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TRANSGRESSIVE SEGREGATION FOR RESISTANCE TO YELLOW RUST IN WHEAT

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SUMMARY

Crosses were made between wheat varieties Joss Cambier, Nord Desprez and Maris Bilbo, all classified as susceptible to yellow rust in field tests, and between Cappelle Desprez and Maris Huntsman, both classified as moderately and durably resistant. Selection for resistance to yellow rust among the progeny was carried out using races of *Puccinia striiformis* able to overcome all the known race-specific components of resistance in both parents of each cross. Lines with greater resistance than in both parents were obtained from each cross, those with greatest resistance being obtained from the cross between the moderately resistant parents. Three lines selected for resistance from the cross of Joss Cambier with Nord Desprez and one from the cross of Cappelle Desprez with Maris Huntsman, together with the parents, were tested in the field with 12 races of *P. striiformis*. Nord Desprez possessed a previously undetected race-specific component. The selected lines also displayed race-specific resistance, some of which was clearly related to race-specificity of the parents, and a component of resistance, greater than in both parents, that was effective against all 12 races. The possible origin and potential durability of this transgressive level of resistance is discussed. It is suggested that such transgressive resistance is more likely to be durable if it is derived from parents that have shown durable resistance.

INTRODUCTION

It has often been suggested that race-non-specific resistance to fungal pathogens such as *Puccinia striiformis* WESTEND. and other diseases exists in wheat and to diseases in other crops. Various authors (e.g. LEWELLEN et al., 1967; NELSON, 1978; ROBINSON, 1976; VANDERPLANK, 1963, 1968) have associated such resistance with minor genes, polygenic inheritance, adult-plant resistance and partial or incomplete resistance that reduces the infection rate. POPE (1965) and SHARP (1972) indicated that increased resistance to yellow rust was obtained through the accumulation of minor resistance genes in progeny from crosses between wheat varieties classified as susceptible to the pathogen. It has been suggested that resistance derived in this way, will (ROBINSON, 1976) or may (LEWELLEN et al., 1967) be race-non-specific. However, JOHNSON & TAYLOR (1972) showed that a minor genetic component of resistance, affecting sporulation of *P. striiformis* in seedlings of Joss Cambier, was race-specific. PARLEVLIET (1977),

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similarly, has shown race-specificity amongst genes that have minor effects in reducing the rate of development of leaf rust on barley. It cannot be assumed, therefore, that either genes with minor effects or resistance that reduces the infection rate are race-non-specific. There is nevertheless, good evidence that many wheat varieties carry incomplete resistance to yellow rust that has remained effective over many years despite their being grown over large areas (JOHNSON, 1978). Little is known of the genetic basis of this durable resistance although studies on Cappelle Desprez (LAW et al., 1978; PINK, 1981), Hybride de Bersée (GAINES, 1976) and Little Joss (LUPTON & JOHNSON, 1970; LABRUM, 1980) have suggested that a number of genes are involved in each variety and that they are mainly effective in adult plants.

This paper describes experiments designed to select for increased resistance from crosses between wheat varieties classified as susceptible or moderately resistant to yellow rust, to test the race-specificity of the resistance and to obtain further information on the genetic control of durable resistance.

MATERIALS AND METHODS

Wheat stocks and crosses. The winter wheat varieties Maris Bilbo, Joss Cambier and Nord Desprez, classified as highly susceptible to race 104 E137(3) of *Puccinia striiformis* WESTEND. in field tests at the Plant Breeding Institute over several years, were intercrossed and F1, F2 and later generations were produced. The winter wheat varieties Maris Huntsman and Cappelle Desprez (a parent of Maris Huntsman), both classified as possessing a moderate level of durable resistance to yellow rust (SCOTT et al., 1980), were crossed and F1, F2 and later generations were produced. Seed of the varieties and progeny from the crosses between them was, in all cases, obtained from ears that had been enclosed in cellophane bags at flowering time to prevent outcrossing.

P. striiformis stocks. The races of *P. striiformis* used to test for resistance are designated according to the nomenclature described by JOHNSON et al. (1972). Further differentiation of the races is indicated by numbers given in brackets, which indicate differential pathogenicity on wheat varieties outside the standard set of differential varieties. Thus, race 104 E137(3) is more pathogenic on Maris Bilbo and Joss Cambier than race 104 E137(1) (JOHNSON & TAYLOR, 1972, 1974). Race 104 E137(3) was chosen for these experiments as being highly pathogenic on these two varieties and also on Nord Desprez. Race 41 E136(3) was chosen as being amongst the most pathogenic on both Cappelle Desprez and Maris Huntsman. The parents and four selected lines were tested with these two races and 10 further races (see below). All the races possessed pathogenicity for the resistance genes *Yr2, Yr3a* and *Yr4a* (LUPTON & MACER, 1962) which were present in some of the parents.

Uredospores of the races, used as inoculum, were multiplied on susceptible wheat seedlings grown in isolation in the glasshouse. All the races behaved as pure clones and many were established from single spores. The uredospores were stored in gelatine capsules in liquid nitrogen vapour and after removal from the vapour were warmed at 37 °C for five minutes before use. Further details of the methods are described by JOHNSON et al. (1981).

Design of trials. Each field trial was planted in a randomised block design with varying numbers of blocks being used in different experiments. Two trials layouts (A and B) were used. In trials of layout A each block was accommodated in one or more 1.5 m wide beds. Within beds each line was represented by six plants 0.3 m apart in a row, each row being separated from the next by 0.3 m. Every third row contained only susceptible spreader plants inoculated prior to transplantation in spring with a specific rust race. Trials of layout A were located as far possible from all sources of other races of *P. striiformis,* although still within the Plant Breeding Institute farm.

One trial (layout B) was used to test lines for resistance to 12 races of *P. striiformis* as described by JOHNSON & TAYLOR (1978). Varieties were sown in approximately circular plots of 0.25 m diameter each containing about 25 plants. The plots of material to be tested were interspersed at regular intervals with plots of a susceptible variety known as Vulgare PP and each set was surrounded by a 1m wide barrier of a mixture of yellow rust resistant wheat and rye plants to reduce cross-contamination. Each set was infected with a single race of *P. striiformis* by transplanting into each plot of the susceptible spreader variety, two seedlings that were infected with yellow rust in the glasshouse. The full set was repeated 24 times and 12 races were applied in two randomised blocks. The races were thus applied to main plots and the varieties to sub plots in this split-plot design.

Each trial received a total of 78 kg/ha of nitrogen in an NPK mixture in two applications, one before sowing, another late in March or early in April and also a herbicide (Ioxynil) spray early in May.

In A trials, scores for individual plants were taken of the percentage area of the flag leaf infected with yellow rust; in the B trial the percentage area of all leaves infected in the whole sub plots was scored. In the latter trial, scores were taken at an early date when it was expected that cross-contamination between races would be lowest. At this early date even the highly susceptible varieties were only moderately infected.

Statistical tests. The performance of lines in different years and generations was compared by correlation coefficients. Mean levels of infection of lines thought to be homozygous were compared by t tests. Low replication of the B trail was due to the large number of other lines being tested simultaneously with those reported here. However, the data of Tables 3 and 5 were analysed separately from those of the other lines. Contamination between races in the B trial would tend to diminish the observed differences between races and comparing means by the least significant difference (l.s.d.) can therefore be considered an adequate test.

RESULTS

Transgressive segregation for resistance to race 104 E137(3). The F1 generations from crosses between Maris Bilbo, Joss Cambier and Nord Desprez were more susceptible than either Joss Cambier or Nord Desprez, indicating that the slight resistance in both these varieties was recessive (Table 1). Transgressive segregation was observed among the F2 and F3 progeny from each cross although the highest levels of resistance occurred among progeny from the crosses between Joss Cambier and Nord Desprez. Individual F3 plants were selected from the 1979 field trials shown in Table 1 and their progeny was tested against the same race in 1980. Correlation coefficients were $r = 0.72$ ($P<0.001$) and $r = 0.61$ ($P<0.01$) for the crosses Maris Bilbo × Nord

Table 1. Frequency distributions of infection levels on 11 July 1979 on progeny from crosses between the wheat varieties Maris Bilbo, Joss Cambier and Nord Desprez infected with race 104 E137(3) of *P. striiformis*.

Lines	% flag leaf area infected																				n	$\bar{x}$
	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100		
Maris Bilbo (M)																			6	17	23	98.7
Joss Cambier (J)														3		2	7	6	6		24	86.5
Nord Desprez (N)												1		2	3	8	5	3	1	1	24	81.5
F_1 M × J																			8	31	39	99.0
M × N																		3	18	10	31	96.1
J × N																	1	4	19	8	32	95.3
F_2 M × J						1		2	3			3	1	8	6	7	16	28	61	100	236	92.1
M × N				1	1		1	4	2	1		4	1	7	11	15	9	36	80	66	239	89.6
J × N			1	2	1	5	3	3	1	7	1	5	4	10	12	9	17	40	69	50	240	84.9
F_3 M × N						4	2	9	1	2	1	5	4	10	8	20	23	43	62	43	237	85.3
J × N	1	2		1	6	5	3	16	3	10	3	12	10	21	9	27	20	27	42	17	235	74.0

Desprez and Joss Cambier × Nord Desprez respectively when F3 plant scores from 1979 were compared with F4 line mean scores from 1980. This showed that much of the variation observed in 1979 was heritable. Similar comparisons made between F4 plants and F5 line mean scores obtained in 1981 yielded correlation coefficients of $r = 0.90$ ($P<0.001$) and $r = 0.88$ ($P<0.001$) respectively.

Transgressive segregation for resistance to race 41 E136(3). In separate trials progeny from crosses between Cappelle Desprez and Maris Huntsman were selected for transgressive segregation to race 41 E136(3). This race was known to be among the most pathogenic on both varieties and to overcome the known adult-plant race-specific component R13 (PRIESTLEY, 1978) in Maris Huntsman. Despite the presence of Cappelle Desprez in the pedigree of Maris Huntsman wide segregation was observed in the F2 generation (Table 2) suggesting that the varieties had few resistance genes in common. Selection for resistance over two generations yielded an F4 line, TP 921 D-4-13(K), which was much more resistant than either parent to race 41 E136(3).

Resistance of transgressive segregant lines to 12 races of P. striiformis. Three of the most resistant transgressive segregant F4 lines from the cross Joss Cambier × Nord

Table 2. Frequency distributions of infection levels of 9 July 1979 on progeny from crosses between the wheat varieties Cappelle Desprez and Maris Huntsman infected with race 41 E136(3) of *P. striiformis*.

Lines	% flag leaf area infected																		n	$\bar{x}$
	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95		
Cappelle Desprez		2	7	6	5	3			1										24	26.0
Maris Huntsman			14	7	2		1												24	23.1
F_1										1	3	7	15	13	1				40	69.9
F_2	5	8	21	13	20	21	20	11	16	8	13	15	13	17	14	9	9	6	239	50.2

Table 3. Percentage leaf area infected on 10 June 1981 on plots of three wheat varieties and three transgressive segregant F_5 lines from the cross Joss Cambier × Nord Desprez, inoculated with 12 different races of *P. striiformis*.

Race	Variety/TP line					
	Maris Bilbo	Nord Desprez	Joss Cambier	926 A-7-2-4(A)	927 B-1-1-6(B)	927 B-1-2-5(C)
41 E136(1)	25.0	80.0	30.0	12.5	12.5	15.0
41 E136(2)	17.5	75.0	77.5	40.0	30.0	30.0
41 E136(3)	27.5	67.5	65.0	40.0	25.0	27.5
41 E136(4)	82.5	72.5	80.0	35.0	37.5	30.0
43 E138	22.5	72.5	77.5	47.5	27.5	37.5
45 E140	37.5	75.0	75.0	42.5	45.0	37.5
104 E137(1)	40.0	75.0	50.0	37.5	15.0	27.5
104 E137(3)	70.0	60.0	60.0	27.5	15.0	17.5
108 E141(1)	22.5	60.0	52.5	27.5	17.5	17.5
108 E141(2)	30.0	67.5	75.0	37.5	20.0	30.0
171 E138	30.0	60.0	50.0	20.0	20.0	22.5
232 E137	37.5	67.5	70.0	37.5	32.5	27.5

l.s.d. ($P = 0.05$) for differences between races within a variety = 15.0.
l.s.d. ($P = 0.05$) for differences between varieties within a race = 15.2.

Desprez were apparently uniform in their reactions and therefore thought to be homozygous. They were tested in the F5 generation for resistance to 12 different races (trial B) in 1981. The F5 lines TP 926 A-7-2-4(A), TP 927 B-1-1-6(B) and TP 927 B-1-2-5(C) were more resistant to all the races than their parents (Table 3), although one difference, between Joss Cambier and line TP 926 A-7-2-4 (A) fell just short of significance at $P = 0.05$. Nord Desprez and Joss Cambier were more susceptible to several of the races than to race 104 E137(3). In contrast, Maris Bilbo was not highly susceptible to some of these, such as race 41 E136(2) and 43 E138, suggesting that the effects were specific for Nord Desprez and Joss Cambier. The F5 lines were also more susceptible to some races (such as 41 E136(2) than to race 41 E136(1) indicating a possible race-specific component in their resistance.

Field trials (layout A) in 1980 and 1981 confirmed that Nord Desprez possessed a component of its adult plant resistance that was more effective against race 104

Table 4. Percentage of flag-leaf area infected with yellow rust on two wheat varieties and transgressive segregant lines for increased resistance or susceptibility derived from a cross between them.

Race	Date	Variety/TP line					
		Nord Desprez	Joss Cambier	926 A-7-2-4(A)	927 B-1-1-6(B)	927 B-1-2-5(C)	927 B-3-11(D)
104 E137(1)	10.7.80	77.5	19.0				
104 E137(1)	6.7.81	75.0	54.5	7.5	7.5	15.0	95.5
104 E137(3)	1.7.80	43.0	61.0				
104 E137(3)	1.7.81	35.0	55.5	6.0	7.0	8.5	90.0

Table 5. Percentage leaf area infected on 23 June 1981 on plots of two wheat varieties and an F_4 transgressive segregant line from a cross between them, inoculated with 12 races of *P. striiformis*.

Race	Variety/TP line		
	Cappelle Desprez	Maris Huntsman	921 D-4-13(K)
41 E136(1)	40.0	17.5	5.0
41 E136(2)	35.0	12.5	3.5
41 E136(3)	40.0	35.0	7.5
41 E136(4)	42.5	17.5	5.0
43 E138	45.0	15.0	5.0
45 E140	35.0	12.5	3.5
104 E137(1)	35.0	12.5	3.5
104 E137(3)	32.5	10.0	2.0
108 E141(1)	25.0	15.0	1.5
108 E141(2)	40.0	32.5	7.5
171 E138	37.5	20.0	3.5
232 E137	40.0	22.5	5.0

l.s.d. (P = 0.05) for differences between races within a variety = 9.5
l.s.d. (P = 0.05) for differences between varieties within a race = 9.8

E137(3) than against 104 E137(1) (Table 4). This race-specific component of its resistance has not been previously reported.

These trials also confirmed the resistance of the three transgressive segregant F5 lines in 1981 and demonstrated transgressive segregation for susceptibility in an F4 line (TP 927 B-3-11 (D) which was selected in the F2 and F3 generations from the cross of Joss Cambier with Nord Desprez. The differential resistance of Joss Cambier to races 104 E137(1) and 104 E137(3) was evident in the 1980 trials but not in 1981, perhaps due to contamination of the race 104 E137(1) trial with a different race or to effects of environment on the expression of resistance.

The F4 line TP 921 D-4-13(K) from the cross between Cappelle Desprez and Maris Huntsman was also tested for resistance to 12 races of *P. striiformis* in Trial B. It was more resistant than both parents to all 12 races (Table 5). However, it was significantly more susceptible to race 108 E141(2) which carries pathogenicity for R13 than to race 108 E141(1) which does not. It was also more susceptible to race 41 E136(3) than to most other races, although many of the differences were not significant, perhaps due to cross-contamination between races. These data suggest that the F4 line possesses R13.

Crosses involving selected resistant lines. Two F4 lines, TP 926 A-7-2-4(A) and TP 927 B-1-2-5(C), selected from the cross between Nord Desprez and Joss Cambier as being uniformly resistant, were intercrossed and backcrossed to their parents. The parents, an F1 between them, the F1 from the intercross and the backcross F1 plants and also F5 progeny from the F4 lines were tested to race 104 E137(3) in an A trial in 1981.

The F4 line C produced two F5 lines that differed in their level of resistance indicating that the F4 line was not homozygous despite itc apparent uniformity. Nevertheless

Table 6. Frequency distributions of infection levels on 1 July 1981 in lines from crosses and backcrosses between Joss Cambier, Nord Desprez and two transgressive segregant lines infected with race 104 E137(3) of *P. striiformis*.

Lines	% flag leaf area infected																	n	$\bar{x}$
	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85		
Joss Cambier							1	2	1	2	5	6	4	1				22	55.7
Nord Desprez					3	6	7	5	2	1								24	35.0
Joss Cambier × Nord Desprez												4	9	5	3	1	1	23	68.0
A* -1	2	5	4															11	8.5
-2	9	3																12	
C -1	5	6	1															12	8.3
-16				1	4	6	1											12	27.9
A × C	1	2	3		5	4		1	1									17	23.5
F_1 Joss Cambier × A			1			3	10	1	1									16	33.6
Joss Cambier × C				1	3	7	5	2	1									20	33.3
Nord Desprez × A				2	2	3	3	1	1	1	1	1						15	35.7
Nord Desprez × C						3	2	4	9	1	3		2					24	44.2

* A = TP926 A-7-2-4(A); C = TP 927 B-1-2-5(C)

most of the F1 plants from the intercross between A and C fell within the range of the F4 derivatives from A and C (Table 6) indicating that the two lines were genetically similar. The resistance of Joss Cambier and Nord Desprez was largely recessive as shown by the susceptibility of their F1, confirming earlier results. The means of F1 plants from backcrosses of lines A and C to Nord Desprez and Joss Cambier were all significantly ($P < 0.001$) more resistant than the mean of the F1 from Nord Desprez and Joss Cambier indicating that lines A and C were homozygous for genes from each of the parents. Except in the backcross line of C to Nord Desprez the backcross F1 hybrids were at least as resistant as the parent to which they were backcrossed. As the resistance was recessive this indicated that the lines possessed all the resistance derived from the parent to which they were backcrossed. The backcross of line C to Nord Desprez was significantly more susceptible ($P < 0.001$) than Nord Desprez itself, indicating that line C lacked one or more recessive genes from Nord Desprez, perhaps the component of resistance for which line C was segregating.

DISCUSSION

The occurrence of transgressive segregation. The data from this study show that transgressive segregation for increased resistance to yellow rust in wheat occurred in all four crosses in which it was sought. This suggests that similar transgressive segregation should be obtainable from many, if not all, other crosses and is not just an occasional phenomenon. These data confirm the findings of NILSSON-EHLE (1911), PESOLA (1927), POPE (1965) and KRUPINSKY & SHARP (1979) who reported transgressive segregation for adult-plant resistance to yellow rust. Whereas their field trails may have involved a mixture of races, the data collected here were obtained using the same known races separately over three years.

The highest levels of resistance obtained through transgressive segregation came from the varieties Cappelle Desprez and Maris Huntsman which themselves possessed the most resistance to the race used. Similarly, crosses between Joss Cambier and Nord Desprez yielded more progeny with greater resistance than did crosses involving the more susceptible variety Maris Bilbo when selection was carried out with race 104 E137(3).

The parental origin of resistance in the selected lines. The transgressive segregation for resistance clearly originated from a combination of the genetic components from both parents of each cross. It was shown, in crosses of Nord Desprez with Joss Cambier and of Cappelle Desprez with Maris Huntsman, that resistance was recessive. Test crosses of two lines from the former cross indicated that both probably contained almost identical resistance and that their resistance was a high proportion of the available resistance from both parents. This evidence, and the rapid accumulation of resistance from both these crosses indicates that the number of genes involved was probably not large. It was interesting to note that Cappelle Desprez and Maris Huntsman, which are genetically related and both durably resistant, differ so greatly in the components of their intermediate resistance, as shown by the wide segregation in the F2 progeny from their cross.

Race-specificity in the parents and the selected lines. Tests with 12 races of *P. striiformis* showed that the transgressive segregrant lines were significantly more resistant than both their parents, usually significantly, to all the races and also that each of the lines contained race-specific components. In some cases these can be related to known race-specific components in the parents, that were overcome by the races used in selection of the transgressive resistance. The inclusion of these race-specific components in the selected lines may be due to chance. However, although our data provide no evidence to support the hypothesis, it cannot be ruled out that the race-specific components may either produce some residual resistance to the races classified as possessing pathogenicity for them, or may interact with other genetic components to increase resistance. Such interactions have been described for genes for resistance to other rusts of wheat, for example for resistance to *P. recondita* (SAMBORSKI & DYCK, 1982). Whatever the cause, the line derived from the cross of Maris Huntsman with Cappelle Desprez apparently possesses the race-specific component R13 derived from Maris Huntsman. The three lines derived from the cross of Joss Cambier with Nord Desprez may possess the component R11 (PRIESTLEY, 1978) from Joss Cambier, as suggested by their greater susceptibility to race 41 E136(2) than to race 41 E136(1). However, if they possesed R11 it would be expected that they would be more susceptible to race 104 E137(3) than to race 104 E137(1). This was not observed (Table 3) probably because the lines possess the previously unknown race-specific component of resistance in North Desprez, giving greater resistance to race 104 E137(3) than to race 104 E137(1) and thus masking the effect of R11. Also cross-contamination between races and perhaps environmental effects may have reduced the differential effect of these two races on R11 as indicated by Joss Cambier in Table 3.

The data also indicated that some races gave higher infection than race 104 E137(3) on Joss Cambier and that the highest infection on the derived lines was due to races giving high infection on both Nord Desprez and Joss Cambier. Although race 104 E137(3) was chosen for selection of the transgressive lines because it was thought to overcome the already recognised race-specific components in Joss Cambier and Nord Desprez, the data presented show that other races might have overcome more race-specific components in these varieties. This illustrates the difficulty of following the advice of Robinson (1976) to choose a single race overcoming all the race-specific components in a group of susceptible varieties to be intercrossed for the selection of supposedly race-non-specific resistance.

Potential durability of resistance in the selected lines. These observations lead to a consideration of whether the resistance accumulated by transgressive segregation will be durable. Insofar as the race used for selection does not overcome all the potentially race-specific components in the parents, the accumulated resistance in the selected lines may be eroded by races matching any such components incorporated in the lines. As shown here, even quite susceptible varieties may contain such race-specific components. It is evident, therefore, that it cannot be asserted that the residual resistance, after already-recognised race-specific components are overcome will be race-non-specific. Nevertheless the component of resistance in the selected lines that was effective against all 12 races with which it was tested merits further investigation and particularly a test of its durability, if this could be achieved. In the case of the lines selected from the cross of Maris Huntsman with Cappelle Desprez, a residual component of resistance in both cultivars was known to be durable and it may be hoped that the derived line carries a combination of the genetic component responsible for this durability and will therefore also possess durable resistance. The line may therefore be a useful source of resistance, but it, and all products from it, will require an adequate test of durability to assess their value. The resistance in the lines from the cross of Joss Cambier with Nord Desprez seems less likely to be durable at its present level because part of it is probably due to the newly-recognised race-specific component from Nord Desprez. Even if this component is overcome the residual resistance could not confidently be predicted to lack further race-specific components. Again, an adequate test of durability would be required to assess the value of the resistance.

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