Incorporation of Additive Genes for Stripe Rust Resistance in Winter Wheat

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ABSTRACT

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Winter wheat cultivars susceptible or intermediate in reaction to stripe rust were crossed. Several generations of selection resulted in progeny with high levels of resistance. Additive genes for resistance were detected in cultivars, which normally appeared susceptible, by maintaining the inoculated plants at a high temperature regime and then comparing the reactions obtained with those of a very susceptible control cultivar. A number of wheat lines were developed that showed uniform resistance to several isolates of *Puccinia striiformis*.

Additional key words: transgressive segregation, uniform resistance, breeding for disease resistance.

Stripe rust caused by *Puccinia striiformis* West is a continual threat to wheats in many areas of the world; cultivars that contain only specific major genes for resistance are particularly vulnerable. In the late 1950's and early 1960's large acreages of wheat in the northwestern USA involved a rather narrow base of resistance germ plasm and losses were considerable. A single plant introduction, P.I. 178383, which was used as a parent in many breeding programs, contributed resistance genes effective against both stripe rust and covered smuts. Two winter wheat cultivars developed during that time were Moro and Crest. Moro contained only one major gene derived from P.I. 178383 conditioning resistance to stripe rust and that was overcome by a race discovered at Bonner's Ferry, Idaho, about 3 years after release (1). The race has since appeared in several other locations in the northwestern USA, including the Gallatin Valley of Montana, and it was one of the cultures used in this investigation.

Earlier studies at this laboratory showed that P.I. 178383, in addition to possessing a major dominant resistance gene, also contained additive genes for resistance that could be accumulated to give good protection against stripe rust (4). Crest is known to contain the major gene from P.I. 178383 and was originally heterogeneous for the additive gene complement (6). Wheat lines containing additive genes from Itana × P.I. 178383 were developed that showed various uniform levels of resistance to the natural population of stripe rust in the northwestern USA. These lines also were evaluated in International Stripe Rust Nurseries for several years and have maintained uniform levels of resistance. Preliminary results with wheat cultivars and lines other than P.I. 178383 indicated that many could contribute other additive genes through selective hybridization (5).

The purpose of this investigation was to determine the feasibility of combining additive genes for stripe rust resistance from P.I. 178383 with those derived from other cultivars.

MATERIALS AND METHODS

The stripe rust reactions of the parental wheat cultivars discussed here are in Table 1. Normal evaluation environments were 2/18 and 15/24 ± 1C (dark/light) for both the preinoculation and postinoculation periods with a 12-hour photoperiod per day (26,900 lx combined incandescent, cool-white fluorescent light). Under these environments, all parents except MT 6531 and Sel A were susceptible. The latter cultivar was susceptible at 2/18 C but intermediate at 15/24 C. However, all parents were known to carry heritable units for resistance that could be detected by evaluation at a temperature regime of 18/24 C. Contrasted to cultivar Lemhi, which was considered to be "a universal suscept", all the cultivars showed some

TABLE 1. Reactions of parental winter wheat plants to stripe rust in the seedling and mature plant stages[a]

Wheat Cultivar	Seedlings at: 2/18 C	Seedlings at: 15/24 C	Mature plants field
Sel A[b]	S	I	I
Lancer, C.I. 13547	S	S	S
Wanser, C.I. 13844	S	S	I
Delmar, C.I. 13442	S	S	S
MT 6531[c]	I	I	I
Itana, C.I. 12933	S	S	S
MT 6930[d]	S	S	S

[a] Reaction type classes: S = susceptible, abundant sporulation with some chlorosis; I = intermediate, moderate sporulation with some chlorosis and necrosis.

[b] Sel A = additive gene selection from P.I. 178383 × Itana.

[c] MT 6531 = Rego × Cheyenne selection.

[d] MT 6930 = Norin 10, Brevor 14, Yogo, Turkey, and Oro in pedigree.

incompatibility at a diurnal temperature regime of 18/24 C for the preinoculation and postinoculation periods of plant growth. The importance of temperature during the dark period of the diurnal cycle and methods of inoculation have been reported previously (3). All evaluations included a 16-hour dark dew period at 7 C. Parent line MT 6531, even though intermediate in reaction to *P. striiformis,* was included in this study because it contained resistance genes derived from Cheyenne and Rego, respectively, that were effective at both the high-and low-temperature regimes.

In the early generations, all progeny of the previously discussed parents were evaluated as seedlings by inoculating them with a field collection of *P. striiformis*. In each segregating generation, at least 200 plants were evaluated and five of the more resistant ones were saved for developing the next generation. At the F_6 generation, all selected wheat lines were evaluated both in the seedling stage and as mature plants in the field. The seedlings were inoculated separately with three cultures of the stripe rust fungus that contained different genes for virulence. Each entry in the field was planted in two 3-m rows, 15 cm apart and was exposed to at least two different pathogenic types of *P. striiformis* that were artificially inoculated onto susceptible spreader rows planted at frequent intervals throughout the rust nursery. Field conditions were favorable for stripe rust development and spread. Stripe rust ratings were made when the disease severity level on the susceptible spreader was near 80% and at successive intervals to detect any possible change over time.

The disease ratings utilized in this study were: susceptible (S), intermediate (I), resistant (R), and very resistant (VR). These corresponded as follows to the infection types given in a previous paper (2): S = 4, 3; I = 3-, 2, 1; R = 1-, 0; and VR = 0-, 00. Only S, I, and R were utilized in rating stripe rust on mature plants and the R class included R and VR as given above.

RESULTS

In the various crosses, the F_1 plants were completely susceptible and resistance was noted only in the segregating generations. Often a significant number of resistant plants were observed among the progeny only after several generations of selection and further selfing, which indicated the presence of many genes conditioning resistance. Many progenies exhibited some segregation after six generations of selfing and selection for the most resistant types in each generation (Table 2). For example, in the cross Sel A × Lancer, six entries were homozygous resistant in the F_6 but two entries of the same cross were still segregating between intermediate and resistant types in the seedling stage. All eight entries of this particular cross showed resistance in the mature-plant stage. The seedling reactions in the F_6 generation were similar, but

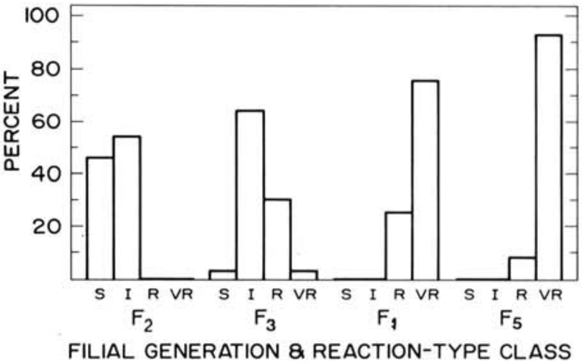

Fig. 1. Distribution of stripe rust reaction type classes in succeeding seedling generations following selection of the five most resistant plants in each generation in the wheat cross Sel A × Lancer. Reaction type classes: S = susceptible; I = intermediate; R = resistant; VR = very resistant.

TABLE 2. Transgressive segregation for resistance of winter wheats to stripe rust

Number of Entries	Cross	F_1 Seedling reaction[a]	F_6 Seedling reaction	F_6 Mature plant reaction
6	Sel A[b] × Lancer	S	R	R
2	Sel A × Lancer	S	Seg (I-R)	R
4	Sel A × Wanser	S	Seg (I-R)	R
1	Sel A × Delmar	S	R	R
1	Sel A × Delmar	S	Seg (I-R)	R
4	Sel A × MT 6531[c]	S	R	R
3	Sel A × Itana	S	Seg (I-R)	I
4	Sel A × MT 6930[d]	S	Seg (I-R)	I

[a] Reaction type classes: S = susceptible, abundant sporulation with some chlorosis; I = intermediate, moderate sporulation with necrosis and chlorosis; R = resistant, no sporulation, necrosis, and chlorosis; Seg (I-R) = population segregation for intermediate and resistant reactions. Seedling plants evaluated at 15/24 C (dark/light) regime in controlled environment chamber. Mature plants evaluated in the field.

[b] Sel A = additive gene selection from P.I. 178383 × Itana.

[c] MT 6531 = Rego × Cheyenne selection.

[d] MT 6930 = Norin 10, Brevor 14, Yogo, Turkey, and Oro in pedigree.

varied to a limited extent.

Figure 1 illustrates a representative approach to increasing the level of rust resistance while obtaining homozygosity by the techniques used in this investigation. Seedling plants were evaluated at 15/24 C. In the F_2 generation, only susceptible and intermediate classes were noted. Plants were selected from the intermediate class for development of the F_3. By selecting the most resistant plants in each succeeding generation, eventually the more resistant classes predominated.

All of the host-pathogen interactions conditioned by the additive gene combinations were influenced by temperature. In general, greater resistance was expressed at the relatively high temperature regime (Fig. 2). There are, however, cases such as in Rego (3) where the greater resistance was expressed at a relatively low temperature regime. Figure 2 shows the F_3 distributions of reaction-type classes for Sel A × Delmar at two temperature regimes, 2/18 and 15/24 C. The differential response to temperature can be utilized judiciously for further accumulation of additive genes for stripe rust resistance. In this particular case, two avenues are open. The very resistant (VR) plants grown at 15/24 C can be selected, increased, and then evaluated at the two temperature profiles while the same can be done for the resistant plants (R) appearing at 2/18 C. It has thus been possible eventually to obtain plants which were very resistant at both temperature profiles. Another somewhat different approach also has been used. Progeny of various crosses were selected through the system as outlined until all plants were homozygous resistant at 15/24 C. Plants were then grown at the lower temperature regime and reselected for resistance at that temperature.

DISCUSSION

The technique used in this investigation resulted in a number of wheat selections with resistance to the prevalent isolates of stripe rust. The resistance was superior to that of either parent. The combining of a large number of genes for resistance logically should result in long-lasting resistance. Differential responses to temperature facilitated the addition of resistance genes and, since major genes were excluded from parental lines, the added gene increments could be followed readily. Generally, it was most desirable first to select for resistance at the higher temperature regime and then to reselect among the same progeny for best resistance at a low-temperature regime because resistance was most readily detected at the higher temperature regime.

Seedling progeny of some crosses showed segregation for rust reaction after six generations of selection, which indicated that a large number of genes conditioned rust reaction. Mature plant reaction was largely stable after six generations, but some segregation for reaction types was observed at the F_5 generation. A number of other wheat selections (not included in this report), even though homozygous for an intermediate or resistant reaction as mature plants, were still segregating between S and R as seedlings in the F_6 generation.

The specific genetic mechanisms involved in this resistance are largely unknown, but it is possible that the dosage effects of additive genes become obvious only when they are homozygous. Specific sequences of hereditary material may also be required for maximum effect. The susceptibility in the F_1 of virtually all combinations supports this hypothesis. Selection of the more resistant types in succeeding segregating generations increases the probability of obtaining plants homozygous for a number of genes and also may provide the particular sequences of genetic material capable of conditioning the greatest resistance.

Since effective resistance can be obtained by crossing normally susceptible wheats, commercially acceptable cultivars can be utilized as parents thus avoiding undesirable traits often associated with exotic plant types or various plant introductions. Trials currently are underway using only commercially acceptable cultivars. To further broaden the germ plasm base, a recurrent selection program is being used in which a number of cultivars known to contain additive genes for resistance are being intercrossed in the early generations prior to selection for the most desirable agronomic types.

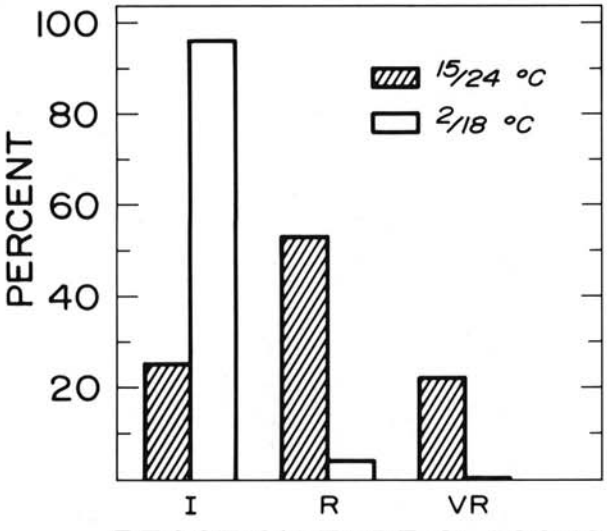

Fig. 2. Distribution of stripe rust reaction type classes at two temperature regimes, 15/24 and 2/18 C (dark/light), of seedlings in the F_3 generation of the wheat cross Sel A × Delmar. Reaction type classes: I = intermediate; R = resistant; VR = very resistant.

LITERATURE CITED

1. BEAVER, R. G., and R. L. POWELSON. 1969. A new race of stripe rust pathogenic on the wheat variety Moro, C.I. 13740. Plant Dis. Rep. 53:91-93.
2. LEWELLEN, R. T., E. L. SHARP, and E. R. HEHN. 1967. Major and minor genes in wheat for resistance to Puccinia striiformis and their responses to temperature changes. Can. J. Bot. 45:2155-2172.
3. SHARP, E. L. 1965. Prepenetration and postpenetration and development of Puccinia striiformis on wheat. Phytopathology 55:198-203.
4. SHARP, E. L. 1968. Interaction of minor host genes and environment in conditioning resistance to stripe rust. Pages 158-159 *in* Proc. 4th Cereal Rusts Conference, August 1-14 Oeiras, Portugal. 238 p.

5. SHARP, E. L. 1972. Additive genes for resistance to stripe rust. Pages 267-269 *in* Proc. 5th Cereal Rusts Conference, July 17-22 Prague, Czechoslovakia. 311 p.

6. SHARP, E. L., and R. B. VOLIN. 1970. Additive genes in wheat conditioning resistance to stripe rust. Phytopathology 60:1146-1147.