Reselection for Improved Resistance of Wheat to Stripe Rust

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ABSTRACT

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Ten acceptable commercial cultivars of spring wheat with resistant, intermediate, and susceptible reactions to stripe rust were intercrossed. The most resistant seedlings (10–20%) were selected in each of four segregating generations, transplanted, and grown to maturity. When evaluated as seedlings in controlled environment chambers, 45 spring wheat crosses showed transgressive segregation. Transgressive segregation was demonstrated in later generations in nine spring wheat crosses that lacked resistant progeny in the F_2 and F_3 generations. Ten commercial cultivars of winter wheat with acceptable agronomic performance and either intermediate or susceptible reactions to stripe rust also were intercrossed. When evaluated as seedlings in controlled environment chambers, 38 winter wheat crosses showed transgressive segregation. Transgressive segregation also was clearly shown in later generations of 17 winter wheat crosses even though the F_2 and F_3 generations of these crosses were totally susceptible. Under field conditions of natural infection, progeny of 27 winter wheat crosses were selected for increased resistance. More resistance was found in the F_3 than in the F_2 progeny. Many F_4 plant progeny were more resistant than the parental cultivars.

Additional key words: general resistance, *Puccinia striiformis* West., transgressive segregation, *Triticum aestivum* L., yellow rust

The stripe rust disease of wheat, *Triticum aestivum* L., caused by *Puccinia striiformis* West. is found on all continents except Australia (9). Economic losses occur in the Pacific Northwest of the United States. The importance of general resistance in controlling plant diseases has been increasingly recognized. For example, apparent general resistance to stripe rust has been shown with minor-gene wheat lines (5–7).

Previous diallel studies involving minor-gene wheat lines (2) indicated that high heritability and a high proportion of additive gene action are associated with this form of general resistance. Thus, once obtained, resistance can be manipulated in a regular breeding program. This study was done to determine if an additive, minor-gene resistance can be obtained from agronomically acceptable spring and winter wheats by selecting for resistance in the seedling stage and by selecting for resistance in winter wheat at the adult stage under field conditions. The use of commercially acceptable cultivars as parents considerably reduces the undesirable traits usually associated with plant introductions, which are the most common new sources of resistance. We intercrossed resistant, intermediate, and susceptible spring wheats and winter wheats with intermediate and susceptible reaction types. The most resistant progeny were selected at each generation.

MATERIALS AND METHODS

Wheat plants were crossed at the Agronomy Field Laboratory near Bozeman, MT, using standard plant-breeding techniques for hand-emasculating and for pollinating with a pollen shower. All heads used for crossing were bagged after emasculation. Heads with hybrid seed were harvested and threshed individually.

Ten commercial cultivars of common spring wheat were intercrossed in the summer of 1973 to give 45 crosses. The varieties were: Bonanza, CI 14077; Centana, CI 12974; Fortuna, CI 13596; Manitou, CI 13775; Polk, CI 13773; Sheridan, CI 13586; Shortana, CI 15233; Thatcher, CI 10003; World Seeds 1809, CI 15012; and World Seeds 1812, CI 14585. Two durum wheats (*Triticum durum*, Leeds, CI 13768, and Wells CI 13333) also were intercrossed.

The 10 winter wheats were: Itana, CI 12933; Lancer, CI 13547; Delmar, CI 13442; McCall, CI 13842; Wanser, CI 13844; Teton, CI 15244; Cheyenne, CI 8885; Centurk, CI 15075; Winalta, CI 13670; and a Montana line, MT 7015. These cultivars were acceptable from agronomic and quality standpoints. All except MT 7015 have been grown commercially. The winter wheat cultivars lacked specific dominant genes for the races of stripe rust against which they were tested. With resistant parents, selection in early generations would have biased toward nonadditive effects and selection of major dominant genes. Conversely, recessive genes and most additive effects would have been masked and not accumulated.

Seedling studies. The hybrids and their parents were evaluated for infection type in the fall of 1973. Starting with the F_2 generation, each segregating generation also was evaluated as seedlings. For four generations, 10–20% of the most resistant progeny were selected, transplanted, and grown for seed for the next generation. Three winter wheat crosses were discarded because of insufficient F_2 seed.

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 ($2.2–3.3 \times 10^4$ ergs/cm^2/sec) at 15/24 ± 1 C (dark/light). Plants were inoculated when the second leaf appeared, 10–12 days after planting. Inoculum prepared directly from field collections of *P. striiformis* included two pathotypes indigenous to the Gallatin Valley of Montana, which Volin (8) designated tentatively as races 3 and 4. For inoculation, leaves were oriented horizontally in a modified settling tower. Urediospores were shot up into the tower with a CO_2 gun and allowed to settle for 4 min (4). After inoculation, the plants were placed in a darkened dew chamber for 20–24 hr at 7 C before their return to the growth chamber. After 1 wk, the leaves above the primary leaf were clipped off. Disease readings were made after a 2-wk incubation. The 10 infection types were assigned values from 1 to 10, with increasing susceptibility (1).

The nine spring wheat populations that were nearly or completely resistant in the F_5 generation were inoculated with five races of stripe rust that Volin (8) designated tentatively as B-1, race 3; VF-Mo, race 4; Cvl-C166, race 8; Msl-We, race 10; and Pn-C166, race 11.

Field studies. The F_1 hybrids from 28 winter wheat crosses were grown in the field in 1974 for F_2 seed production. In 1975 27 F_2 populations were planted. Five 10-ft rows of space-planted, segregating material were planted between rows of parents. Rows of a susceptible rust-spreader cultivar, Itana, separated parents of different groups.

Spreader rows surrounding the nursery were inoculated with field collections of *P. striiformis* early in the spring to insure adequate development of rust. The field collections of *P. striiformis* were indigenous to Montana's Gallatin Valley and contained two pathotypes tentatively designated races 3 and 4 by Volin (8).

At the 10.5 heading stage of growth (3), each plant in each F_2 population was rated for reaction to stripe rust. Plants were classified as susceptible, intermediate, or resistant. Susceptible plants had high densities of uredia and prominent striping of the leaves. Plants exhibiting intermediate reactions had moderate numbers of uredia and restricted striping of the leaves. Resistant plants had no uredia or few uredia with restricted striping. Field infections were suitably high in all years of the study to evaluate the segregating plants.

The most resistant plants were saved and bulked for the F_3 generation. In 1975, a few plants in eight populations were tagged as more resistant than most other selected plants. These few plants were bulked separately for each population and planted separately for the F_3 generation.

The 35 segregating F_3 populations in 1976 were evaluated by the methods used in 1975. The most resistant plants, an average of 11 plants (12%) per population, were saved and harvested individually for evaluation in plant rows in 1977. The data for the F_2 and F_3 generations were tabulated.

In 1977, F_4 plant rows from individually selected F_3 plants and the parents were planted and inoculated by the methods used in 1975. Tissue damage on flag leaves was rated as the percent of necrosis of total leaf area and as the percent of leaf area covered by pustules. Three weeks later, the amount of head infection was determined. Two florets from five heads, selected at random from each row, were examined. Each floret that contained rust spores was counted as one. For example, if six florets contained spores, the row would be given a rating of six. An average of 10.5 progeny rows (range 7–18) were examined for each cross. The parent cultivars, planted next tc their F_4 progeny rows, were evaluated similarly. Thus, parental varieties were replicated as many times as they were involved in the parentage of the crosses.

RESULTS

Spring wheat seedling studies. The spring wheat parents were classified as resistant (Bonanza, Fortuna, Polk, World Seeds 1809, World Seeds 1812), intermediate (Manitou, Thatcher, Sheridan), and susceptible (Centana, Shortana). Resistant plants were readily detected in some F_2 populations (Table 1). Of 45 crosses, 15 had no resistant F_2 plants. For nine crosses, no resistant plants were obtained in the F_2 or F_3 generation.

The percentage of resistant, intermediate, and susceptible plants changed with each successive generation of selection (Table 1). Resistant types continually increased from 14.3% in the F_2 to 86.1% in the F_6. Intermediate types made up about 29% of the F_2, F_3, and F_4 populations and eventually decreased to 19 and 13% for the F_5 and F_6 generations, respectively. The susceptible types continually decreased from 56.3% in the F_2 to 0.7% in the F_6 (Table 1). Thus, the susceptible types were essentially eliminated by the F_6, with only 42 plants susceptible of 5,830.

The nine spring wheat crosses that did not result in resistant progeny in the F_1, F_2, and F_3 generations were considered to lack major specific genes for resistance (Table 2). These nine crosses were: Manitou × Centana, Manitou × Thatcher, Sheridan × Centana, Sheridan × Thatcher, Shortana × Thatcher, Shortana × World Seeds 1809, Thatcher × Centana, Thatcher × Sheridan, and World Seeds 1809 × Manitou. Once resistant progeny (3.9%) were obtained in the F_4, resistance increased to 12.7% in the F_5 and 59.9% in the F_6. Conversely, susceptible types decreased continually from 77.4% in the F_2 to 2.5% in the F_6 (Table 2). A representative sample was the Manitou × Centana cross (Table 3), which does not contain the resistant parent, World Seeds 1809, or Thatcher, a variety with specific resistance (R. E. Allen, *personal communication*). Of the F_2 plants rated, 11% were intermediate in

TABLE 1. Development of resistance to stripe rust as a result of selection of resistant plants and selfing of segregating populations of 45 spring wheat crosses[a]

Generation	Crosses evaluated	Plants evaluated	Infection type (%) Resistant	Intermediate	Susceptible
Parental[b]	...	...	44.4	31.1	24.4
F_1	45	...	8.9	33.3	57.8
F_2	45	6,304	14.3	29.4	56.3
F_3	42	3,397	28.2	28.2	43.5
F_4	44	5,929	40.0	28.8	31.1
F_5	41	6,072	68.3	19.1	12.6
F_6	38	5,830	86.1	13.1	0.7

[a] Plants were evaluated as seedlings in controlled environment chambers.
[b] Total of 90 (two parents for each cross); each parent (Bonanza, Centana, Fortuna, Manitou, Polk, Sheridan, Shortana, Thatcher, World Seeds 1809, World Seeds 1812, Leeds, and Wells) was used several times.

TABLE 2. Development of resistance to stripe rust as a result of selection and selfing of segregating populations of nine spring wheat crosses[a] that lacked resistant progeny in the F_2 and F_3 populations[b]

Generation	Crosses evaluated	Plants evaluated	Infection type (%) Resistant	Intermediate	Susceptible
Parental[c]	...	...	11.1	61.1	27.8
F_1	9	...	...	22.2	77.7
F_2	8	1,200	...	22.6	77.4
F_3	9	703	...	26.5	73.5
F_4	9	1,578	3.9	31.6	64.4
F_5	7	1,144	12.7	43.3	44.1
F_6	7	870	59.9	37.6	2.5

[a] Manitou × Centana, Manitou × Thatcher, Sheridan × Centana, Sheridan × Thatcher, Shortana × Thatcher, Shortana × World Seeds 1809, Thatcher × Centana, Thatcher × Sheridan, and World Seeds 1809 × Manitou.
[b] Plants were evaluated as seedlings in controlled environment chambers.
[c] Total of 18 (two parents for each cross).

reaction type compared with 100% of the F_6 plants rated as resistant or intermediate (Table 3). Thus, the pattern was similar when the resistant cultivars were not in the parentage.

Progeny of another nine crosses were totally resistant in the F_5 generation; the F_6 plants were inoculated with five races. Only 28 (2.17%) of the 1,466 F_6 plants from these nine crosses were classified as intermediate; the rest were resistant.

The parents and F_1 through F_4 progeny of the two *T. durum* crosses were susceptible. In the Leeds × Wells cross, an intermediate infection type was found in 46 plants (45.5%) of the F_5 and in 38 plants (73.0%) in the F_6 generation. No F_5 or F_6 data were available for the Wells × Leeds cross.

Winter wheat seedling studies. The winter wheat parents were classified as intermediate (Lancer, Delmar, Teton, Cheyenne, Centurk) and susceptible (Itana, McCall, Wanser, Winalta, MT 7015). All F_1 hybrid progeny of the 41 crosses were susceptible in seedling tests (Table 4). All F_2 progeny from 35 of the 38 crosses evaluated were susceptible. Only eight individual plants from three crosses—Itana × Teton, Teton × McCall, and Teton × MT 7015—were intermediate in reaction type. Teton, an intermediate resistant variety, was the female parent in two of these crosses and the male parent in the other cross.

Twenty crosses had F_3 progeny with intermediate infection types, and 18 crosses had F_3 progeny with susceptible infection types only. Seven of 38 crosses had at least one plant with a resistant infection type. Teton was a parent in five of the seven crosses: Teton × Delmar, Teton × Lancer, Teton × McCall, Teton × MT 7015, and Wanser × Teton. The other two—Delmar × Winalta and Winalta × Cheyenne—had one resistant F_3 individual.

Of 35 F_4 crosses, 34 had progeny that were classified as having intermediate infection types. Three crosses—Lancer × Itana, Lancer × Wanser, and MT 7015 × Itana—had progeny with susceptible infection types only. Sixteen of 35 crosses had resistant F_4 progeny.

In the F_5 generation all 36 crosses had progeny with intermediate levels of resistance; 31 crosses had progeny with resistant infection types. All 25 crosses evaluated in the F_6 generation had plants with intermediate levels of resistance, and 23 crosses had progeny with resistant infection types. Transgressive segregation was evident when the infection types of F_6 progeny were compared with that of the parents. Of the F_6 plants, 27% had resistant infection types, even though no resistant parents were used (Table 4).

The 17 crosses that lacked progeny with intermediate and resistant infection types in the F_2 and F_3 also showed transgressive segregation. The resistant types increased from 1% in the F_4 to 15% in the F_6 generation. The intermediate types increased from the F_4 to the F_5 generation but then decreased in the F_6 generation (Table 5). The five crosses involving susceptible parents showed a similar pattern for recovery of resistance: McCall × Itana, McCall × MT 7015, McCall × Wanser, MT 7015 × Itana, and MT 7015 × Winalta. Of the 771 F_4 plants evaluated, 14 (1.8%) showed an intermediate reaction type. Of the 769 F_5 plants rated, 26 (3%) were resistant, 572 (74%) were intermediate, and 171 (22%) were susceptible. Of the 833 F_6 plants rated, 13 (2%) were resistant, 388 (47%) were intermediate, and 432 (52%) were susceptible. A representative sample was the McCall × Itana cross (Table 6). All of the F_2 and F_3 plants were rated as susceptible, whereas 66 % of the F_5 plants were rated as intermediate.

Field studies on adult winter wheat plants. An average of 100 individual plants (range 72–151) were rated for each of 27 F_2 populations. Of the 2,686 rated, 80.7% were susceptible, 19.9% were intermediate, and 0.5% were resistant. Only six of 27 crosses showed resistant plants: Cheyenne × Delmar, Centurk × Lancer, Delmar × Centurk, Delmar × McCall, Lancer × Delmar, and MT 7015 × Lancer. Delmar was involved in the parentage of four of these six crosses.

An average of 89 plants (range 60–115) were rated for stripe rust for each of 35 F_3 populations. Of the 3,104 plants rated, 44.7% were susceptible, 51.2% were intermediate, and 4% were resistant. Of 35 populations, 22 (63%) had resistant plants. Delmar was involved in parentage of 10 (45%) of those crosses.

The best 10 crosses were selected on the basis of the percentage of F_2 plants in intermediate and resistant classes in 1975: Teton × Delmar (59%), Lancer × Delmar (55%), Teton × McCall (51%), Teton × MT 7015 (44%), Wanser × Centurk (37%), Cheyenne × Delmar (33%), Delmar × MT 7015 (28%), Delmar × Winalta (28%), Delmar × Centurk (27%), and Itana × Delmar (23%). Delmar was involved in the parentage of seven of 10 crosses. Teton was a parent for three of the best five crosses.

From the percentage of F_3 plants in the intermediate and

TABLE 3. Development of resistance to stripe rust as a result of selection of resistant plants and selfing of segregating populations of the Manitou × Centana cross[a]

	Number of plants for each infection type[b]									
	Resistant				Intermediate		Susceptible			
Generation	00	0−	0	1−	1	2	3−	3	4	Total
Parental	...	...	...	...	...	P_1	P_2	...	...	...
F_1	...	...	...	...	...	...	F_1	...	...	...
F_2	...	...	...	0	0	11	48	37	0	96
F_3	...	...	0	0	0	3	10	10	0	23
F_4	...	0	2	4	8	32	46	75	4	171
F_5	0	0	0	0	22	39	57	23	0	141
F_6	0	8	148	8	9	4	0	0	0	177

[a] Plants were evaluated as seedlings in controlled environment chambers.
[b] Infection types of Brown and Sharp (1) were used.

TABLE 4. Development of resistance to stripe rust as a result of selection and selfing of segregating populations of 38 winter wheat crosses[a]

			Infection type (%)		
Generation	Crosses evaluated	Plants evaluated	Resistant	Intermediate	Susceptible
Parental[b]	...	...	0	51.3	48.6
F_1	38	...	0	0	100.0
F_2	35	6,012	0	0.13	99.9
F_3	38	6,271	0.4	6.1	93.4
F_4	35	5,280	9.9	23.9	66.2
F_5	36	6,342	22.9	58.4	18.7
F_6	25	5,106	27.2	49.2	23.4

[a] Plants were evaluated as seedlings in controlled environment chambers.
[b] Total of 76; two parents were used for each cross; each parent (Itana, Lancer, Delmar, McCall, Wanser, Teton, Cheyenne, Centurk, Winalta, and MT 7015) was used several times.

resistant classes in 1976, the best 10 crosses were: MT 7015 × Lancer (100% resistant), Teton × Delmar (100% resistant), Teton × McCall (96%), Teton × MT 7015 (93%), Wanser × Centurk (93%), MT 7015 × Lancer (90%), Teton × Delmar (89%), McCall × Wanser (88%), Wanser × Delmar (87%), and Winalta × Centurk (87%).

Transgressive segregation was evident when the F_4 progeny rows were compared with the parental material. The overall average for the 380 F_4 progeny rows evaluated was 40% necrosis of the flagleaf, 22% of the leaf area covered with pustules, and 2.6 florets of 10 with stripe rust spores. The overall average for the 72 parent rows evaluated at the same time was 73% necrosis of the flagleaf, 58% of the leaf area covered with pustules, and 6.4 florets of 10 with stripe rust spores. The progeny rows showed less infection than did the parent material in all three categories for disease rating.

When each cross was considered individually, the pattern of transgressive segregation was similar. By comparing the average of the progeny rows with the average of each parent, 72 comparisons were possible. In 65 comparisons, the progeny rows had less infection than the parents had in all three categories (Table 7). In comparisons of MT7015 × Cheyenne and MT7015 × Itana with MT 7015 the progeny rows had less infection in two ratings. In two ratings, Teton had less infection than its progeny in Itana × Teton. In only the four comparisons of Cheyenne × Itana with Cheyenne, Delmar × MT 7015 with MT 7015, Itana × Wanser with Wanser, and McCall × MT 7015 with MT 7015, the parent had less infection than the progeny did for all three categories of disease rating (Table 7).

DISCUSSION

Spring wheat seedling studies. Transgressive segregation for resistant plants in the F_5 and F_6 generations was demonstrated for the 45 spring wheat crosses. Because some populations contained susceptible and intermediate F_6 individuals, their distributions can possibly be shifted further towards greater resistance with continued selection and selfing. Plants from nine populations with totally resistant progeny in the F_5 were inoculated in the F_6 with five pathotypes having different virulence. Their resistance to all pathotypes was uniform.

TABLE 5. Development of resistance to stripe rust as a result of selection and selfing of segregating populations of 17 winter wheat crosses[a] with susceptible progeny in the F_2 and F_3 populations[b]

Generation	Crosses evaluated	Plants evaluated	Infection type (%) Resistant	Intermediate	Susceptible
Parental [c]	...	...	0	38	62
F_1	17	...	0	0	100
F_2	16	2,922	0	0	100
F_3	17	2,709	0	0	100
F_4	17	2,743	1	11	88
F_5	16	2,798	10	69	23
F_6	13	2,637	15	46	39

[a] Cheyenne × Itana, Centurk × Lancer, Delmar × McCall, Delmar × MT 7015, Itana × Delmar, Lancer × Itana, Lancer × McCall, Lancer × Wanser, McCall × Centurk, McCall × Itana, McCall × MT 7015, McCall × Wanser, MT 7015 × Itana, MT 7015 × Winalta, Wanser × Centurk, Wanser × Delmar, and Winalta × Centurk.
[b] Plants were evaluated as seedlings in controlled environment chambers.
[c] Total of 36, because two parents were used for each cross; each parent was used several times.

TABLE 6. Development of resistance to stripe rust as a result of selection of resistant plants and selfing of segregating populations of the McCall × Itana cross[a]

Generation	Number of plants for each infection type: Intermediate 1	Intermediate 2	Susceptible 3−	Susceptible 3	Susceptible 4	Total
Parental	...	...	...	P_1, P_2	...	...
F_1	...	...	...	F_1	...	...
F_2	0	0	8	240	0	248
F_3	0	0	5	110	57	172
F_4	0	3	16	139	10	168
F_5	6	132	60	11	0	209

[a] Plants were evaluated as seedlings in controlled environment chambers.
[b] Infection types of Brown and Sharp (1) were used.

TABLE 7. Averages of field reactions to stripe rust for the F_4 progeny rows and for the parents of each individual cross[a]

Cross	F_4 plant rows: Rows (no.)	Necrosis of flagleaves (%)	Pustule coverage of flagleaves (%)	Head infection[b]	Female parent: Necrosis of flagleaves (%)	Pustule coverage of flagleaves (%)	Head infection[b]	Male parent: Necrosis of flagleaves (%)	Pustule coverage of flagleaves (%)	Head infection[b]
Cheyenne × Delmar	10	32	17	0.1	63	45	5.0	95	91	7.8
Centurk × Lancer	15	31	11	3.2	81	61	7.1	38	15	6.3
Delmar × McCall	10	38	19	2.4	95	91	7.8	84	71	8.4
Delmar × Winalta	9	49	32	2.2	95	91	7.8	58	45	4.5
McCall × Wanser	10	43	22	6.6	84	71	8.4	68	44	7.2
Teton × MT 7015	10	14	3	0.7	30	7	2.6	61	35	1.3
Cheyenne × Itana	11	88	77	7.7	63	45	5.0	100	95	9.5

[a] Representative examples of progress.
[b] The number of florets infected with stripe rusts, 0 through 10, increasing with increased susceptibility.

Transgressive segregation for resistance was evident in the F_6 generation of another nine populations that did not have highly resistant plants in F_2 and F_3. The absence of resistant segregants in F_1, F_2, and F_3 indicated that these resistance genes did not have major effects.

The data from the two *T. durum* crosses were a good indication of progress even when susceptible parents were crossed. Although a high level of resistance was not achieved, progress was still measurable and the level of resistance exceeded that of the parents. In conclusion, sources of resistance can be selected from crosses of moderately resistant and susceptible commercial cultivars of spring wheat.

Winter wheat seedling studies. The methods used to accumulate stripe rust resistance were effective in all 38 crosses. Resistance appeared more quickly in some crosses than in others. By the F_5 generation, all crosses showed transgressive segregation for a level of resistance greater than that of the parents and F_1 hybrids. By the F_5 and F_6 generation, 86 and 92% of the crosses, respectively, had some resistant progeny. Thus, highly resistant progeny were selected even though only susceptible plants of infection types 3−, 3, and 4 were present in the early generations. The continued selection of the most resistant plants, those rated reaction type 3− in the early generations, could lead to homozygosity of recessive factors for higher levels of resistance in later generations. Progress can be made in future studies that avoid parental cultivars with high levels of resistance or specific resistance. Small differences in susceptible reaction types, possibly due to genes with minor effects, can be detected and selected when they are not masked by genes with major effects. Another possible method would be to use a pathotype that overcomes the specific gene present so that detection and selection can be made by small differences in susceptible reaction types.

The lack of resistant infection types in the F_2, the low percentage of resistant types in the F_3, and the low percentage of intermediate infection types in the F_2 support the statement that the parents lacked major specific genes for stripe rust resistance to the pathotypes evaluated. The performance only of Teton indicated the possible presence of other than minor genes. Teton was involved in the parentage of three crosses with progeny of the intermediate type in the F_2 generation and in five of the seven crosses with resistant progeny in the F_3 generation.

The 17 winter wheat crosses that lacked F_2 and F_3 progeny with resistant and intermediate reactions showed the effectiveness of careful selection for developing resistance. The resistant and intermediate progeny showed an increase in resistance, with successive selfing, inoculation and selection with 12% in the F_4, 79% in the F_5, and 61% in the F_6 generation. The 18% increase in susceptible progeny in the F_6 is probably from continued segregation for susceptible types.

Conclusions reached from this study are similar to those from the study on spring wheats. With the spring wheats, resistance was obtained in the F_4, F_5, and F_6 generations in nine crosses that had F_2 and F_3 progeny with only intermediate and susceptible reaction types. The winter wheat study is even more significant, because resistance was obtained in later generations of 17 crosses even though only susceptible progeny were present in the F_2 and F_3 generations (Table 5). Also, resistance was obtained in five of these 17 crosses when only susceptible cultivars were used as parents. Although only 2 and 47% of the F_6 progeny of these five crosses were recorded as resistant and intermediate, respectively, progress was measurable, and 49% of the F_6 progeny exceeded the parents. This resistance was developed from parental material with susceptible infection types and thus was accumulated more slowly. The next step would be to intercross these intermediate progeny from crosses involving different parents. Perhaps much higher levels of resistance could be selected and developed.

In conclusion, selection for significant resistance from crosses of susceptible commercial cultivars or cultivars with an intermediate level of resistance is a valid method for accumulating sources of resistance. Once the resistance is accumulated, it can be manipulated, as demonstrated with the additive, minor-gene lines (2). Elite progeny are likely to be frequent if all parental genotypes have satisfactory agronomic and quality performance. Thus, acceptable segregants could probably be selected from space-planted, advanced bulk populations of genotypes carrying minor gene resistance.

The demonstration of resistance from susceptible cultivars emphasizes possible future uses. Many potential sources of resistance may have been inadvertently discarded in the past because they were not detected in the F_2 and F_3 generations. Careful observation and selection through the F_4 generation should facilitate the detection of new recombinant types of resistance.

Field studies with adult winter wheat plants. Selection in the F_2 population mainly for intermediate resistance types effectively shifted the F_3 population to a higher level of resistance. Plants with the intermediate reaction type increased from 19.9% in the F_2 to 51.2% in the F_3. Resistant plants increased from 0.5% in the F_2 to 4% in the F_3.

When the F_2 and the F_3 rankings of the best 10 crosses were compared, Teton stood out as a good source of resistance. It was the female parent in the crosses ranked one, three, and four in 1975 and in the crosses ranked two, three, and four in 1976. In 1976, Teton was rated as intermediate in the field. The good performance of the three crosses involving Teton could be due to high penetrance of genes conditioning resistance from Teton.

The number of top-ranked crosses having Delmar in their parentage was reduced in the F_3 generation. Perhaps the resistance in the F_2 was due to nonadditive effects, which were reduced in the F_3 progeny, or perhaps the genotype-environment interaction was important in the expression of resistance in Delmar crosses. Conversely, progeny from Wanser crosses showed dramatic improvement from the F_2 to F_3 generation. Only one cross with Wanser in its parentage ranked at the top in the F_2; in the F_3, three of the five Wanser crosses were so ranked. The apparent improvement of Wanser crosses may be due to genotype-environment interaction, or linkage groups may have been broken that allowed additional resistance gene combinations to be expressed.

The comparisons between the F_4 progeny rows and the parent varieties showed that the selection for resistance in the F_2 and F_3 bulk populations was effective when we started with intermediate and susceptible parents. In only four of 72 comparisons was one parent better than the average of the progeny rows in all three categories of disease rating. We assume that even further progress can be made with additional selection in the F_4 generation.

The F_2 and F_3 comparisons and the F_4 and parent comparisons clearly show that progress has been made and that resistant lines can be selected from progeny of crosses between intermediate and suscpetible varieties under natural field conditions. These results agree with the studies done under controlled environmental conditions with seedlings of spring and winter wheats.

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