

Additive Resistance in Wheat to *Puccinia striiformis*

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ABSTRACT

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Gene action for resistance to *Puccinia striiformis* was determined in minor gene lines of wheat derived from crosses of PI 178383/Itana//commercial cultivars. The minor gene lines were intercrossed in one diallel and intercrossed with susceptible winter wheat cultivars in a second diallel. The two

diallel analyses showed the presence of additional gene action and high heritabilities and indicated that this apparently general type of resistance could be manipulated easily in a breeding program.

Additional key words: general resistance, yellow rust, minor gene resistance, diallel analysis.

The stripe rust disease of wheat, *Triticum aestivum* L., caused by *Puccinia striiformis* West. is found on all continents except Australia (25). The disease caused large economic losses in the Pacific Northwest region of the United States in 1960–1964, and has caused moderate damage since then (1,2,6). In 1974 the disease caused severe damage in central California (12). The use of resistant varieties was proposed in 1924 (8) and is still considered the most feasible means of control (7). Specific resistance has been the most common type of disease resistance used (5), but an apparent general type of resistance has been developed (19,21,23).

In 1963, Allan et al (2) reported moderate resistance to infection by *P. striiformis* in several fourth-backcross lines derived from the two susceptible parents Norin 10-Brevor 14 and Burt. They cited it as an example of transgressive segregation and suggested that complementary gene action was involved in the expression of resistance within these backcross lines. Allan et al (1) also observed transgressive segregation for adult resistance to stripe rust in a cross of Itana × Burt. They reported that W. K. Pope and W. L. Nelson had made similar observations in progeny of crosses involving Itana. Pope (13,14) concluded that susceptible wheats contained at least 20 genes that might confer partial resistance to progeny of appropriate crosses. In 1971, Henriksen and Pope (6) reported on the segregation of minor genes for additive levels of resistance.

Lewellen et al (10,11) studied the inheritance of both major and minor genes for stripe rust resistance by

crossing PI 178383 and Chinese 166 (both resistant) with Lemhi (susceptible) and by using two diurnal temperature profiles for growing the plants. The presence of minor genes was clearly shown in F₃ plants at the 15/24 C temperature profile (10,11).

Inoculation, continuous selfing, selection, and diallel-cross analysis was used to isolate lines of PI 178383/Itana that contained one, two, and three detectable minor genes (17,20). These lines were then crossed with commercial wheat varieties to develop new minor-gene lines (PI 178383/Itana//commercial wheat cultivars). In general, these genes (i) behaved as recessives, (ii) were temperature sensitive, (iii) conferred higher levels of resistance when combined together, (iv) probably existed in many commercial wheat cultivars, and (v) were a possible source of long-lasting general resistance (17–19,21,22).

The general nature of this form of resistance was reported by Stubbs (23), who worked with four minor gene lines isolated by Sharp over a period of 8 yr. Sharp demonstrated its general nature by testing these minor gene lines with four pathotypes from the United States and five pathotypes from Europe. These pathotypes contained different virulence factors and virulence genes for all cultivars included within the differential host set for the determination of stripe rust races (19; Sharp, *unpublished*).

In recent years, the importance of general resistance in controlling plant diseases has been recognized increasingly. Minor gene resistance is one example of general resistance that has been demonstrated. This study was undertaken to determine the gene action associated with general resistance moderated by minor genes and to determine whether such resistance can be manipulated in a regular breeding program.

MATERIALS AND METHODS

Wheat seeds were planted in a row across the diameter of 10.5-cm clay pots that contained steamed soil. The pots were placed in a growth chamber with a 12-hr daily photoperiod ($2.2-3.3 \times 10^4$ erg/cm²/sec) at $15/24 \pm 1$ C (dark/light). Plants were inoculated when the second leaf appeared, 10–12 days after planting. Inoculum was prepared directly from field collections of *P. striiformis*. It included two pathotypes indigenous to the Gallatin Valley of Montana, which Volin (24) has tentatively named races 3 and 4. For inoculation, leaves were oriented horizontally in a modified settling tower. Urediospores were shot up into the tower with a CO₂ gun and were allowed to settle for 4 min (16). After inoculation, the plants were placed in a darkened dew chamber for 20–24 hr at 7 C and were returned to the growth chamber. After 1 wk, the leaves above the primary leaf were clipped off. Disease readings were made after a

total incubation period of 2 wk. The ten infection types were assigned numerical values increasing from 1 to 10, as susceptibility increased (3) to facilitate computer analysis.

First diallel cross.—Six minor gene lines, derived from crosses of PI 178383/Itana//commercial cultivars and resistant in their reaction type were included in this diallel cross. The lines were: 1/Lancer, infection type 0-, 75-312; 1//Rego/Cheyenne, infection type 0, 75-333; 1/Delmar, infection type 1-, 75-344; 3/Delmar, infection type 00, 75-249; 2/Delmar, infection type 0, 75-277, and 1/Lancer, infection type 1-, 75-317. Head rows of F₆ plants were used as parents for the reciprocal crosses to form a complete 6 × 6 diallel.

Second diallel cross.—Three minor gene lines that were stable for infection type were intercrossed with four susceptible winter wheats to form a complete 7 × 7 diallel. The three minor gene lines were: 3//Rego/Cheyenne, infection type 0-, 75-1787; 1//Rego/Cheyenne, infection type 0-, 75-333; and 1/Lancer, infection type 0-, 75-312.

TABLE 1. Infection types obtained from a diallel cross of minor gene lines (PI 178383/Itana//commercial wheat cultivars)^a

Minor gene lines	Infection type ^b					
	1/Lancer	1//Rg/Cnn 37-3-6	1/Delmar	3/Delmar	2/Delmar	1/Lancer
1/Lancer	3.4 ^c	4.0	5.4	4.0	5.5	4.4
1//Rg/Cnn 37-3-6	4.0	3.9	4.4	3.6	4.0	5.0
1/Delmar	5.2	4.7	5.0	4.6	5.4	6.9
3/Delmar	4.0	3.3	4.3	2.1	4.3	4.6
2/Delmar	4.6	4.7	6.9	4.2	3.9	5.0
1/Lancer	4.5	5.1	5.5	4.4	5.2	4.8

^aDiallel analysis of F₁ hybrids and parents; 1//Rg/Cnn is 1//Rego/Cheyenne.

^bInfection type ratings 1 through 10, with increasing susceptibility (3).

^cInfection type of parent indicated by selfed value (above line).

TABLE 2. Mean squares from analyses of first diallel, in which minor gene lines (PI 178383/Itana//commercial wheat cultivars) resistant to stripe rust were intercrossed, and of second diallel, in which resistant minor gene lines were intercrossed with susceptible commercial wheat cultivars^a

Source	First diallel ^b		Second diallel ^b	
	DF	MS	DF	MS
General combining ability (additive)	5	32.0** ^c	6	433.9**
Specific combining ability (nonadditive)	9	3.0**	14	31.7**
Maternal	5	0.9**	6	107.4**
Reciprocal	10	3.3**	15	35.2**
Error (experimental error)	345	0.3	697	3.1
Total genetic variance		35.0		465.6

^aAnalyses according to Schaffer and Usanis (15).

^bAnalysis of infection-type ratings increasing from 1 to 10 as susceptibility increased (3).

^c**Significant at 1% level.

The four susceptible winter wheats were: McCall, CI 13842; Sundance, CI 15327; Trader, CI 13998; and Itana, CI 12933.

The parents and their F_1 crosses were tested simultaneously for each diallel. Because the first diallel was replicated 14 times and the second diallel 18 times, weighted means of the infection types were calculated for presentation in a table. The number of individual plants

for each infection type was multiplied by the infection type value (1 through 10), summed together, and divided by the total number of individuals tested. The data from parents and reciprocal crosses were analyzed by use of the general least-squares analysis of diallel experiments that Schaffer and Usanis (15) developed. All data from the two diallel crosses were analyzed individually by the Data Systems Application Division, SEA, USDA, Beltsville, MD. Information in the diallel analyses was used to estimate gene action, genetic variance, and heritability according to the methods of Finkner et al (4).

TABLE 3. Gene action and heritabilities from analyses of first diallel, in which minor-gene lines (PI 178383/Itana//commercial wheat cultivars) resistant to stripe rust were intercrossed, and of second diallel, in which resistant minor gene lines were intercrossed with susceptible commercial wheat cultivars^a

Source	First diallel	Second diallel
Gene action, additive genetic variance (%)	91.4	93.2
Gene action, nonadditive genetic variance (%)	8.6	6.8
Broad-sense heritability (%)	99.0	99.3
Narrow-sense heritability (%)	90.6	92.6

^aAnalyses according to Finkner et al (4).

RESULTS

First diallel cross.—The weighted means of the infection types of the parents were all resistant (Table 1). They ranged from 2.1 (infection type, 00) to 5.0 (infection type 1-). All of the hybrids were resistant except two, which were intermediate at 6.9 (infection type 2). The general combining ability, specific combining ability, and maternal effects were significant (Table 2). Additive genetic variance made up the largest percentage of gene action (Table 3). Broad-sense and narrow-sense heritability estimates were 99 and 91%, respectively (Table 3).

Second diallel cross.—The resistant/resistant and susceptible/susceptible crosses were easily distinguished from the resistant/susceptible and the susceptible/resistant crosses (Table 4). The three resistant

TABLE 4. Infection types obtained from diallel cross of minor gene lines with wheat susceptible to stripe rust^a

Line	Infection type ^b						
	3//Rg/Cnn	1//Rg/Cnn	1/Lancer	McCall	Sundance	Trader	Itana
3//Rg/Cnn	2.5 ^c R ^d	3.0 R	3.1 R	7.0 I ^e	7.1 I	5.8 I	7.2 I
1//Rg/Cnn	2.8 R	2.9 R	4.2 R	7.1 I	7.8 S ^f	7.0 I	7.0 I
1/Lancer	2.5 R	3.8 R	3.0 R	7.4 I	6.9 I	8.6 S	7.3 I
McCall	7.1 I	7.4 I	8.9 S	8.7 S	9.0 S	8.9 S	8.8 S
Sundance	7.5 S	5.8 I	7.7 S	9.0 S	8.0 S	8.7 S	8.9 S
Trader	7.5 S	7.0 I	7.8 S	9.0 S	8.9 S	8.3 S	8.9 S
Itana	6.5 I	6.6 I	7.1 I	9.1 S	9.0 S	8.9 S	7.7 S

^aDiallel analysis of F_1 hybrids and parents; minor gene lines: 3//Rego/Cheyenne, 1//Rego/Cheyenne, and 1/Lancer.

^bInfection type ratings 1 through 10, increasing with increased susceptibility (3).

^cInfection type of parent indicated by selfed value (above line).

^dR = resistant.

^eI = intermediate.

^fS = susceptible.

parents and the six resistant/resistant hybrids were highly resistant. The four susceptible parents and the 12 susceptible/susceptible crosses were all susceptible. Ten of the resistant/susceptible crosses were intermediate in reaction type, and only two were susceptible. Seven of the susceptible/resistant crosses were intermediate in reaction type, and five were susceptible (Table 4).

General combining ability, specific combining ability, and maternal effects were highly significant (Table 2). Additive genetic variance again made up the largest percentage of gene action (Table 3). Broad-sense and narrow-sense heritability estimates were 99 and 93%, respectively (Table 3).

DISCUSSION

First diallel cross.—The general combining ability, a measure of additive gene action, was highly significant (Table 2) and accounted for a high proportion of the gene action (Table 3). The specific combining ability, a measure of nonadditive gene action, was significant; however, the mean square for the general combining ability was ten times that of the specific combining ability. This additive minor gene resistance could be manipulated easily in a breeding program because of a high level of additive gene effects and the high heritabilities. The cytoplasm of the female parent probably contributes maternal effects to the expression of resistance.

Second diallel cross.—Ten of the resistant/susceptible crosses were intermediate in reaction type and only two were susceptible. Seven of the susceptible/resistant crosses were intermediate in reaction type and five were susceptible (Table 4), indicating possible maternal effects in which the cytoplasm of the female parent contributed to the expression of resistance. In resistant/susceptible and corresponding reciprocal crosses, the intermediate hybrids predominated with 17 out of 24 hybrids being intermediate in reaction type (Table 4). This intermediate reaction type of the F_1 hybrids is for any plant character that is controlled by additive gene action: the hybrids are intermediate to the two parents. Additive resistance was present in the minor gene lines.

The high percentage of additive genetic variance, the low percentage of nonadditive genetic variance, and the high heritability from the second diallel agree with the same parameters from the first diallel.

This conclusion is further supported by preliminary studies in which minor gene lines (P_1/P_2) and F_1 minor gene lines ($P_1/P_2//P_3/P_4$) were intercrossed (9). A high level of resistance was selected in the F_2 and maintained in the F_3 segregating progeny.

Results of intercrossing the minor gene lines with commercial cultivars indicated that the commercial cultivars carried genes for resistance (19,21). Thus, the next stage in development of this additive resistance would be to cross cultivars that are commercially acceptable. By using acceptable commercial cultivars as parents, undesirable agronomic traits associated with sources of exotic germplasm can be avoided.

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