TN1, Mudgo, ASD7, Towada and Delta.

On occasions in some selected lines survival was very low. To prevent complete loss of a line, when survival fell below 20% the remaining survivors were transferred back to their original host variety to provide nymphs for the next generation. This happened for the Australian line on TN1 in generations 1, 3 and 5 and with biotype 1 on ASD7 in generation 2.

RESULTS

Philippine biotype populations. The results of the selection experiments are presented in 2 forms. The first (Table II) gives the changes in (A) % survival, (B) weight in ♀♀ at emergence, and (C) time taken for 50% of the survivors to become adults at each generation. Second, the values for the combined index of these 3 variables were plotted for the 3 lines on each of the 3 standard cultivars, TN1, Mudgo and ASD7 (Fig. 1).

In all experiments lines on resistant varieties improved dramatically after 4 or 5 generations of selection. After 10 generations of selection

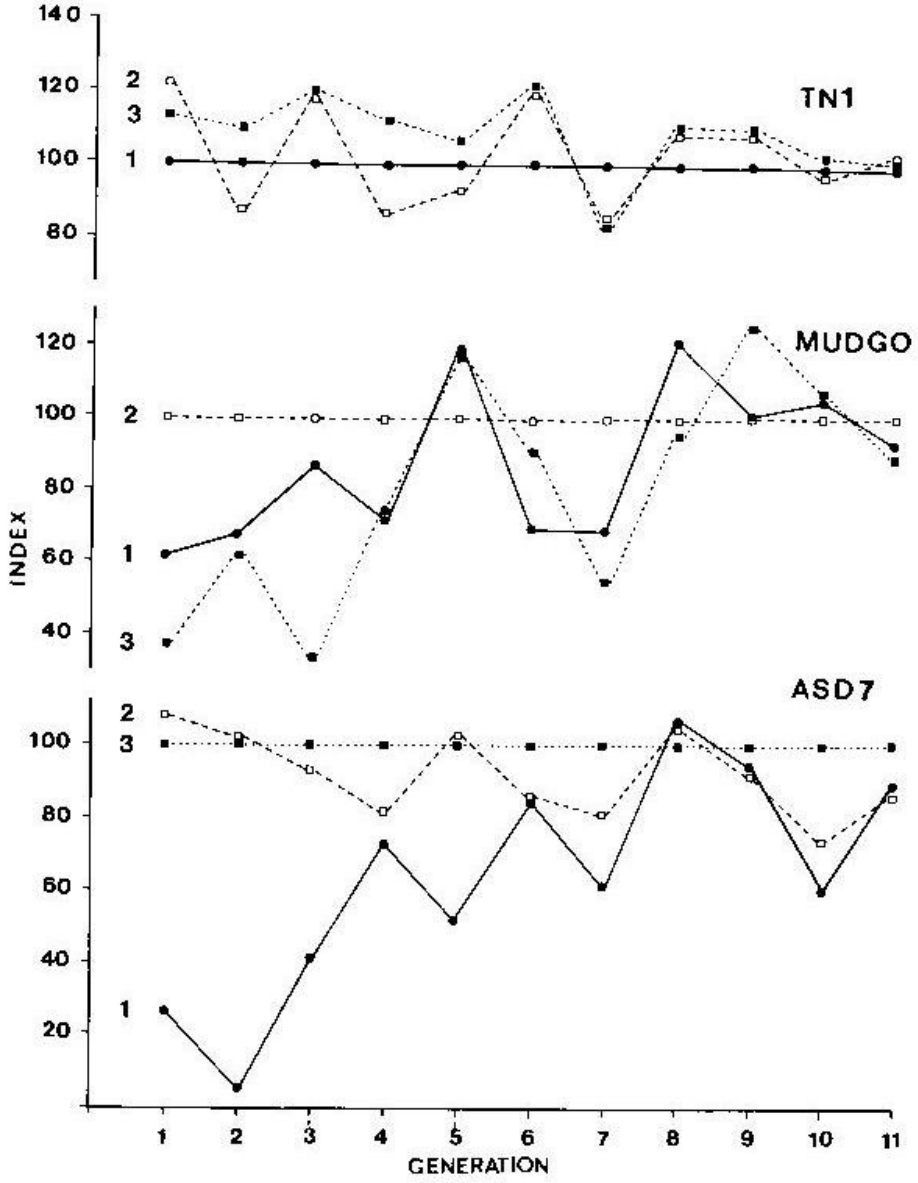

Fig. 1. Combined index of % survival, weight change and time taken for 50% survivors to become adult of Philippine *N. lugens* biotypes, 1, 2 and 3 for 11 generations of selection of TN1, Mudgo and ASD7.

TABLE II

N. lugens *Philippine biotype populations selected on TN1, Mudgo and ASD7, and Australian population selected on TN1. Means and s.d. for % survival (A), and weight of first 10 ♀♀ to emerge (B), and time taken for 50% population to become adult (C), for each of 11 generations of selection*

			Generation																					
			1		2		3		4		5		6		7		8		9		10		11	
Bio-type.	variety.		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
		A	90	3.5	81	14.5	80	4.0	82	6.0	93	5.2	86	4.5	86	8.2	80	103	79	10.4	85	6.8	78	6.6
1	TN1	B	2.08	0.18	3.19	0.37	2.41	0.34	2.69	0.61	2.53	0.72	2.16	0.34	2.45	0.47	2.15	0.41	2.30	0.39	2.41	0.31	2.31	0.22
		C	13		13		12		13		12		12		13		14		15		14		14	
		A	74	7.2	82	4.5	80	14.4	85	6.6	95	6.6	76	5.7	74	8.2	86	4.5	73	12.8	83	7.1	89	5.0
1	Mudgo	B	1.84	0.37	2.05	0.20	2.23	0.20	2.03	0.14	1.08	0.14	1.95	0.19	2.00	0.13	2.60	0.34	2.36	0.27	2.32	0.23	2.18	0.35
		C	14		14		14		13		14		16		15		14		16		15		14	
		A	40	4.9	—		68	4.04	83	11.9	55	7.7	68	3.3	72	8.6	81	9.5	79	8.2	73	7.7	80	11.8
1	ASD7	B	1.51	0.30	—		1.92	0.36	1.96	0.34	1.95	0.18	2.19	0.26	2.13	0.28	2.32	0.28	2.30	0.28	2.06	0.25	2.23	0.29
		C	16		—		15		13		16		15		15		14		15		16		16	
		A	93	3.3	89	14.5	88	7.5	81	14.2	89	1.7	90	4.5	87	1.7	86	8.7	75	6.8	85	10.3	88	4.9
2	TN1	B	2.30	0.17	2.54	0.49	2.59	0.41	2.13	0.28	2.43	0.35	2.40	0.30	2.24	0.21	2.25	0.14	2.44	0.28	2.40	0.38	2.25	0.19
		C	12		13		12		12		12		12		14		14		14		14		15	
		A	88	4.9	94	6.0	91	7.1	85	7.7	82	6.0	87	1.7	88	4.9	79	6.6	77	3.3	82	8.7	88	10.2
2	Mudgo	B	2.54	0.16	2.75	0.26	2.22	0.35	2.55	0.27	1.95	0.16	2.02	0.2	0.19	2.63	0.41	2.26	0.31	2.30	0.33	2.22	0.24	14
		C	14		13		14		12		14			14		15		16		15		14		73
		A	82	11.8	98	2.0	90	4.5	84	5.7	82	2.0	9.5	81	3.3	78	2.0	70	18.2	81	7.1	73	3.3	2.04
2	ASD7	B	2.45	0.36	2.43	0.31	2.42	0.34	2.23	0.27	2.25	0.28	0.25	2.39	0.13	2.61	0.30	2.37	0.23	2.34	0.38	2.20	0.22	15
		C	15		13		13		14		14			14		15		14		16		15		93
		A	91	3.3	95	3.3	85	7.2	95	6.6	95	1.7	4.4	83	10.3	84	6.3	78	2.0	85	3.3	90	8.2	2.49
3	TN1	B	2.18	0.20	2.89	0.45	2.67	0.39	2.35	0.34	2.69	0.47	0.37	2.29	0.20	2.31	0.28	2.39	0.29	2.54	0.33	2.14	0.26	12
		C	12		13		12		12		12			14		14		14		14		15		86
		A	53	20.8	71	5.2	40	12.3	82	4.5	87	11.8	2.0	58	10.0	82	7.2	78	10.8	84	7.5	89	8.2	1.98
3	Mudgo	B	1.95	0.29	2.13	0.23	1.77	0.49	2.18	0.59	2.17	0.15	0.20	2.17	0.30	2.32	0.20	2.57	0.30	2.52	0.42	2.29	0.29	15
		C	18		14		15		13		14			16		15		15		16		16		80
		A	78	6.0	88	4.9	91	5.2	88	5.7	89	4.4	6.3	95	4.4	81	8.7	82	3.5	92	3.3	85	1.7	2.02
3	ASD7	B	2.09	0.26	2.64	0.22	2.56	0.22	2.24	0.24	2.15	0.40	0.27	2.28	0.41	2.28	0.21	2.18	0.24	2.33	0.33	0.22	2.14	0.27
		C	13		13		13		12		13		14		13		14		14		14		15	
		A	—		34	25.3	—		50	8.2	—		35	8.2	50	27.5	82	8.2	78	6.0	81	1.9	81	9.5
Aust.	TN1	B	—		1.38	0.19	—		1.67	0.11	—		1.40	0.14	1.95	0.33	2.40	0.19	2.50	0.23	2.37	0.47	2.35	0.28
		C	—		15		—		16		—		17		16		15		14		14		15	

all lines were performing similarly regardless of the variety on which they were selected or from which they were derived.

Of the 3 variables measured at each generation, % survival showed the most satisfactory separation of populations in the early generations. However, taking account of % survival alone, biotype 1 on Mudgo appeared to survive well in the early generations (Table II), but the combined index showed it to do less well than biotype 2 on Mudgo (Fig. 1). Biotype 2 on ASD7 did well in the initial generations using both % survival and the combined index, but honeydew and weight change data (presented below) indicate that it fed less on ASD7 before selection than on Mudgo, or on ASD7 after selection.

The results of the honeydew and weight change measurements are presented in Table III. The differences between the responses on the 3 varieties for each of the 3 control lines (boxed in solid lines, Table III) were significant ($p < 0.0001$). Although these differences were very significant, the standard deviations were large, indicating great variation within each population. After 10 generations of selection, all lines initially started on a resistant variety had mean honeydew and weight gains comparable to those of the biotype normally on the resistant variety. The 3 lines selected on Mudgo and tested on Mudgo did not differ significantly either for honeydew production or weight gain (horizontal cross-hatched, Table III). The lines selected and tested on ASD7 did not differ significantly for honeydew production, but did show a significant difference for weight gain ($p = 0.02$) (diagonal cross-hatch). The lines selected on TN1 and tested on TN1 showed no significant difference for honeydew ($p = 0.06$), but a just significant weight gain ($p = 0.04$). However, the importance of these results lies in the obvious trends of improvement in performance by lines on resistant varieties after only 10 generations of selection, rather than in precise levels of significance.

The performance of each biotype on its original host variety after 10 generations of selection on either a susceptible or a resistant variety (boxed in broken lines) did not show a dramatic loss of virulence, although in all experiments, except biotype 1 selected on Mudgo, there was a slight decline. The differences in honeydew and weight change for biotype 2 on Mudgo after selection on the 3 standard varieties were not significant, but those for biotype 1 on TN1 (honeydew $p = 0.003$, weight change $p = 0.003$) and biotype 3 on ASD7 ($p = 0.006$ and 0.04) were significant.

Australian population. The most remarkable result was the reaction of the Australian population to TN1, which has been considered universally susceptible to feeding by *N. lugens* (Khush, 1979; Seshu & Kauffman; 1980). When first imported to Cardiff we had great difficulty in maintaining cultures until we transferred them either to the French variety Delta or the Japanese Towada.

Measures of honeydew production by ♀♀ on 5 cultivars show great individual variation

TABLE III

Means and s.d. for mg honeydew produced (A) and weight change in 24 hr (B) of newly emerged ♀♀ Philippine N. lugens *biotypes, each selected for 10 generations on TN1, Mudgo and ASD7. Standard biotype reactions: boxed in solid lines. Columns outlined by broken lines: results of selecting same initial population on the 3-test varieties. Populations from different biotypes, but selected on same variety, shown in same hatching in same horizontal rows*

SELECTED ON		BIOTYPE 1 TESTED ON: TN1 MEAN	TN1 SD	MUDGO MEAN	MUDGO SD	ASD7 MEAN	ASD7 SD	BIOTYPE 2 TESTED ON: TN1 MEAN	TN1 SD	MUDGO MEAN	MUDGO SD	ASD7 MEAN	ASD7 SD	BIOTYPE 3 TESTED ON: TN1 MEAN	TN1 SD	MUDGO MEAN	MUDGO SD	ASD7 MEAN	ASD7 SD
TN1	A	26	15	4	3	4	3	17	8	9	8			15	10			7	7
	B	32	19	-10	6	-10	5	22	27	8	27			18	16			9	16
MUDGO	A	14	8	-6	6			16	9	-6	4	4	3			-7	4	8	7
	B	27	20	-8	20			34	18	-20	22	-4	9			-12	19	16	24
ASD7	A	10	9			12	9			7	7	12	8	12	11	3	2	12	13
	B	16	22			21	18			15	21	34	24	12	17	1	8	23	17

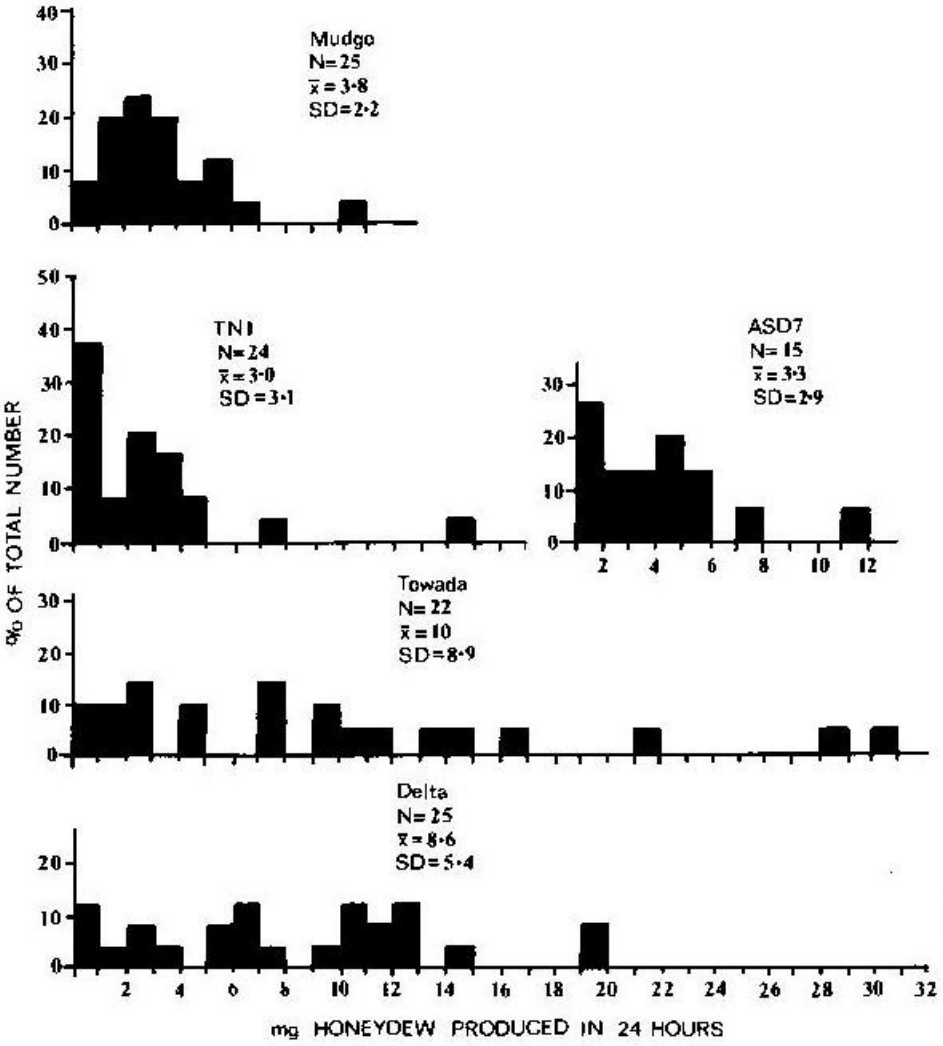

Fig. 2. Honeydew produced by individuals of Australian population of *N. lugens* tested on Delta, Towada, TN1, Mudgo and ASD7.

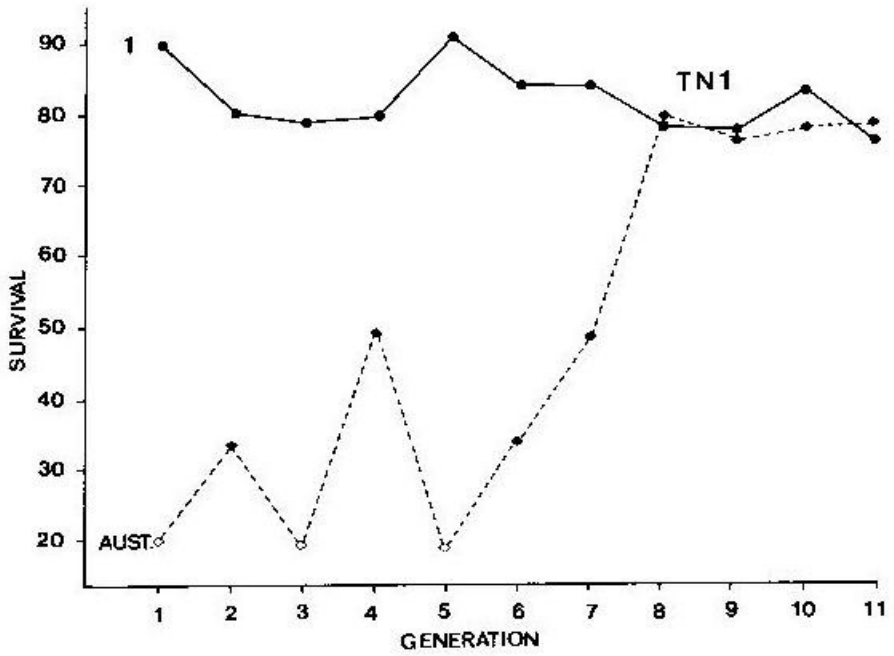

Fig. 3. Percentage survival of *N. lugens* Australian population and Philippine biotype 1 population, each selected on TN1 for 11 generations.

(Fig. 2). Most individuals produce little honeydew (less than 6 mg/24 hr) on TN1, Mudgo and ASD7, and indeed there is no significant difference in the response to those varieties. The results for performance on Delta and Towada closely resemble similar data for the Philippine biotypes on their normal host varieties (Claridge & Den Hollander, 1980).

Results of the selection experiment on the Australian population were even more striking than those of the biotypes (Fig. 3, Tables II & IV). Only with great difficulty could the line be maintained on TN1 in the early generations, but after 10 generations the performance of the population approached that of Philippine biotype 1 on TN1 although honeydew production and weight gain were significantly different ($p = 0.03$ and 0.01, respectively) (Tables III & IV).

CONCLUSIONS

It may be concluded from the experiments on both the Philippine biotypes and the Australian population that performance on different varieties is both very variable within populations and also susceptible to selection over only a few generations to give populations with very different patterns of virulence. Thus what are often termed distinct biotypes may be converted one to another with little difficulty. Also, from our present virulence data (Table III) and from those previously published (Claridge & Den Hollander, 1980), it is clear that there is a relationship between amount of honeydew produced and weight change on different varieties. However, amount of honeydew produced for the same weight change differs between varieties, for example biotype 2 on Mudgo and biotype 3 and ASD7. Honeydew produced is generally thought to reflect food intake (Sogawa, 1977), so that such differences may indicate differences either in the efficiency of food utilisation by different populations or in the quality of different varieties as food.

TABLE IV

Means and s.d. for mg honeydew (A) and weight change (B) in 24 hr of ♀♀ N .lugens *from Australia after 10 generations of selection on Towada and TN1*

Selected on		Australian population tested on: TN1 Mean	TN1 S.D.	Towada Mean	Towada S.D.
TN1	A	11.0	10.3	20.6	15.4
	B	16.2	21.5	10.0	26.0
Towada	A	3.0	3.2	10.0	8.7
	B	5.7	15.2	18.0	19.3

DISCUSSION

Previously we have argued against the assigning of Brown Planthopper populations to biotypes as this implies marked and clear-cut differences between them and presumes a gene for gene relationship between virulence and resistance (Claridge & Den Hollander, 1980; Den Hollander & Pathak, 1981).

All our evidence indicates that the criterion used to separate the biotypes — virulence on different varieties — is an extremely variable character, probably controlled by a system of polygenes. We suggested previously that because of the variability of each biotype, such populations would respond rapidly to selection by new resistant rice varieties. The observations reported here confirm this prediction and are supported by other published work (Kaneda & Kisimoto, 1979; I.R.R.I., 1979a). It is now clear that it is possible to convert one biotype into another after only a few generations of selection, thus strengthening the argument for discontinuing the use of the term at least in any strict sense of numbering or naming within this species.

A particular problem with the use of the term biotype for such variable populations as are found in *N. lugens* arises when comparing geographically isolated populations. For example, the population capable of surviving on TN1 from Australia and derived from our selection experiment resembles Philippine biotype 1 closely in virulence. However, we know from hybridisation and behaviour studies (Claridge *et al.*, 1982) that they are quite distinct in many features. It would be misleading therefore to give them the same name or biotype number.

The high level of resistance of TN1 to the Australian population of Brown Planthopper questions the assumption of the use of TN1 as a universally susceptible variety, lacking any resistance genes. It indicates that the level of resistance of a variety to a particular population depends to a large extent upon the history of that population, particularly the variety to which it has been exposed in the relatively recent past.

It has been stated often that virulence in a population is developed at the expense of fit-

ness and therefore that natural selection should elimenate unnecessary virulence from a population (Van der Plank, 1963, 1976). This assumption is important as it forms the theoretical basis for the multiline use of varieties and the recycling of resistant varieties. In all of our experiments, except for biotype 1 selected on Mudgo, after selection on either a resistant variety or on a susceptible variety lacking resistance genes, virulence to the original variety did decline (Table III). However, this decline was never very great, certainly not enough to regard the original variety as being resistant. Thus, it appears that virulence is not readily lost once acquired. If this is generally so, then the strategy of recycling resistant cultivars will not be useful in minimizing the impact of *N. lugens*.

Also from our results it appears that virulence may be compounded by successive selection on different resistant cultivars. For example, Philippine biotype 2, which is normally virulent to Mudgo (with Bph 1 gene for resistance), after 10 generations of selection on ASD7 (with bph 2), performed on ASD7 like biotype 3. However, when tested back on Mudgo the population retained its virulence. Thus this population had compounded the characteristics of biotypes 2 and 3. It is interesting that similar results have been reported for field populations in Taiwan (Cheng & Chang, 1979) and in the laboratory at I.R.R.I. (Pathak & Khush, 1979). Again if this compounding of virulence is generally applicable, then control strategies using multiline-resistant varieties may not be expected to succeed in combating *N. lugens*.

Since the response of *N. lugens* populations to selection in our experiments was rapid, even for highly inbred laboratory cultures, it might be expected that more variable field populations might show more dramatic responses. However, under field conditions some varieties have maintained their resistance over several years. For example, IR36 (resistance based on bph 2) has retained its field resistance in the Philippines for 6 years despite the earlier failure of IR26 (based on bph 1) after only 2 years (Heinrichs, pers. comm.). With up to 10 generations possible each year on 3 or 4 successive crops, the survival of IR36 under intense selection is surprising. It may be explained partly by ecological factors, including parasitism and predation. These may operate more intensely on such a cultivar since laboratory populations of *N. lugens* with similar patterns of virulence show reduced fecundity on varieties incorporating bph 2 (Sogawa, 1981). Additionally, in the field, migration from populations developing on different varieties may serve to dilute the selection for virulence operating on a particular crop. Thus, the evolution of virulence might be expected to occur most rapidly in large areas of monoculture of a single variety, whereas it would be much slower where several different varieties are grown in close proximity or in rotation. Relevant data might be forthcoming if it were possible to monitor the field virulence of insects on one crop in one area over a complete growing season.

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RÉSUMÉ

Virulence de populations de Nilaparvata lugens *sur des cultivars de riz et évolution de ce caractère au cours de sélections*

Les caractéristiques de la virulence des populations, appelées "biotypes" 1, 2 et 3 de *N. lugens* des Philippines, ont été précisées sur des variétés de riz contenant respectivement, aucun gêne de résistance (TN1), Bph 1 (Mudgo) et bph 2 (ASD7). Ces populations ont été sélectionnées pendant 11 générations sur chacune de ces variétés et comme témoins sur des variétés hôtes normales. Pour chaque génération, les performances de chaque lignée ont été précisées par le taux de survie, le poids des adultes à l'émergence et le temps nécessaire à l'obtention de 50% d'adultes. Ces critères ont été combinés pour fournir un indice de performance. La virulence des lignées sur les 3 variétés standard a été examinée après 10 générations, en mesurant le poids de miellat

produit et le changement de poids de femelles en 24 h.

Dans toutes les expériences, les performances et la virulence de chaque lignée ont évolué nettement vers celles du "biotype" de chaque variété de riz. Il est ainsi possible de transformer un biotype en un autre. Quand elles ont été sélectionnées sur une variété différente et testées à nouveau sur leur hôte habituel, la plupart des populations n'ont montré qu'une faible diminution de leur virulence originelle. Ceci est la preuve de la complexité des caractéristiques des biotypes.

Une population allopatrique de Queensland (Australie) a d'abord réagi à TN1 (considéré généralement comme intégralement sensible) comme à une variété résistante. Après 11 générations de sélection, elle a ressemblé au biotype 1 Philippin par ses performances et sa virulence sur TN1.

On peut en conclure que les individus de *N. lugens* ont des performances alimentaires très hétérogènes. La variabilité est importante et les populations peuvent répondre rapidement à une sélection pour les caractères de virulence. Ainsi le terme de biotype dans un sens étroit peut conduire à des malentendus sur la nature de la variabilité dans cette espèce.

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