

Inheritance of durable adult plant resistance to stripe rust (*Puccinia striiformis* f. sp. *tritici*) in ‘Otane’ wheat (*Triticum aestivum*)

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Abstract Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici*, is an important disease of wheat (*Triticum aestivum*) in New Zealand and throughout the world. The wheat cultivar ‘Otane’ carries durable resistance to stripe rust that has remained effective in New Zealand since the cultivar’s release in 1984. To determine the mode of inheritance of this durable adult plant resistance to stripe rust, ‘Otane’ was crossed with the stripe rust susceptible ‘Tiritea’, and 140 F₁-derived double haploid (DH) lines were evaluated in glasshouse and field experiments for their reaction to the stripe rust pathogen. Transgressive segregation occurred, indicating that both cultivars possess resistance

genes. Genetic gain as a percentage of the moderately resistant parent for the most resistant 5% of the DH lines was statistically significant (83% and 68% in the glasshouse and field experiments, respectively). The distribution of DH lines assessed through infection types (IT) in the glasshouse supported a digenic ratio, whereby resistance genes from both parental cultivars act additively to produce resistant DH lines. Moderately resistant DH lines were produced when only the gene from ‘Otane’ was present, and the absence of the ‘Otane’ gene produced susceptible DH lines. The distribution of reaction of DH lines in the field fitted a trigenic ratio. This model proposed that resistant DH lines were produced when at least two genes from both parents interact; moderately resistant DH lines were produced when either two genes (one modifier) or one gene from ‘Otane’ were present, and susceptible DH lines were produced when either resistance genes from both parents or the major gene from ‘Otane’ were absent. Segregation of final disease severity measured in the field also supported the segregation of three genes in the DH population. The demonstrated durability of stripe rust resistance in ‘Otane’ in New Zealand, which is influenced by environment, may be the result of a combination of resistance alleles at two loci at least.

Keywords *Triticum aestivum*; durable disease resistance; double haploid; transgressive segregation; genetic models

INTRODUCTION

Stripe rust (also called yellow rust), caused by *Puccinia striiformis* West. f. sp. *tritici*, is generally considered one of the most damaging diseases of wheat (*Triticum aestivum* L.) throughout the world, especially in moist and cool environments. This disease can cause up to a 50% yield reduction in an infected crop due to the shrivelling of grains and reduction in the number of spikes, while in extreme situations losses can reach 100% (Roelfs et al. 1992).

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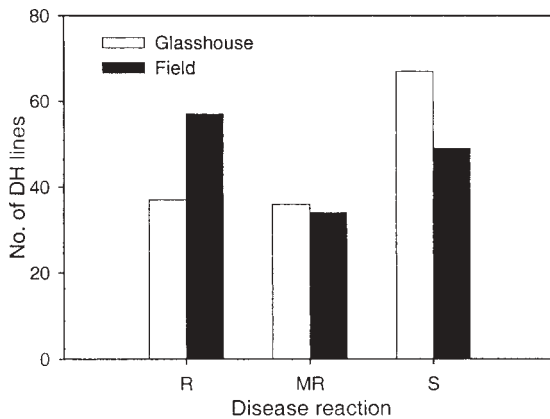


Fig. 1 Distribution of adult plant stripe rust reactions which were resistant (R), moderately resistant (MR), and susceptible (S) from the double haploid (DH) lines in the glasshouse and field experiments. Data were obtained from a 'Tiritea' × 'Otane' wheat (*Triticum aestivum*) population inoculated with pathotype 106E139A⁺ of *Puccinia striiformis* f. sp. *tritici*.

In New Zealand, where yield losses of up to 60% in susceptible cultivars have been reported (Beresford 1982), stripe rust has become a threat to the wheat industry because of the occurrence of new virulent races (Cromey 2000). Stripe rust is controlled primarily by genetic resistance or the use of fungicide chemicals and, to a lesser extent, by cultural practices. Of these, breeding for disease resistance is an economical and environmentally safe measure to reduce crop losses. However, the development of cultivars that confer durable resistance to stripe rust requires the availability of the desired genetic resources, a better understanding of the genetics of the host-pathogen interaction, and suitable techniques to utilise the desired genes.

Genetic resistance to stripe rust can be divided into seedling and adult plant resistances. Seedling resistance is usually effective throughout the plant growth cycle and is assumed to follow a gene-for-gene relationship (Flor 1959). Plants that are susceptible at the seedling stage, but resistant at the adult plant stage, are described as possessing adult plant resistance (Allan et al. 1966). Some lines and cultivars express intermediate infection types as seedlings and at the adult plant stage (Zwer & Qualset 1994). Plant breeders are mostly interested in adult plant (non-specific) resistance, which usually lasts longer, but the genetics of non-specific resistance have been studied by only a few

researchers (Chen & Line 1993; Bariana & McIntosh 1995; Börner et al. 1999). Understanding the genetics of resistance to disease is valuable for planning crosses in breeding programmes, identifying resistance genes, understanding genetic diversity, and developing genetic markers to assist in selection. The genetic basis of resistance in the New Zealand wheat 'Otane', which has conferred durable adult plant resistance since its release in 1984 (Cromey & Munro 1992), has not been studied. This study was conducted to characterise the genetics of durable adult plant resistance conferred by 'Otane', and to determine the expression of this resistance under glasshouse and field environments using a double haploid (DH) population.

MATERIALS AND METHODS

Host

To study the inheritance of adult plant resistance in 'Otane' a segregating population comprising 140 DH lines was produced by crossing 'Otane' with the stripe rust susceptible 'Tiritea' as described by Imtiaz et al. (2003).

Pathogen

Stripe rust (*P. striiformis* f. sp. *tritici*) pathotype 106E139A⁺ was used in this study. The collection of inoculum and method of inoculation have been described by Imtiaz et al. (2003).

Experimental design

Three replicates of one seed of each DH line, two seeds of the F₁, and four seeds of both parents were sown on 20 August 1999 in individual pots in a glasshouse following the design outlined by Imtiaz et al. (2003). After c. 63–66 days, when the plants had a fully expanded flag leaf, they were inoculated using the method described for seedling inoculation (Imtiaz et al. 2003). For the field trial, seeds of the 140 DH lines and their parents, 'Tiritea' and 'Otane', were sown on 3 August 2000 at the New Zealand Institute for Crop & Food Research Limited, Lincoln, Canterbury. Six g (3 g per row) of seeds were drilled in rows 1.28 m long with 18 cm spacing between rows. Each test plot consisted of two 1.28 m rows of two DH lines with a disease spreader row of 'Tiritea' on each border of the plot. The trial was a randomised block design with three replicates. The susceptible 'Tiritea' was also sown at the end of each replicate. The susceptible line 96WFM5568

was sown on the border of the field trial to further facilitate the spread of stripe rust within the trial.

Field inoculation

The field plots were first inoculated on 9 September 2000 when the first leaves on plants had emerged and the second leaves were just appearing. Glasshouse-grown 'Tiritea' plants infected with pathotype 106E139A⁺ of *P. striiformis* f. sp. *tritici* were planted in the middle of the spreader rows on the border of each experimental plot. To ensure good epidemic development, the entire experimental area was further spray-inoculated with 106E139A⁺ on 27 September 2000, 18 days after the first inoculation. For the spray inoculation, a suspension of 106E139A⁺ uredospores in distilled water with 50 mg Tween 20/litre was prepared. The suspension was sprayed using a battery-powered, hand-held boom sprayer (Yellow 02) with low volume nozzles (08 nozzle size; 3 litre/min) in the late evening when there was no wind or cloud. Uredospores were applied at a rate of 5.6 g/ha, which equates to 1000 spores per plant (Stubbs et al. 1986).

Disease assessments

All 140 DH lines and the two parents were evaluated in the glasshouse for infection types (IT), and in the field for IT and final disease severity (FDS). Infection types produced by the host-pathogen interaction were recorded 18 days after glasshouse inoculation using the 0–9 infection type scale (Line et al. 1974) as tabulated previously (Imtiaz et al. 2003). Infection type scores from 0 to 3 were interpreted as resistant (R), 4 to 6 as moderately resistant (MR), and 7 to 9 as susceptible (S). However, in a separate analysis, infection types were also grouped into two classes: 0–6 were considered resistant and 7–9 were susceptible. Furthermore, in the field, IT was recorded on five fully expanded flag leaves of each row (growth stage (GS) 41–45; Zadok's scale modified by Tottman & Makepeace 1979). The FDS, defined as the maximum disease on the flag leaf of each DH line, was recorded before senescence of each flag leaf. In most instances data for severity at GS 61–69 were used, but in some susceptible lines leaf senescence had occurred before this stage, and hence FDS was recorded earlier.

Statistical analysis

Chi-square (χ^2)-goodness of fit was used to compare the observed distribution in the DH population with those predicted by various genetic models for each measure of resistance. Models used were

single-, two-, and three-gene models, as well as gene-interaction models. Contingency table χ^2 analysis was used to compare sets of data from the two environments (glasshouse and field). Least significant difference (LSD) was used to compare the means of parents and DH lines. The mean of the 140 DH lines was also compared with that of the parents. The most resistant DH line as well as the 5% of DH lines showing the highest resistance to the pathogen (low IT values) were compared with the resistant parent. To measure genetic variability in the DH population, percent genetic gain (El Attari et al. 1998) was calculated as follows:

$$GG = 100 (BDH - BP)/BP \text{ and} \\ GG = 100 (SDH - BP)/BP$$

where GG is the genetic gain; BDH is the best DH line; SDH is the most resistant 5% of the DH lines; and BP is the best parent.

RESULTS

Disease evaluations were made under the hypothesis that gene(s) involved in the resistance of 'Otane' would be identified at the adult plant stage. The genetic model hypothesis for the DH population disease reaction was based on the classification of three phenotypes—R, MR, and S. Analysis of variance of the 140 DH lines and their parental cultivars, 'Tiritea' and 'Otane', showed a highly significant ($P < 0.001$) genotype effect both in glasshouse and field experiments.

Glasshouse studies

Cultivar 'Tiritea' had a mean IT of 7.7 whereas that for 'Otane' was 6.3. The F₁ phenotype fell in a category near to resistant with a mean IT of 3.9. Three distinct phenotypic classes, R, MR, and S, were observed in the DH progeny of 'Tiritea' × 'Otane' against pathotype 106E139A⁺ (Fig. 1).

Transgressive segregation was apparent in the DH progeny of the cross. The mean DH population IT was 5.8, but DH-119 had a low IT value of 0.3. At the other extreme, DH-96 was S, with an IT of 9 (Fig. 2). The numbers of DH lines that showed R, MR, and S ITs were 37, 36, and 67 respectively. This segregation fits a 1:1:2 digenic ratio (Table 1), suggesting an additive/modifying action of two genes, and does not fit the other models tested.

This model suggests that R lines were produced when genes from both parents were present. MR

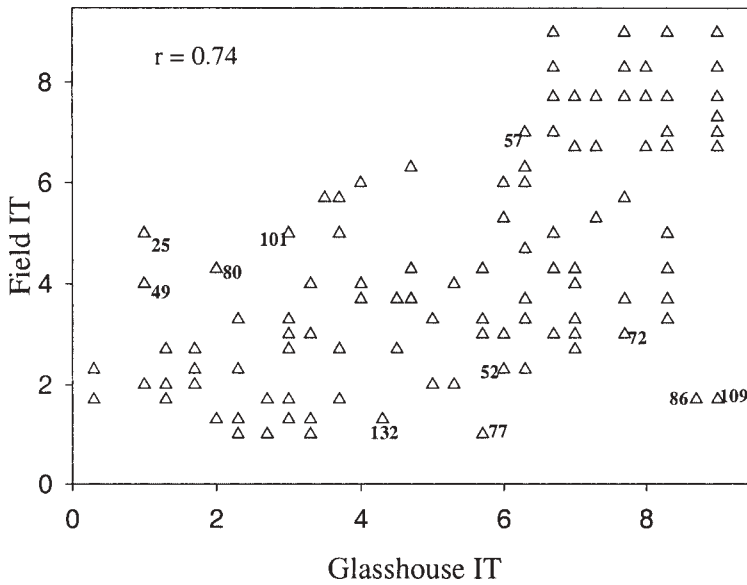


Fig. 2 Comparison of field and glasshouse infection type (IT) for double haploid (DH) lines through simple linear regression. Numbers identify DH lines with very different glasshouse and field IT scores.

Table 1 ‘Tiritea’/‘Otane’, F₁ infection types (IT), double haploid (DH) segregation, and Chi-square (χ^2) fit to genetic models for adult wheat (*Triticum aestivum*) plants inoculated with *Puccinia striiformis* f. sp. *tritici*, pathotype 106E139A⁺ under glasshouse and field conditions. (R, MR, and S refer to resistant, moderately resistant, and susceptible respectively. MR* represents an IT which was closer to R than MR and recorded in the glasshouse only.)

Cultivar/ generation	Phenotype	Obs. infection types	Number of plants			Tested ratio R:MR:S	χ^2	Probability
			R	MR	S			
Glasshouse								
Tiritea	S	8						
Otane	MR	6						
F ₁	MR*	4						
DH lines	R	1, 2, 3	37	36	67	1:1:2	0.27	0.86
	Mr	4, 5, 6						
	S	7, 8, 9						
Field								
Tiritea	S	8						
Otane	MR	4						
DH lines	R	1, 2, 3	57	34	49	1:1:2	20.15	<0.00001
	MR	4, 5, 6						
	S	7, 8, 9						
DH lines	R	1-6	91		49	5:3 (R:S)	0.37	0.55
	S	7-9						

lines were produced when only the resistant genes from ‘Otane’ were present, while S plants were produced when the resistance gene from ‘Otane’ was absent. This is the simplest model to fit these data. Other models tested (which did not fit the data) included simple one-, two-, or three-gene models, and various other gene-interaction models.

Field studies

Infection type

‘Otane’ expressed a moderate level of resistance with an IT of 3.7 in the field compared with an IT of 6.3 in the glasshouse. The reaction of ‘Tiritea’ was almost the same in the field and glasshouse with IT

values of 8.3 and 7.7 respectively. The field ITs for DH lines ranged from a minimum of 1 to a maximum of 9, with a mean value of 4.8. The mean IT value was 5.8 in the glasshouse (Fig. 2). When glasshouse disease reactions were compared with field reactions (Fig. 2), in the field 57 DH lines were in the R category compared with 37 DH lines in the glasshouse. The number of DH lines in the MR and S classes changed from 36 to 34 and 67 to 49 respectively for the glasshouse and field. Eight DH lines were categorised S in the glasshouse, but R in the field. Five DH lines were R under glasshouse conditions but categorised MR in the field. DH-57 was MR (IT 6.3) when sown in the glasshouse, but was S in the field (IT 7). Out of 67 DH lines which were categorised S in the glasshouse, eight were R and 11 were MR in the field.

The Chi-square for independence ($\chi^2 = 95.65$ with 4 d.f.) was highly significant ($P < 0.001$) with a correlation (r) value of 0.68 for glasshouse versus field data. The segregation for IT under field conditions was 57R:34MR:49S. This was a major deviation from the simple 1:1:2 digenic ratio proposed under controlled conditions, but this observed segregation closely fitted a 3:2:3 trigenic ratio (Table 1). This model proposes that R DH lines were produced when either three genes (ABC), or at least two genes (AB), from both parents interact, while MR DH lines are produced when either two genes (BC) or one gene (B) of ‘Otane’ are present. S DH lines are produced when either R genes (AB) from both parents or a R gene (B) from ‘Otane’ are absent. The R gene ‘C’ of ‘Otane’ acts only as a modifier. To further validate this model, the DH progeny were grouped into just two phenotypic classes, those having infection types of 0–6 (R) versus those having infection types of 7–9 (S), for

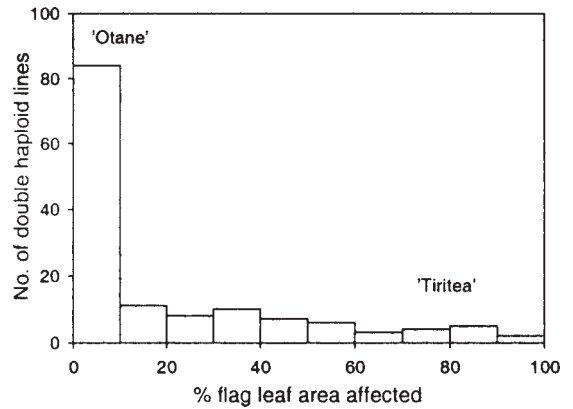


Fig. 3 Distribution of final disease severity of stripe rust in the field for ‘Tiritea’ × ‘Otane’ wheat (*Triticum aestivum*) double haploid lines after inoculation with *Puccinia striiformis* f. sp. *tritici*. Severity scores are based on the modified Cobb scale (Peterson et al. 1948).

which a segregation ratio of 91R:49S occurred. This segregation also fitted a 5:3 trigenic ratio, indicating involvement of three genes under field conditions (Table 1).

Final disease severity (FDS)

‘Tiritea’ had a mean FDS of 76.7% whereas ‘Otane’ had a mean FDS of 7.7%. DH-96 and DH-100 were the most severely infected lines with FDSs of 96.7 and 90% respectively. DH-22, DH-81, and DH-139 also had FDS values higher than the S parent ‘Tiritea’. The distribution of the mean FDS was skewed towards the MR parent, as shown in Fig. 3 with 85 DH lines having mean FDSs between 0.7 and 10%. Most of the lines that had low ITs in the field had a low FDS, which means the measures were

Table 2 Ratios of resistant (R) to moderately resistant (MR) to susceptible (S) plants and χ^2 values of observed against expected 5:1:2 or 5:3 ratios, based on final disease severity (FDS) of the double haploid (DH) population obtained from ‘Tiritea’ × ‘Otane’ wheat (*Triticum aestivum*) inoculated with *Puccinia striiformis* f. sp. *tritici*, pathotype 106E139A⁺.

Cultivar/ generation	FDS division point	No. of plants observed			Tested ratio R:MR:S	χ^2	Prob.
		R	MR	S			
DH lines (FDS)	0.7–10% (R) 11–30% (MR) 31–100% (S)	85	17	38	5:1:2	0.35	0.85
DH lines (FDS)	Similar to Otane (MR) Different from Otane (S)	–	90	50	5:3	0.19	0.60

related ($r = 0.78$; data not presented)). Conversely, ITs recorded under glasshouse conditions were poorly correlated with FDS ($r = 0.48$; data not presented).

The DH lines were grouped into three classes: those having mean FDSs of 0.7 to 10% being R, those with mean FDSs of 11 to 30% being MR, and those with mean FDSs of 31 to 100% being S. This produced 85 DH lines in the first group, 17 lines in the second group, and 38 lines in the third group. This segregation of 17MR:38S:85R again fits a 1:2:5 trigenic ratio, suggesting involvement of three genes (Table 2). To test the validity of this model, DH lines were divided into two groups—those having mean FDSs statistically similar to ‘Otane’, and those having mean FDSs statistically different from ‘Otane’. This produced 90 DH lines in the first group and 50 DH lines in the second group (Table 2). This observed segregation ratio of 90:50 is close to the expected ratio of 87.5:52.5 for a 5:3 ratio of three segregating loci ($\chi^2 = 0.19$; $P > 0.60$).

Genetic gain was measured in this population to assess genetic variability for resistance to stripe rust caused by *P. striiformis* f. sp. *tritici*. The comparison between the best DH line and the best parent (‘Otane’) showed a statistically significant difference for resistance to stripe rust in both experiments, with genetic gains of 95 and 73% in the glasshouse and field experiments respectively (Table 3). The same trend was observed when the

best parent was compared with the mean of the most resistant 5% of the DH lines; genetic gains were 83 and 68% in the glasshouse and field experiments respectively (Table 3).

DISCUSSION

Inheritance of resistance to stripe rust has frequently proved to be complex (Bariana & McIntosh 1995). The objective of the present research was to study the inheritance of resistance in ‘Otane’, which closely fits the Johnson (1983) durability definition, i.e., resistance that has remained effective while a cultivar possessing it has been widely cultivated in an environment favouring the disease for a long sequence of generations or period of time. In an attempt to separate simple major gene resistance from adult plant resistance the DH progeny from a ‘Tiritea’ × ‘Otane’ cross were evaluated under controlled glasshouse as well as field conditions. To limit environmental variation a multi-inoculation strategy was applied to the field experiment. ‘Otane’ had a moderate level of resistance at the adult stage and ‘Tiritea’ was susceptible, but transgressive segregation occurred in the DH population.

Plants that are susceptible to *P. striiformis* f. sp. *tritici* at the seedling stage may develop adult plant resistance during the post-seedling phases. This resistance may be described as adult plant resistance

Table 3 Genetic gain (GG) for resistance to stripe rust in double haploid (DH) lines of wheat (*Triticum aestivum*). Values represent the mean of the host infection types for a scale ranging from 0 to 9, from three replicates. (NS, not statistically significant ($P > 0.05$); XDH, mean of all DH lines; BP, best parent (‘Otane’); GG, genetic gain when the best DH line or 5% of the selected DH lines were compared with the best parents (‘Otane’).)

Parents or DH lines	Glasshouse expt	Field expt
Otane (P1)	6.3	3.7
Tiritea (P2)	7.7	8.3
P1 – P2	–1.4 NS	–4.6 $P < 0.05$
XP = (P1 + P2)/2	7.0	6.0
XDH	5.8	4.8
XDH – XP	1.2 NS	1.2 NS
Best DH (BDH)	0.3	1.0
BDH – best parent (BP)	–6.0 $P < 0.05$	–2.7 $P < 0.05$
GG = 100(BDH – BP)/BP	–95.2 $P < 0.05$	–72.9 $P < 0.05$
5% Selected DH (5% SDH)	1.1	1.2
5% SDH – BP	–5.2 $P < 0.05$	–2.5 $P < 0.05$
GG = 1 – (5% SDH – BP)/BP	–82.6 $P < 0.05$	–67.6 $P < 0.05$
Least significant difference (LSD)	1.7	1.3

or post-seedling resistance (Bariana & McIntosh 1995). Adult plant resistance can be race-specific or race non-specific (Johnson 1988). In contrast to seedling resistance, little is known about the genetic basis of adult plant resistance. Studies on the inheritance of adult plant or race non-specific resistance in wheat to stripe rust have been reported (Zwer & Qualset 1994; Boyd & Minchin 2000; Johnson et al. 2000). However, in these studies it is generally not clear whether resistance is due to genes effective at the seedling stage, to genes effective only at the adult stage, or to combinations of both types. Adult plant resistance to stripe rust in wheat has been used widely (Johnson 1992); in some cases it has eroded (Johnson 1988, 1992) whereas in others it has proved durable (Milus & Line 1986). Race-specificity for *P. striiformis* f. sp. *tritici* was also observed for adult plant resistance as reported in 'Brock' in New Zealand (Cromey 1992).

The New Zealand spring wheat 'Otane' has conferred a quantitative and durable adult plant resistance since its release in 1984 (Cromey & Munro 1992). Understanding the genetics of 'Otane' resistance should be helpful for exploiting the resistance in gene deployment, gene pyramiding, and multi-line development. If observations of cultivar-race interactions with different cultivars are used in combination with the results reported here, then further understanding of the genetic basis for virulence in stripe rust races could be developed. In this study, transgressive segregation was observed for resistance and susceptibility at the adult plant stage under both glasshouse and field conditions, which is in complete agreement with the comments of Wallwork & Johnson (1984) that transgressive segregation is not an occasional phenomenon; rather it should be obtainable from many if not all crosses. In our study, under controlled conditions, IT segregation fitted the 1:1:2 digenic ratio, suggesting that genes from 'Otane' are likely to confer moderate resistance when present alone but interact in an additive manner when present together with a resistance factor from 'Tiritea'. The heterozygote major gene would probably condition an MR reaction by itself, but with the modifying influence of the resistance factor it appeared to condition the IT near to an R type in the F_1 of 'Tiritea' \times 'Otane'. This kind of additive and major/minor gene resistance has been reported by many workers (Lewellen et al. 1967; Milus & Line 1986; Ma & Singh 1997) for resistance to stripe rust in wheat.

The segregation of DH lines in the field environment did not fit a 1:1:2 digenic ratio; rather

it fitted a 3:2:3 or a 5:3 trigenic ratio, suggesting the involvement of three genes. Environmental influence on the reaction of wheat to *P. striiformis* f. sp. *tritici* has been found in several studies (Lewellen et al. 1967; Lewellen & Sharp 1968; Milus & Line 1986) and this probably occurred in the present study. Sharp (1965) observed that cultivars showed characteristic responses to increasing temperature profiles. An improvement in the parental resistance of 'Otane' to pathotype 106E139A⁺ of *P. striiformis* f. sp. *tritici* was observed under the field environment in the present study. However, the high IT on 'Tiritea' indicates that temperatures in the field environment were suitable for stripe rust infection to occur. When the FDSs were grouped into two classes, similar to 'Otane' and different from 'Otane', the distribution of DH lines fitted a 5:3:1 trigenic ratio for R to S. When stripe rust IT is divided into R and S classes, only the major genes are recognised, and no information on important minor genes is gained (Lewellen et al. 1967). Therefore, for studies on minor gene action, more resistance categories would be helpful. As in the present study, Ghannadha (1993) observed transgressive segregation in the F_2 and F_3 at the adult plant stage involving 'Tiritea' in different crosses.

Shifts in resistance level of some susceptible DH lines between the glasshouse and field environments observed are common (Hooker 1967). The number of DH lines in the R category increased under field conditions, mainly due to shifts of MR lines to the R category. This could be due to a genotype \times environment interaction favouring the better expression of resistance of MR lines under these conditions. An association in the genetic mechanisms was found between adult-seedling and adult-adult reactions under both environments. The greatest relatedness between seedling and adult reactions occurred in the glasshouse ($\chi^2 = 102.23$, d.f. = 4, $P < 0.005$), which indicated that the loci governing seedling and adult reactions may be closely linked or identical. The same relationship was observed under field conditions, but the association was less strong ($\chi^2 = 69.20$, d.f. = 4, $P < 0.005$), probably because some DH lines were susceptible at the seedling stage (Imtiaz et al. 2003) but resistant at the adult stage. This indicates that some loci conditioning adult plant resistance probably do not influence seedling resistance under field conditions. Allan et al. (1966) observed a similar association between adult plants and seedlings in the glasshouse and field. Under glasshouse and field environments, the dependency

was stronger for seedling-seedling ($\chi^2 = 121.70$, d.f. = 4, $P < 0.005$) than adult-adult ($\chi^2 = 95.65$, d.f. = 4, $P < 0.005$) reactions. This might be due to the involvement of minor genes in adult plant resistance, whose expression is strongly affected by environmental changes, especially temperature (Dyck et al. 1966) and light (Wellings et al. 1988). The different results obtained from the controlled and field environments in this study suggest that 'Otane' possesses at least two genes, one major and one minor, operating at the adult plant stage when the minor gene is more vulnerable to environmental conditions, possibly temperature (Sharp 1965).

The present study indicates that high genetic variability for resistance to stripe rust caused by *P. striiformis* f. sp. *tritici* can be obtained in DH lines from F_1 progeny of a MR and S cultivar, and thus significant genetic gain can be obtained by selecting the most resistant lines. DH lines resistant to fusarium head blight in wheat (Simmonds et al. 1993) and resistant to stem rust, leaf rust, powdery mildew, and bacterial leaf streak in barley (Steffenson et al. 1995; El Attari et al. 1998) have been reported. Therefore, DH production can be used as an efficient method of breeding for disease resistance.

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