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Components of partial resistance to powdery mildew in wheat mutants

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Abstract

Components of resistance to powdery mildew (latent period, pustule density and conidium production) were analysed on glasshouse-grown artificially inoculated plants of wheat mutants ($n = 11$) derived from either induced mutagenesis or adventitious regeneration of cv. Guardian. These mutants had previously been shown to be partially resistant to the disease in the field over a two-year period. Analyses were carried out at three stages of development: seedling, tillering and heading. None of the mutants exhibited a latent period significantly different from that of the susceptible parent 'Guardian' at any stage of development tested. With respect to pustule density, one mutant (M61) was significantly more resistant than 'Guardian' at all stages of development, two mutants (M19 and SC100) were more resistant at tillering and heading, and two (M156 and SC267) were more resistant only at heading. Significantly reduced conidium production per pustule (as a measure of pustule size) over a 24 h period was observed on three mutants (M61, SC100 and SC231) at tillering and heading, while mutant SC68 exhibited this trait at heading only. On the basis of resistance components and relative grain yield in the presence of mildew, the eleven mutants were categorised into five categories. Tests for associations between field resistance score and components of resistance measured in the glasshouse, both measured at heading, revealed a significant positive correlation only between pustule density and field score. To assess the effects of combining different components (i.e. pyramiding different partial resistance genes), mutants were crossed. Transgressive segregation for at least one component was observed in the F_2 generation in crosses between mutants with complementary modes of action (i.e. involving different components of partial resistance), but not in cases where the parents exhibited the same component of resistance.

Introduction

Whereas complete resistance has been a major weapon used by plant breeders to control fungal pathogens such as wheat powdery mildew (*Blumeria* (*Erysiphe*) *graminis* f.sp. *tritici*), the generally race-specific and hence non-durable nature of this resistance has shifted the focus to race-non-specific partial resistance. Unfortunately, the fact that partial resistance is the resultant effect of many genes, each with a small individual effect, has made investigation of partial resistance genes (a vital study, if breeding for this relatively low heritability trait is to be made more efficient) a difficult process. Partial disease resistance is expressed as a reduction in the rate of development of the disease in the host. It can be caused by alterations in one or more of the following components: increased incubation period (time from inoculation to appearance of symptoms), increased latent period (time from inoculation to sporulation on the resulting colony), reduced infection frequency (number of colonies per unit leaf area), reduced infectious period (length of time the colony produces viable spores), reduced infection size (colony size), and reduced spore production (number of spores produced per infection or per unit leaf area over a particular length of time).

Assessment of partial resistance in the field can be subject to large experimental error, because of the effects of environmental factors such as field heterogeneity and other pathogens or pests. On the other hand, measurement of single components of resistance under a controlled environment involves much smaller experimental error values. If a single component were highly correlated with field partial resistance, then it would be possible to assess this component only, and hence select indirectly (and more efficiently) for increased resistance. Significant correlations between one component of resistance and partial resistance in the field have been reported, e.g., adult plant latent period with partial resistance to leaf rust (*Puccinia hordei*) on barley (Parlevliet et al., 1980) and lesion size with partial resistance to bacterial blight in rice (Koch et al., 1991). In these examples, it was necessary to measure only the specific component in order to obtain an accurate estimate of partial field resistance.

For plants grown in a glasshouse or growth chamber, leaves can be inoculated while attached to or detached from the plant. For increased control over the experimental environment, detached leaf experiments are often preferred. However, the responses of many genotypes in detached leaf experiments deviate from those in field trials. Roderick and Clifford (1995) reported a poor association between field results for adult plant resistance to powdery mildew on oats and results from detached leaves; the detached leaf test did not appear to be sensitive enough to distinguish small differences observed in the field between genotypes. Thus, in the analysis of different levels of partial resistance, it is preferable to maintain a certain degree of control over the experimental environment, e.g., by conducting studies in a glasshouse or a growth chamber, with the inoculated leaf being kept attached to the plant.

Whereas complete resistance is usually expressed during all stages of plant development, certain forms of partial resistance are only expressed as the plant develops. Thus, to analyse components of partial resistance, plants should be evaluated at both the seedling stage and an adult plant stage, e.g. heading. It is also desirable to evaluate components of resistance at one stage of development between these two extremes (e.g., during tillering) to characterise the resistance further.

Most investigations into the mechanisms of partial resistance have compared crop varieties exhibiting different degrees of this resistance (e.g., Jones, 1978; Bennett, 1981; Roderick and Clifford, 1995). Identification of causal relationships in such studies is difficult because of the large number of genes by which the resistant and susceptible genotypes differ. Such studies would be facilitated by the use of more nearly isogenic material. The development of such lines by backcrossing is difficult because the small effects of individual genes and the large influence of the environmental factors on the expression of resistance makes the introgression of a single gene problematic. An alternative strategy involves mutagenesis. As with backcrossing, it can be difficult to isolate mutants with partial disease resistance, but recently several authors (Varghese, 1985; Worland and Law, 1991) have demonstrated that such mutants can be identified efficiently from small M_2 or M_3 populations. We screened a small population ($n = 135$) of M_3 (derived by induced mutagenesis) and SC_3 (derived by adventitious regeneration) progeny rows of wheat cv. Guardian to isolate mutants exhibiting increased resistance to powdery mildew (Kinane and Jones, 2000a). Eleven mutants, which exhibited high levels of partial resistance (compared with the parent variety Guardian) to natural infection by powdery mildew in the field over two seasons, were isolated (Kinane and Jones, 2000a).

The availability of these eleven independent mutants permitted the analysis of the modes of action of single genes affecting partial mildew resistance in wheat. Previous varietal studies had indicated that partial resistance to wheat powdery mildew was associated predominantly with one or more of the following modifications of resistance components: increased latent period, reduced pustule density or reduced conidium production (Shaner, 1973a; Rouse et al., 1980; Bennett, 1981; Nass et al., 1981). Each of these components was analysed in cv. Guardian and in the eleven mutants at seedling, tillering and heading. The near-isogenic nature of the genetic material also permitted determination of causal relationships between individual components and field resistance. Finally, hybridisation between selected 'complementary' mutants exhibiting alterations in different components of resistance, and subsequent analysis of the F_1 and F_2 progeny, could provide fundamental information on the interaction between resistance genes, as well as an assessment of the potential for increasing partial resistance by pyramiding individual genes into a single genotype.

Methods

Plant material

The wheat variety 'Guardian' and eleven mutants (M, following ethyl methane sulphonate-induced

mutagenesis, or SC, following adventitious regeneration from immature wheat embyros; Kinane and Jones, 2000a) which had exhibited increased partial resistance to powdery mildew in the field (Kinane and Jones, 2000a) were grown in potting compost (Bord na Mona, Ireland), three plants per 2 l pot, and maintained in a heated glasshouse (minimum temperature 16 °C), with a 16-h photoperiod supplemented with artificial (400 W sodium vapour lamps) lighting. The pots were arranged in a replicated randomised block design. Six replicate plants were grown of each line for inoculation at stages GS12 (seedling), GS27 (tillering) or GS45 (heading), (Zadoks et al., 1974). Six weeks after sowing, the plants were fed with 0.05% (w/v) aqeuous solution of a proprietary plant nutrient source (Phostrogen; Corwen, UK) (containing 10% nitrogen, 8.8% phosphorus, 22.5% potassium) at a rate of 1 l per pot; this was repeated every two weeks. Earlier opportunist mildew infection on the plants to be inoculated at tillering or heading was prevented by misting them with water for 15 min every two hours for approximately four weeks prior to inoculation.

Fungal material

The universally susceptible wheat variety 'Cerco' was grown in potting compost, at a rate of approximately 200 seedlings per seed tray, in a separate unheated glasshouse (minimum temperature 10 °C) under natural lighting. When the 'Cerco' seedlings were seven days old, they were inoculated with a heavy inoculum from a local population of powdery mildew consisting of a mixture of four pathotypes: 2, 4b, 5, 6, 8; 2, 4b, 5, 6, 8, Ta2; 2, 4b, 5, 6, 8, Ta2, 3d, To; and 2, 4b, 5, 6, 8, d, 3d, To, Ax (Kinane and Jones, 2000b). The plants were covered with a transparent lid to ensure a high relative humidity during disease development. The day before use as sources of inoculum, the infected seedlings were shaken to dislodge aged conidia.

Inoculation and disease assessment

Inoculation was carried out at three stages of development. At the seedling stage, the first leaf was inoculated at complete emergence of the second-formed leaf. At the end of tillering the youngest fully emerged leaf on the main shoot was inoculated, and at the heading stage, the fully emerged flag leaf of the main stem was inoculated. The leaf to be inoculated was laid (adaxial surface uppermost) at the base of a settling tower and inoculated to a density of approximately five conidia per mm^2. Inoculum density was monitored by placing a glass slide covered with double-sided adhesive tape beside the experimental leaves in the settling tower and counting the number of conidia which landed on it until it reached the desired density. Inoculated plants were then incubated in the glasshouse under conditions described earlier. Latent period was determined as the number of days after inoculation to when conidia were visible on 50% of the colonies. To determine conidium production, a modification of the method of Shaner (1973b) was used. Three days after the end of the latent period, plants were shaken to remove any conidia; 24 h later, two segments, each approximately 3 cm long were gently excised from the centre of each infected leaf and laid with the adaxial (inoculated) surface face down on water (10 ml) in a 60 ml glass jar, and shaken gently on an orbital shaker for 6 h at 22 °C and the concentration of conidia present in the water was determined using a haemocytometer slide. The pustule number on each leaf segment was counted with the aid of a hand lens and the leaf segment area was measured using Delta-T™ DIAS (Delta-T Devices Ltd., Cambridge, UK) image analysis system. Thus pustule number per cm^2 leaf area and conidium production per pustule and per cm^2 leaf area were calculated.

Pyramiding experiment

A cross was carried out between SC68 (egg parent) and SC267 (pollen parent). The resulting F_1 (3 plants) and F_2 ($n = 15$) generations, plus both parents ($n = 9$) were grown in a glasshouse as described above. When the main stem flag leaf had fully emerged (GS 39, Zadoks et al., 1974), the flag leaves were inoculated with a local powdery mildew population in a settling tower, and the pustule density and conidium production per pustule and per unit cm^2 leaf area were assessed as described above. The mean values for each parent were calculated (P_1 and P_2). From these values the mid-parent value (m) were calculated ($m = (P_1 + P_2)/2$). The additive effect (a) (the difference between either parent value and the mid-parent value i.e. ($P_1 - m$) or ($m - P_2$)) and the dominance effect (d) (the difference between the F_1 value and the mid-parent value) were calculated. From this, the dominance ratio was calculated (d/a). A dominance ratio value of 1 indicates that 100% of the genetic variation exhibited dominance effects and a value of 0 indicates that 100% of the genetic variation exhibited additive effects; an intermediate ratio indicates that both additive and dominance

effects applied. The experiment was repeated with the crosses SC68 × SC231 and SC231 × SC267.

Results

Effect of plant development on resistance

Resistance increased in 'Guardian' and the mutants as the plants aged (Table 1); as the plants at different stages were not inoculated at the same time, the observed increase in resistance may have been due to environmental factors, but the trend of more mutants exhibiting significant changes in resistance components (relative to 'Guardian') as plant age increased indicates that partial resistance in the mutants was more pronounced in older plants. Mean latent period averaged over the twelve tested lines (eleven mutants plus 'Guardian') was a day shorter ($P < 0.01$) at the seedling stage than at either tillering or heading. While there was a reduction in pustule density and both conidium production parameters as the plants developed, only plants at heading were significantly different ($P < 0.01$) from those at other stages with respect to these components.

Components of resistance

None of the mutants exhibited a latent period significantly different from 'Guardian' at any stage of development tested (data not shown). Significant differences from 'Guardian' were observed, however, when pustule density was measured (Figure 1a). One mutant, M61, exhibited significantly reduced pustule number per cm^2 leaf area compared with 'Guardian' at all three stages of development tested. Two lines, M19 and SC100, exhibited reduced pustule density at tillering and heading, and two, M156 and SC267, at heading only (Figure 1a).

Conidium production per pustule over a 24 h period (Figure 1b) in the mutants showed stage-specific differences in expression similar to those in pustule density. This component was not altered in any of the mutants at the seedling stage, whereas three mutants, M61, SC100 and SC231, showed decreased conidium production per pustule at tillering and four, M61, SC100, SC231 and SC68, exhibited this trait at heading (Figure 1b).

Pustule number per cm^2 leaf area and conidium production per pustule were multiplied to give conidium production per cm^2 leaf area. This value gives an indication of the effect of resistance on overall inoculum production in a 24-h period by each of the lines. Any line that exhibited either significantly reduced pustule density or reduced conidium production per pustule also produced significantly fewer conidia per cm^2 leaf area in the 24-h period (Figure 1c). Thus seven of the eleven mutants tested should significantly reduce disease development in the field at the adult plant stage (by reducing inoculum production); three of these lines should reduce it also at tillering, while only one (M61) would be effective from the seedling stage onwards (Figure 1c).

Correlations between components of resistance to powdery mildew indicated that the only significant associations were those between conidium production per cm^2 leaf area and both pustule density and conidium production per pustule. These significant correlations were attributable to autocorrelation (Table 2).

When testing for any association between the field resistance score and components of resistance measured in the glasshouse at the heading stage, field infection results (expressed as % flag leaf area covered

Table 1. Comparison of components of resistance at three stages of development in 'Guardian' and eleven partially resistant mutants

	Latent period (day)	Pustule density (number per cm^2)	Conidium production per pustule ($\times 10^{-3}$) in 24 h	Conidium production per cm^2 leaf area ($\times 10^{-4}$) in 24 h
Seedling	6.2 ± 0.39a*	9.9 ± 2.71a	14.7 ± 2.69a	14.9 ± 5.43a
Tillering	7.2 ± 0.39b	8.3 ± 2.56a	13.1 ± 4.62a	11.1 ± 5.02a
Heading	7.2 ± 0.39b	5.7 ± 2.58b	11.3 ± 5.29b	6.9 ± 3.72b
ANOVA	$F(2, 34) = 5.3$; $P < 0.01$	$F(2, 34) = 6.1$; $P < 0.01$	$F(2, 34) = 5.6$; $P < 0.01$	$F(2, 34) = 6.0$; $P < 0.01$

Any two samples in a column sharing a common letter are not significantly different at $P = 0.05$ using the Tukey test, following ANOVA.

*Values indicated are mean ± standard deviation.

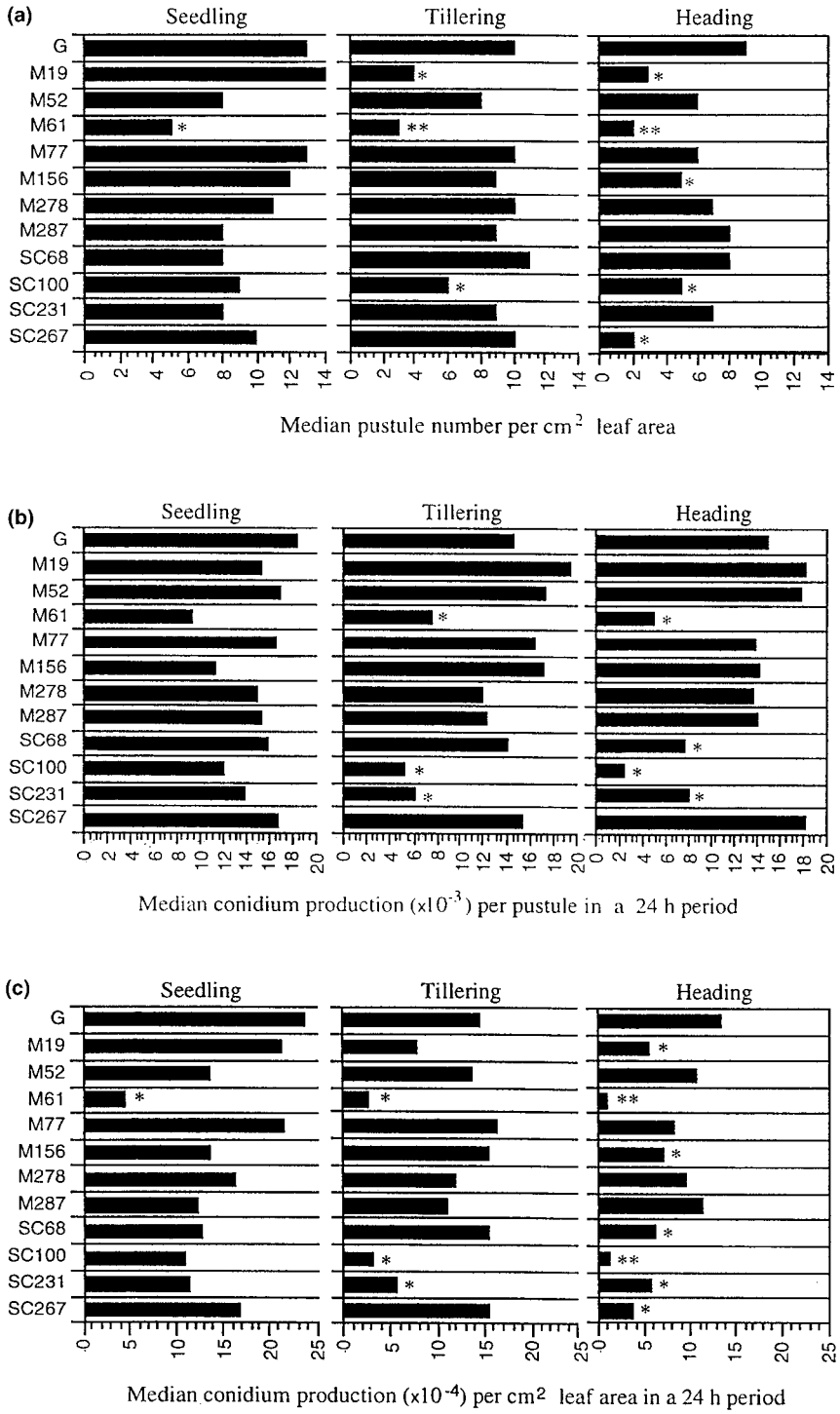

Figure 1. Comparison of 'Guardian' and the partially resistant mutants at three stages of development with respect to (a) pustule density, (b) conidium production per pustule, and (c) conidium production per cm^2 leaf area. Asterisks indicate significant differences from 'Guardian' at $P \leq 0.05$ (*) and $P \leq 0.01$ (**) using the Kruskal–Wallis test.

Table 2. Correlation coefficients between components of resistance to powdery mildew in eleven partially resistant mutants and the susceptible parent 'Guardian'

	Latent period	Pustule density	Log_{10} conidium production per pustule	Log_{10} conidium production per cm^2
Latent period		−0.43	−0.18	−0.40
Pustule density			0.09	0.68*
Log_{10} conidium production per pustule				0.76**

For each correlation $n = 12$. Correlations are denoted by * ($P \leq 0.05$) and ** ($P \leq 0.01$).

by pustules) were averaged over the two growing seasons (Kinane and Jones, 2000a). There was a moderate significant positive correlation ($r = 0.60$; $n = 12$; $P < 0.05$) between pustule density and field infection, but correlations between field score and latent period ($r = 0.03$), conidium production per pustule ($r = -0.25$) or per cm^2 ($r = -0.03$) were not significant.

Pyramiding resistance genes

The mutant SC267, which exhibited a lower pustule density at heading than 'Guardian' (Figure 1a), was crossed with mutant SC68, which exhibited lower conidium production per pustule (Figure 1b) than the parent; both mutants exhibited conidium production per unit leaf area significantly lower than that of 'Guardian' (Figure 1c). For the three characters recorded (pustule density and conidium production per pustule or per unit leaf area), the responses of the F_1 plants were intermediate between those of their parents (Figure 2). The calculated dominance ratio of 0.55 (pustule density), 0.40 (conidium production per pustule) and 0.89 (conidium production per cm^2) indicated that both dominance and additive effects play a role in the genetic control of the characters analysed. Transgressive segregation was observed for the F_2 generation for all three traits (Figure 2). Of particular interest was the identification of F_2 plants with increased resistance compared with the parents. In the F_2 progeny, one plant showed a pustule density below the range of either parent (Figure 2a), while conidium production per pustule of two other F_2 plants was lower than that of either of the parents (Figure 2b). With regard to conidium production per cm^2 leaf area, four F_2 plants gave lower values than any individual plant of either parent (Figure 2c).

When SC267 was hybridised with SC231 (another mutant which exhibited reduced conidium production per pustule; Figure 1c), transgressive segregation was again observed in the F_2 generation for low conidium production, on both a pustule and leaf area basis (Table 3). The third cross, involving two mutants exhibiting reduced conidium production (SC68 and SC231), however, failed to result in transgressive segregation for any component of partial resistance (Table 3).

Discussion

Improvement of partial resistance in breeding programmes could be facilitated by screening for an easily identifiable character which is highly correlated with field resistance. In this study, there was a positive correlation between field infection score and pustule density; although the latter trait is easier to quantify than infected leaf area (the standard field infection measure), the coefficient of determination of the relationship ($r^2 = 0.36$) would appear to be insufficient. Although reduced pustule density (infection frequency) was the most frequently affected component among the mutants, several mutants (e.g., SC68, SC231) did not exhibit reduced infection frequency, and would have been over-looked if screening for partial resistance were based purely on pustule number.

The eleven mutants analysed had previously exhibited significant partial resistance in the field, compared to 'Guardian' in trials conducted over two years (Kinane and Jones, 2000a). The four pathotypes present in the inoculum in these artificial inoculation studies were the same as those in the natural inoculum in the studies in which the mutants were isolated (Kinane and Jones, 2000a). The field resistance measure (percentage leaf area affected) reflects the product of the density of pustules and the mean size of the pustule. 'Pustule density' was not only the component most affected in the mutants, but also the only component positively correlated with field resistance. This may reflect the importance of this component in determining partial resistance and/or the mutation frequency of gene(s) controlling this character. Roderick and Clifford (1995) reported that, of the three components they analysed (latent period, infection frequency and conidium production) in ten unrelated oat genotypes exhibiting adult plant resistance to powdery mildew, only pustule density showed

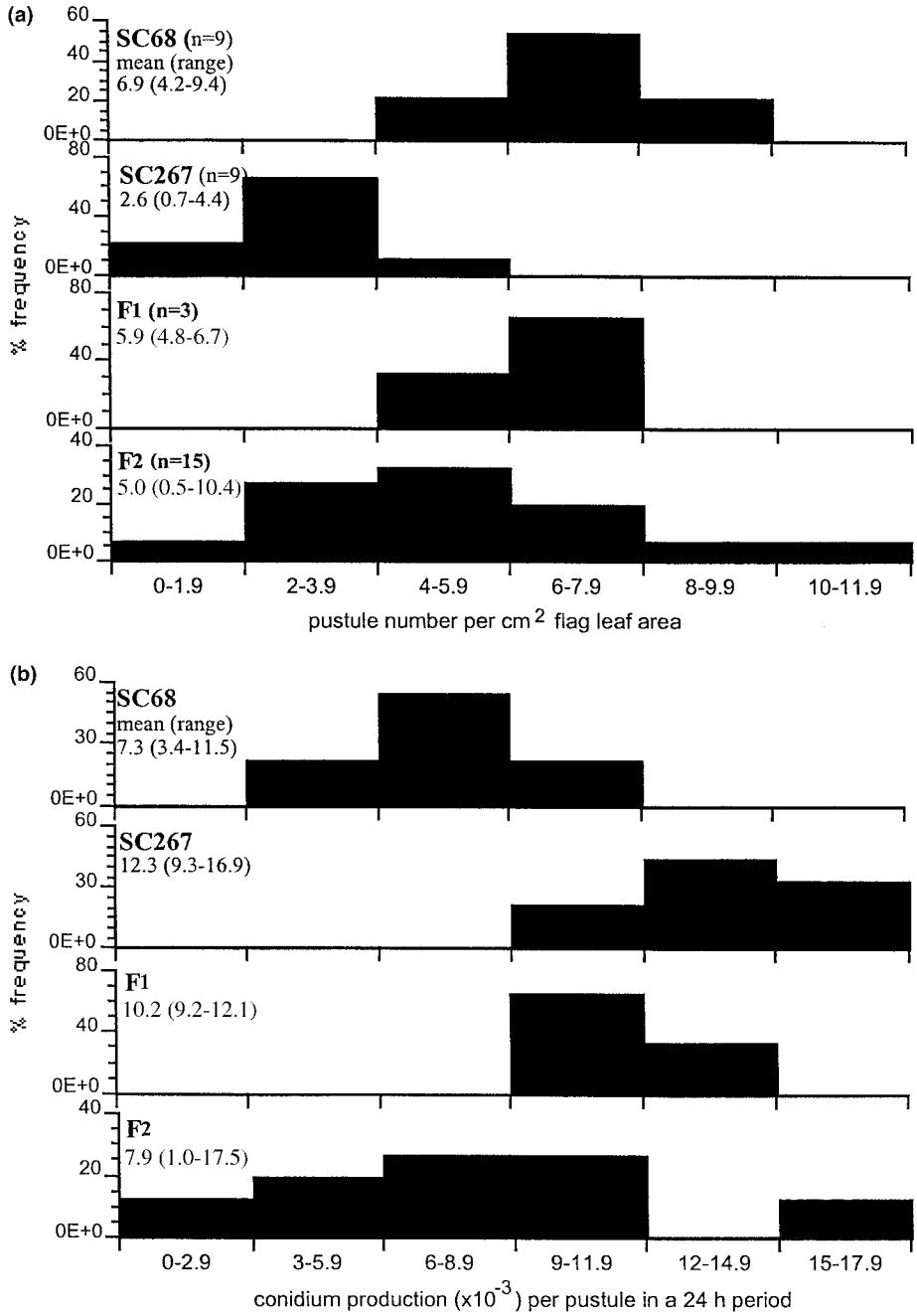

Figure 2a and b. Frequency distributions of (a) pustule density, (b) conidium production per pustule for SC68, SC267 and their F_1 and F_2 progeny.

a significant correlation with partial resistance in the field. Similarly, Mastebroek and Balkema-Boomstra (1991) found highly significant positive correlations between powdery mildew level in the field and pustule density in the glasshouse for the corresponding growth-stage up to node three among barley varieties.

In this study, conidium production per pustule was used as a measure of pustule size, because of technical

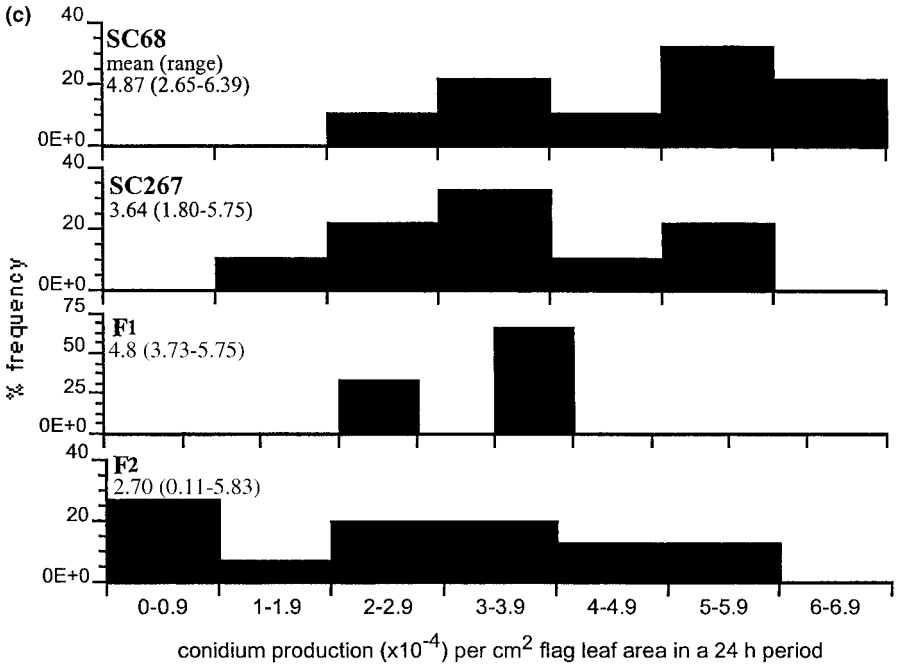

Figure 2c. Frequency distributions of conidium production per cm^2 leaf area for SC68, SC267 and their $F_1$and F_2 progeny.

difficulties, encountered in preliminary experiments, in obtaining reproducible direct estimates of pustule size. Reduced conidium production per pustule could be achieved, however, without a parallel decrease in pustule size. With conidium production being so prolific (glasshouse studies indicated 2000–19 000 conidia per pustule over a 24-h period), it is highly unlikely that an increased field resistance score in a mutant associated with reduced conidium production per pustule in these mutants was due to reduced inoculum production *per se*. Given the air-borne nature of the inoculum and the fact that the original population ($n = 135$) which was screened was genetically heterogeneous (M_3 and SC_3 lines), with each mutant planted in replicated 1 m long rows, 15 cm apart, differences in conidium production between the mutants would not be expected to result in local differences in infection levels between these mutants. It is more probable that the observed partial resistance was due to reduced pustule size.

Characterisation of the seven mutants which exhibited significant changes in components of partial resistance in terms of mechanisms of resistance (including the effect on grain yield; Kinane and Jones, 2000a), identified five distinct classes (Table 4). Further analysis may permit additional subdivision such as in Class 5, where mutant M61 exhibited reduced pustule number at all three stages, whereas SC100 expressed this trait only at tillering and heading. Mutants in Classes 1 and 2 appeared to cause general attenuation of the infection process, affecting all components of the infection process and expressed as reduced infection frequency and conidium production per pustule, whereas mutants in other classes exhibited modified response to infection only with respect to specific components of the infection process.

Four mutants, M52, M77, M278 and M287, were consistently more resistant than 'Guardian' to powdery mildew in the field over a two-year period (Kinane and Jones, 2000a) but they did not differ significantly from 'Guardian' with respect to any of the components of resistance tested in the glasshouse trials. In each case, pustule number in the mutants was lower than that in 'Guardian' at one (M77) or more stages (M52, M278, M287) (Figure 1a), but the difference was not significant. The results may be a reflection of difficulties associated with identifying small differences in quantitative resistance as significant. Alternative explanations may be environmental (e.g., under the glasshouse conditions, resistance mechanisms observed in the field may not be expressed) or

Table 3. Components of mildew resistance in F_2 progeny of crosses between mutants exhibiting partial resistance

	Population			
	SC231 mean (range)	SC267 mean (range)	SC68 mean (range)	F_2 mean (range)
SC231 × SC267 Pustule density (pustule number cm^{-2} leaf area)	6.7 (4.2–9.3)	2.6 (0.7–4.4)		3.7 (0.5–9.1)
Conidium production per pustule ($\times 10^{-3}$)	6.6 (3.6–9.8)	12.3 (9.3–16.9)		8.0 (0.3–15.2)
Conidium production cm^{-2} ($\times 10^{-4}$)	4.08 (3.03–6.24)	3.64 (1.80–5.75)		2.95 (0.30–6.40)
Number of plants tested	9	9		11
SC231 × SC68 Pustule density (pustule number cm^{-2} leaf area)	6.7 (4.2–9.3)		6.9 (4.2–9.4)	7.1 (4.2–9.0)
Conidium production per pustule ($\times 10^{-3}$)	6.6 (3.6–9.8)		7.3 (3.3–11.5)	7.3 (3.9–10.3)
Conidium production cm^{-2} ($\times 10^{-4}$)	4.08 (3.03–6.24)		4.87 (2.56–6.39)	4.18 (2.71–6.21)
Number of plants tested	9		9	12

Table 4. Classification of mutants exhibiting partial resistance on the basis of effect on resistance components and yield

	Effect on yield*		
	($P < 0.05$) Increased yield	No effect	($P < 0.05$) Reduced yield
Reduced pustule number	M19 Class 1	M156 Class 2	SC267 Class 3
Reduced conidium production $pustule^{-1}$		SC68, SC231 Class 4	
Reduced pustule number, conidium production		M61, SC100 Class 5	

*Data from Kinane and Jones (2000a).

mechanistic (e.g. resistance mechanisms operating at the level of mildew epidemiology in the field may not be detected in the single generation studies in the glasshouse).

Since partial resistance is, by definition, incomplete in nature, one strategy to increase the level of resistance involves the hybridisation of plants exhibiting partial resistance to pyramid several partial resistance genes into a single plant. Of course this is only possible if the partial resistance in both parents is controlled by independent genes. The identification of mutants from different classes with different modes of action opens up the possibility of combining different components of partial resistance into single lines by hybridisation. Following hybridisation of SC68 (which reduced conidium production by the fungus) with SC267 (which reduced pustule density) the inheritance of components of partial resistance in the two mutants involved in the crossing programme showed both dominance and additive effects. Similar results were reported by Röbbelen and Heun (1990), when they combined powdery mildew partial resistance genes that were induced through mutagenesis in barley (although no data were presented), while transgressive segregation of partial

resistance to leaf rust have been reported from crosses between varieties of wheat (Kloppers and Pretorius, 1997) and barley (Parlevliet et al., 1985). The isolation of individual F_2 plants exhibiting transgressive segregation with respect to the specific resistance components (decreased pustule density or reduced conidium production per pustule) indicates an interaction between the two mutant genes, so that the reduced conidium production of SC68 accentuated the decreased pustule number in SC267. Transgression was most marked for the multiplicative character, conidium production per unit leaf area. Very similar results were obtained when SC267 was crossed with a second low spore production mutant (SC231), from the same resistance class as SC68 (Table 4). When two mutants exhibiting reduced conidium production were crossed, however, no transgressive segregation was observed. This result supports the categorisation of mutants SC68 and SC231 into the same resistance class; it also suggests that the mutations in SC68 and SC231 operate via similar mechanisms and may even be in the same gene locus.

The marked reduction in conidium production per cm^2 leaf area in selected F_2 plants from crosses between complementary parental mutants from 18 000 (for the better parent, SC267) to 1100–3000 would be expected to considerably retard an epidemic of the disease in the crop; such an effect is characteristic of partial resistance. The studies need to be extended to include progeny testing of homozygous segregants (e.g., from doubled haploids derived from the F_1 hybrid of these and other combinations of mutants). Nevertheless the results are exciting; the observation that pyramiding of small numbers of genes can result in such high levels of resistance could have marked potential in breeding programmes. The availability of the individual resistance genes in such near-isogenic lines would facilitate the identification of the gene concerned (e.g., using AFLP or subtractive hybridisation), as it would increase the probability that a polymorphism between 'Guardian' and a specific mutant was in the disease response gene itself.

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