

# Reaction of F<sub>2</sub> Seedlings of Several Crosses of Susceptible and Resistant Wheat Selections to *Puccinia striiformis*

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## ABSTRACT

We classified F<sub>2</sub> progeny of crosses among nine sources of wheat (*Triticum aestivum*) with seedling resistance (Nord, Spaldings Prolific, Holzapfel Fruh, Rouge Prolifique Barbu, Heines Kolben, Ottawa/Renacimiento, Alba, P.I. 178383, and Suwon 92/3\*Omar, 63301) and two seedling-susceptible selections (Omar and Gaines) for reaction to a culture of *Puccinia striiformis*. We also studied certain crosses among the nine seedling resistant sources. Pre- and postinoculation temp were 15 ± 2 C. In general, crosses of resistant parents with Omar produced higher proportions of plants in the resistant classes than crosses with Gaines. Resistant × susceptible crosses demonstrated monogenic control of

reaction with P.I. 178383, Spaldings Prolific, and Sel.63301, whereas digenic control prevailed with Nord, Holzapfel Fruh, and Ottawa/Renacimiento. Eight resistant × resistant crosses indicated digenic control, but the crosses Nord/Spaldings Prolific, Nord//Ottawa/Renacimiento, P.I. 178383//Ottawa/Renacimiento, Nord/Rouge Prolifique Barbu, and P.I. 178383/Alba gave trigenic reaction patterns. No suitable interpretation could be made of the reaction pattern of the Sel.63301//Ottawa/Renacimiento cross. Evidence suggests that Nord, Heines Kolben, and P.I. 178383 have in common at least one gene that governs an intermediate reaction type. *Phytopathology* 60:1368-1372.

The breeding of cultivars of wheat (*Triticum aestivum*) resistant to *Puccinia striiformis*, the pathogen that causes stripe rust, has been intensified in the Pacific Northwest, since a major outbreak of stripe rust occurred in 1960. In addition to some indigenous sources, numerous exotic sources of resistance have been incorporated into the plant breeding programs of the region.

There is limited information concerning the inheritance of host resistance for much of the germ plasm currently in use, particularly the exotic sources. Several genetic studies concerned with the inheritance of host reaction to the stripe rust fungus have direct bearing on the present study, however.

Metzger & Silbaugh (7), in field studies at Corvallis, Oregon, reported that the near immunity of P.I. 178383 to *P. striiformis* was conditioned by a single dominant gene. This gene was linked within two map units of a brown chaff gene of P.I. 178383.

Sharp (11) demonstrated the importance of environmental control in genetic studies involving the host and *P. striiformis*. Lewellen et al. (5) and Lewellen & Sharp (4) described the genetic control of host resistance to a single pathogenic type of *P. striiformis* for P.I. 178383, Chinese 166, and Rego. Two types of resistance factors were found to condition disease reaction (5). Single "major" genes and an undetermined number of "minor" genes were found in P.I. 178383 and Chinese 166. The minor genes were temp-sensitive, but capable of conditioning usable levels of resistance in additive combinations. They hypothesized that minor genes are possibly nonspecific and do not adhere to corresponding gene-for-gene systems. The study of Lewellen & Sharp (4) suggested that the reaction of Rego was conditioned by complementary dominant

genes and one or more temp-sensitive minor genes. Minor host genes of P.I. 178383 in combination with the minor host genes of Rego gave an additive interaction for greater resistance under high and low temp profiles.

Allan & Purdy (1) reported monogenic control of reaction to *P. striiformis* for P.I. 94349 and Kansas Sel.587023. These two host genes appeared to fit the "major gene" category of Lewellen et al. (5).

Pope (8) tested several populations of wheat under field conditions at Moscow, Idaho, and believed a min of 20 different host genes were represented. Numerous genetic studies made outside of the United States, particularly in Europe, have been reviewed by Macer (6).

The purpose of this study was to gain background information on the inheritance of host reaction of nine sources of resistance to a culture of *P. striiformis* under controlled environmental conditions.

**MATERIALS AND METHODS.**—Material tested for seedling reaction to culture 61-1 of *P. striiformis* West consisted of 33 F<sub>2</sub> wheat crosses and their parents. Parental germ plasm included nine resistant and two susceptible selections to stripe rust culture 61-1. This culture is virulent on Chinese 166 and avirulent on P.I. 178383, Triumph, and Suwon 92/3\*Omar, 63301 (10). The parents, their infection types, and their abbreviations are described in Table 1. Parents and F<sub>2</sub> populations of the crosses were classified for reaction when inoculated with culture 61-1.

All populations were grown in galvanized metal flats in rows spaced 2 inches apart; single rows contained approximately 30 F<sub>2</sub> plants or 30 parental plants. Between 200 and 450 F<sub>2</sub> seedlings of each cross were classified. Seedlings grew before and after inoculation in a plastic greenhouse bench maintained at 15 ± 2 C.

Plants received 12 hr of supplemental light (6 AM to 6 PM) from fluorescent tubes in addition to natural light. Seedlings were inoculated in the one- to two-leaf stage with a mixture of urediospores in talc (9). Infection types that developed on seedlings were determined 14 to 16 days after inoculation. The system followed to assign infection types has been previously described (9).

To facilitate direct comparison between the reactions obtained between the host and the pathogen, crosses of the resistant parents to Gaines and Omar were tested simultaneously. Chi-square analyses were used to evaluate goodness of fit tests.

In order to test various hypothetical ratios offered to explain the genetic control of reaction type, the intermediate class was combined with either the resistant or susceptible class in several instances. This pooling of classes seemed justified, since unpublished results from our laboratory in several instances have shown that the progeny of  $F_2$  plants classed as intermediate (type 2) have given both resistant and susceptible reactions. Similarly, Lewellen & Sharp (4) reported considerable discrepancy between the reaction of  $F_2$  plants and their  $F_3$  progeny to stripe rust in a Rego  $\times$  Lemhi cross.

**RESULTS.**—The nine resistant parents produced similar infection types when inoculated with culture 61-1 of stripe rust (Table 1). Holzapfel Fruh (H.F.) and Ottawa (OT)/Renacimiento (Rcm) gave infection type 0, but a few plants of these two parents also classed as type 1. Omar seedlings were completely susceptible (type 4); most seedlings of Gaines also gave type 4 but a few plants classed as type 3.

Reactions to *P. striiformis* of  $F_2$  plants of crosses with the nine resistant parents to Gaines (Gns) and Omar were not in general agreement (Table 2). The cross Gns/Sel.63301 yielded insufficient seed for testing. Reactions of  $F_2$  plants of the 17 crosses tested segregated into three general categories; i.e., resistant, intermediate, and susceptible. Resistant plants demonstrated infection types of 0 or 1, intermediate plants showed type 2, and susceptible plants consisted of types 3 or 4.

In general, crosses with Omar produced a higher percentage of plants within the resistant class than did crosses with Gaines (Table 2). Exceptions to this pattern included Spaldings Prolific (S.P.) and P.I. 178383,

which had relatively the same percentage of resistant plants in both their Omar and the Gaines crosses. The Gns/Alba cross was unique and had a considerably greater number of resistant plants than did the Omar/Alba cross (25 versus 6%). Five of eight crosses with Gaines had 14 to 26% more  $F_2$  plants classified susceptible than their respective Omar crosses (Table 2). Crosses with Ottawa/Renacimiento and P.I. 178383 had comparable proportions of susceptible  $F_2$  plants.

**Inheritance in susceptible  $\times$  resistant crosses.**—Although we recognize that  $F_2$  data alone do not allow for precise interpretation, some conclusions concerning the inheritance of reaction to collection 61-1 could be reached from the Omar and Gaines crosses. Crosses of P.I. 178383 with Omar and Gaines suggested that a single dominant gene of P.I. 178383 governed reaction; similarly, a single dominant gene, presumably from Suwon 92, regulated  $F_2$  seedling reaction to culture 61-1 in the Sel.63301/Omar cross.

$F_2$  populations of both Omar/S.P. and Gns/S.P. crosses fit a 1 resistant:3 moderately susceptible-susceptible ratio (Table 2). The reaction of the Gns/Rouge Prolifique Barbre (R.P.B.) cross also fit a similar one factor ratio when the resistant and intermediate groups were pooled; but no suitable interpretation of the Omar/R.P.B. reaction pattern could be made.

When the intermediate and susceptible groups are combined, the reaction of the Gns/Alba cross suggested monogenic control (Table 2), but digenic control was suggested in the Omar/Alba cross (1 resistant:15 intermediate-susceptible ratio, Table 2). The  $F_2$  plant reactions of crosses of Omar and Gaines with Heines Kolben produced monogenic and digenic patterns, respectively (Table 2). Segregation in crosses of Omar and Gaines with Holzapfel Fruh, Nord, and Ottawa/Renacimiento followed typical digenic control. Different hypothetical digenic ratios were proposed for each of these three resistant parents when crossed to Omar and Gaines (Table 2).

**Inheritance in resistant  $\times$  resistant crosses.**—Relationships for the inheritance of stripe rust reaction to collection 61-1 of 14 crosses among 9 resistant parents gave evidence of considerable genetic diversity in control of stripe rust reaction. Susceptible plants were recovered when Spaldings Prolific was crossed to Nord, Sel.63301, and P.I. 178383 (Table 3). Similarly, Holzapfel Fruh and Ottawa/Renacimiento segregated sus-

TABLE 1. Wheat parents, their abbreviations, identification numbers, source, and infection type to culture 61-1 of *Puccinia striiformis*

Parent	Abbreviation	Identification No.	Source	Infection type
Nord		P.I. 174677	France	0(57) <sup>a</sup>
Spaldings Prolific	S.P.	C.I. 11766	Germany	0(62)
Holzapfel Fruh	H.F.	C.I. 11771	Germany	0(54), 1(5)
Rouge Prolifique Barbu	R.P.B.	C.I. 11774	Germany	0(52)
Heines Kolben	H.K.	P.I. 180619	Germany	0(39)
Ottawa/Renacimiento	Ot/Rcm	Ks 79847	Kansas	0(46), 1(14)
Alba		C.I. 13256	Oregon	0(55)
P.I. 178383		P.I. 178383	Turkey	0(58)
Suwon 92/3*Omar, 63301	Sel. 63301	A 63301	Wash.	0(63)
Omar		C.I. 13072	Wash.	4(93)
Gaines	Gns	C.I. 13448	Wash.	3(13), 4(74)

<sup>a</sup> Value inside parentheses represents the number of plants classified as to infection type.

TABLE 2. Plant reactions, infection types, hypothetical ratios, and probability values for 17 F<sub>2</sub> populations involving Omar and Gaines wheat inoculated with collection 61-1 of *Puccinia striiformis*

Cross	Reaction and infection type			Total	Hypothetical ratio	P
	Resistant 0-1	Intermediate 2	Susceptible 3-4			
Gaines/Nord	96	56	222 <sup>a</sup>	374	3:13	.80-.70
Omar/Nord	122	56	148	326	7:9	.05-.02
Gaines/S.P.	74		180	254	1:3	.20-.10
Omar/S.P.	85	79	154	318	1:3	.50-.30
Gaines/H.F.	22	25	267	314	1:15	.70-.50
Omar/H.F.	67	78	261	406	3:13	.30-.20
Gaines/R.P.B.	117	35	252	404	1:3	.10-.05
Omar/R.P.B.	266		148	414		
Gaines/H.K.	67	51	233	351	3:13	.90-.80
Omar/H.K.	65	37	112	214	1:3	.10-.05
Gaines/ /Ot/Rcm	28	137	259	424	1:15	.80-.70
Omar/ /Ot/Rcm	48	63	174	285	3:4:9	.20-.10
Gaines/Alba	100	106	197	403	1:3	.95-.90
Omar/Alba	19	86	209	314	1:15	.90-.80
Gaines/P.I. 178383	319		103	422	3:1	.90-.80
Omar/P.I. 178383	329		117	446	3:1	.70-.50
Omar/Sel. 63301	329		127	456	3:1	.20-.10

<sup>a</sup> Classes connected by horizontal line pooled for purposes of analysis.

ceptible F<sub>2</sub> plants when crossed with the same three selections. F<sub>2</sub> populations of Nord/R.P.B. and Sel. 63301/R.P.B. had 2 and 4% susceptible plants, respectively.

No highly susceptible F<sub>2</sub> plants were recovered from the crosses of Heines Kolben (H.K.) with Nord or P.I. 178383 (Table 3). Plants with intermediate or moderately susceptible reactions occurred in both populations at frequencies of 23% (Nord/H.K.) and 7% (P.I. 178383/H.K.).

This study did not allow for a complete genetic analysis of the inheritance of reaction in regard to the specific genes carried by all the parents. F<sub>2</sub> plant reactions of certain crosses did warrant tentative conclu-

sions about the inheritance of reaction to culture 61-1 for several sources of resistance, however.

When the intermediate and susceptible plants are grouped together, segregation of the P.I. 178383/S.P. cross closely fit a 15 to 1 ratio (Table 3). The reaction of Sel.63301/S.P. cross gave a good fit for a 15 resistant:1 intermediate-susceptible ratio (Table 3). The inheritance of F<sub>2</sub> plant reaction in the Nord/S.P. cross was more complex (Table 3). If resistant and intermediate plants were combined, the pattern fit a three factor (57:7) ratio.

Crosses of Holzapfel Fruh to Nord and P.I. 178383 demonstrated digenic control (15 resistant:1 susceptible ratio) of F<sub>2</sub> reaction to stripe rust (Table 3)

TABLE 3. Plant reactions, infection types, hypothetical ratios, and probability values for 14 F<sub>2</sub> populations of wheat (resistant × resistant parents) inoculated with collection 61-1 of *Puccinia striiformis*

Cross	Reaction and infection type			Total	Hypothetical ratio	P
	Resistant 0-1	Intermediate 2	Susceptible 3-4			
Nord/S.P.	370	17	40 <sup>a</sup>	427	57:7	.20-.10
Sel. 63301/S.P.	390	4	21	415	15:1	.90-.80
P.I. 178383/S.P.	413	2	20	435	15:1	.50-.30
Nord/H.F.	352	54	25	431	15:1	.80-.70
Sel. 63301/H.F.	394	12	24	430	15:1	.70-.50
P.I. 178383/H.F.	360	8	14	382	15:1	.70-.50
Nord/ /Ot/Rcm	164	177	6	347	63:1	.80-.70
Sel. 63301/ /Ot/Rcm	362	68	13	443	?	
P.I. 178383/ /Ot/Rcm	349	72	10	431	63:1	.30-.20
Nord/R.P.B.	352	88	8	448	63:1	.80-.70
Sel. 63301/R.P.B.	416	10	19	445	15:1	.50-.80
Nord/H.K.	212	62		274	13:3	.20-.10
P.I. 178383/H.K.	411	32		443	15:1	.30-.20
P.I. 178383/Alba	387	39	15	441	57:7	.50-.30

<sup>a</sup> Classes connected by a horizontal line were pooled for purposes of analysis.

when the intermediate class is combined to the susceptible class (P.I. 178383/H.F.) or to the resistant class (Nord/H.F.). The Sel.63301/H.F. cross was inconclusive. When resistant and intermediate groups were combined, digenic control was indicated (Table 3); whereas when the intermediate and susceptible classes were pooled, a 57:7 ratio occurred.

Two of three crosses of resistant selections to Ottawa/Renacimiento gave trigenic inheritance of  $F_2$  plant reaction. Both the Nord//Ot/Rcm and the P.I. 178383//Ot/Rcm cross fit a 63 to 1 ratio when  $F_2$  plants classed as type 2 are grouped with the type 0 and 1 plants. The  $F_2$  reaction of the Sel.63301//Ot/Rcm cross did not fit either a 2 or 3 factor pattern.

Crosses of Rouge Prolifique Barbu with Nord and Suwon 92/3\*Omar, 63301 gave trigenic and digenic  $F_2$  reaction patterns to culture 61-1. The Nord/R.P.B. cross fit a 63:1 ratio when only type 3 and 4 plants are considered susceptible; and the Sel.63301//R.P.B. cross gave a 15 resistant:1 intermediate or susceptible ratio (Table 3).

The reaction pattern of the P.I. 178383/Alba cross proved complex. By combining the intermediate and susceptible plants, the distribution of plant reaction conformed to a trigenic ratio of 57 to 7 (Table 3).

DISCUSSION.—Gaines and Omar have nearly comparable susceptible infection types to culture 61-1, yet they possess genes that produce completely different gene action patterns in combination with the factors carried by several parents. These differences in gene action result in a reduced proportion of resistant plants and increased proportion of susceptible plants for crosses of Gaines to Holzapfel Fruh, Heines Kolben, Rouge Prolifique Barbu, and Nord when compared to the crosses of these same resistant parents to Omar. Crosses with Spaldings Prolific suggest that a single recessive gene controls reaction type, but considerably fewer plants had infection types of 3 or 4 in the S.P./Omar than S.P./Gaines cross. Omar must carry at least one gene not present in Gaines which interacts with the Spaldings Prolific genotype to give the intermediate infection type 2.

Lewellen & Sharp (4) have shown that combining minor additive host genes can produce resistant infection types. Although complete evidence is lacking, we believe that, unlike Gaines, Omar has one or more genes that contribute additive or complementary genetic effects when combined with exotic resistant sources. Sharp (11) has established that Omar gives resistant infection types when seedlings are grown at high temp (21 and 24 C) prior to and after inoculation with *P. striiformis*. Therefore, Omar must have a gene or genes that conditions resistance to certain cultures of *P. striiformis*. Perhaps the gene(s) for host resistance detected by Sharp (11) also operates at the constant  $15 \pm 2$  C regime used in this study.

Lewellen et al. (5) reported that minor genes may modify the expression of major genes so that a lower infection type results. We suggest that one or more genes of Omar function similarly.

Crosses of Gaines and Omar to Alba did not follow the general pattern previously mentioned. The Omar

genetic background may act epistatically to gene(s) of Alba and thus account for the divergent reaction patterns. We cannot rule out the possibility that Gaines may also have gene(s) that modify certain major genes for resistance. The occurrence of modifiers appears to be rare; Lewellen et al. (5) pointed out that evidence for complementary, additive gene action in the expression of stripe rust resistance has been reported frequently.

Since both Omar and Gaines appear to have genes capable of influencing the expression of resistance, we could not determine the number of major genes possessed by all of the resistant sources employed as parents in susceptible  $\times$  resistant crosses.

Reactions of  $F_2$  seedlings from resistant  $\times$  resistant crosses aided in the determination of host genes possessed by certain resistant parents. We believe that P.I. 178383 and Sel.63301 have a single but different major gene which conditions infection type when inoculated with culture 61-1. Recently we described a culture that is pathogenic on Sel.63301 but not on P.I. 178383 (10). Nord also probably differs from either P.I. 178383 or Sel.63301. Under Pullman, Washington, field conditions in some seasons, Nord becomes susceptible to *P. striiformis* after heading and infection types as high as type 4 have been recorded. Similar observations have not been detected with P.I. 178383 and Sel. 63301. These three resistant sources were used as tester parents in crosses with the seven remaining resistant sources because of these earlier observations.

Previous studies (2, 5, 7) as well as the present study indicate that P.I. 178383 and Sel.63301 have a single major gene that conditions low infection types to culture 61-1. The current study suggests that Spaldings Prolific also has a single major gene inherited independently of either the P.I. 178383 or Sel.63301 gene. No positive conclusions could be formed about the remaining seven sources of resistance, however.

Although crosses with Gaines and Omar would suggest that Holzapfel Fruh, Ottawa/Renacimiento, and Nord carry two major genes for expression of infection type, the crosses with other resistant sources do not entirely verify this conclusion. Crosses of Ottawa/Renacimiento to Sel.63301 and P.I. 178383 substantiate that Ottawa/Renacimiento has two major genes for expression of infection type; the reaction of this selection when crossed to Sel.63301 could not be explained. Digenic control was indicated in crosses of Holzapfel Fruh with P.I. 178383 and Sel.63301. Complementary gene action could account for these results wherein Holzapfel Fruh may have two complementary genes for resistance. P.I. 178383 and Sel.63301 may have one of the Holzapfel Fruh genes plus another major gene detected in crosses to the two susceptible parents. Alba may carry two major genes since like Ottawa/Renacimiento, when crossed with P.I. 178383, the reaction suggested trigenic control.

Crosses with Nord most frequently indicated complex genetic control of the expression of infection type. A previous study (3) indicated that Nord may have two genes governing reaction to collection 61-1. The occurrence of digenic control when Nord was crossed

to susceptible parents as well as trigenic control when crossed to certain resistant parents substantiates this conclusion. Epistasis or complementary gene action or both could account for the digenic ratios encountered in the Nord/H.F. cross.

Our results also indicate that Nord and P.I. 178383 each has at least one gene in common with Heines Kolben that conditions an infection type 2. No susceptible  $F_2$  plants (types 3 or 4) were recovered from these two crosses. Lewellen et al. (5) showed that P.I. 178383 has a major gene and an undetermined number of minor genes. The minor genes are expressed only under high temp conditions. P.I. 178383 may have still another gene which is expressed at the  $15 \pm 2$  C temp regime. This gene apparently is not detected in certain crosses of P.I. 178383 with Gaines, Omar, Spaldings Prolific, and Holzapfel Fruh, which suggests it may be vulnerable to epistatic influence. Similarly, Nord may have a gene in common with Heines Kolben that conditions infection type 2. The Nord/H.K. cross consisted of only 274 plants and, therefore, we cannot rule out the possibility that small sample size accounted for the lack of susceptible plants. Likewise, linkage between host genes of P.I. 178383 and Heines Kolben, as well as between Nord and Heines Kolben, could also explain the failure to recover susceptible progeny.

According to Lewellen et al. (5), inheritance studies conducted under a nonvarying environment would fail to identify so-called minor host genes. The host genes demonstrated in our study probably represent major genes. The resistant  $\times$  resistant crosses do not suggest complexity of inheritance of these genes. Although the inheritance of reaction for the one cross (Sel. 63301//Ot/Rcm) could not be interpreted, the other crosses suggested digenic or trigenic control. None of the resistant sources represent germ plasm with multi-major gene resistance to stripe rust.

An important objective of the applied breeding program at Pullman is to transfer exotic host resistant genes into locally adapted germ plasm. The relatively simple genetic control of rust resistance shown in this study suggests that this objective can be obtained for most of the resistant sources studied.

Recently, Lewellen & Sharp (4) and Lewellen et al. (5) stressed the value of minor additive host genes for disease protection. They pointed out that major host genes are specific to corresponding pathogen genes, and frequently are compromised by mutation or new recombinants in the pathogen. They stress use of minor additive genes which they believe are nonspecific for pathogenicity. A disadvantage of minor, temp-sensitive genes is that often they do not confer resistance throughout the entire life cycle of the wheat plant. Lewellen & Sharp (4) suggest that this disadvantage

could be overcome through combination of low and high temp sensitive genes for resistance, and thus provide resistance over a wider temp range.

Utilization of combinations of both major and minor host genes for disease protection is a logical suggestion (1, 5). In actual plant breeding practice, incorporating both forms of resistance may be difficult, particularly if major host genes are epistatic to minor host genes.

A plant breeding method now used in our program involves a modified backcross system wherein the recurrent parent has minor but no major genes for resistance. Major gene resistance is recovered in successive backcrosses. After two or three backcrosses to appropriate minor gene parents, a majority of the backcross progeny should have both major and minor gene resistance. This system provides a flexible procedure wherein the primary criteria for recurrent parents would be that they contain minor genes. In this way, several parents identified to have minor genes for host resistance could be introduced into the backcross program.

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