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There have been high levels of stripe rust (*Puccinia striiformis* West.) in much of the Pacific Northwest since 1960. Interactions of many wheats with intermediate levels of resistance to the rust have been noted at Moscow, Idaho, in numerous crosses to the three commercial wheat varieties Lemhi C.I. 11415, Cheyenne C.I. 8885, and Idaed or Idaed 59 C.I. 11706 and 13631. Crosses to Lemhi, which has no genes influencing the reactions to stripe rust, gave estimates of gene number. Cheyenne and Idaed, each with two genes conditioning intermediate levels of rust resistance, showed transgressive segregation for higher levels of resistance in crosses with each other and with many other wheats revealing a system of many (20 or more) interacting genes for resistance to stripe rust (POPE, 1965). This paper summarizes these interactions (Table 1) with information on further crosses with Exchange and Golden.

METHODS

Rust readings, using a pustule type of 0 (necrosis, no sporulation) to 4 (abundant sporulation, no necrosis) and the percentage of the plant leaf area covered, were made at several growth stages on field grown plants infected by natural spore showers. Values shown are typical rather than maximum.

RESULTS AND DISCUSSION

Segregation Patterns

Four broad patterns of behaviour have been observed:

1. Highly resistant wheats such as P.I. 178383 and Sonora C.I. 3036 with very dominant genes that could be followed in F_1 plants in successive backcrosses to the susceptible Lemhi. These dominant resistances were utilized in breeding work but avoided in further genetic studies.

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2. Highly resistant wheats with multiple minor genes for resistance, only a portion of which could be maintained in a backcross to Lemhi. Hohenheimer C.I. 11458 (Fig. 1) behaved in this way. It was easy, however, to maintain a better-than-Cheyenne level of resistance in a Cheyenne backcross recovering presumably only a portion of the contribution of Hohenheimer.

3. Moderately resistant wheats with more than single genes for resistance that could be dominant or recessive and that usually segregated for high levels of resistance in crosses where the genes were non-allelic.

4. Wheats classed as susceptible but which contributed genes that gave moderate to spectacular increases in resistance in some progeny segregates. The hard red winter wheats Itana C.I. 12933, Ponca C.I. 12128, Westar C.I. 12110, the soft winter club wheats Omar C.I. 13072 and the related Awned Elgin C.I. 13450, the white spring wheats Lemhi 62 C.I. 13435 (Kenya sel. x $Lemhi^6$) and Federation C.I. 4734 were all of this type.

Cheyenne Derivatives

Fig. 1 shows the F_1 and most resistant progeny in crosses of Cheyenne to 11 other varieties with a range of phenotypic resistances. All populations showed highly susceptible plants indicating the Cheyenne genes were not in common. Transgressive segregation was recognized for all but the two most resistant varieties. Lee C.I. 12488 is the only variety in this group with a relatively dominant resistance.

Exchange Derivatives

The spring variety Exchange C.I. 12635 showed a simple segregation (Fig. 2) in which its weak resistance (2/30) was conditioned by two genes recovered in 1/16 of the progeny (P = .40) when crossed to Lemhi. This weak resistance was additive with genes from the susceptible Dicklow C.I. 3663, Marfed C.I. 11919 (2/50), and the moderately resistant Idaed (1/20). Peculiarly the genes for resistance in Idaed x Marfed, though non-allelic as indicated by susceptible progeny, failed to show segregates for additive levels of resistance. This is the only case where this has been noted.

Strong Interactions

Derivatives of Golden C.I. 11063 formed a separate class of segregates with large increases in resistance. Golden (4/20 +) crossed to Lemhi 62 (4/70) produced a few selections that have remained highly resistant to date. Lemhi 62 had a very weak resistance just detectably better than the fully susceptible Lemhi, yet its contribution to Golden behaved as a "missing ingredient". It is therefore not surprising that Lemhi 62 was also additive in a less spectacular way with Idaed 59, Ridit C.I. 6703 and Burt C.I. 12969 (Table 1). Golden x Idaed 59 segregated for strong interactions with over one half of 290 F_2 progeny more resistant than either parent and one third highly resistant. This was the only situation in which anything that could be called a dominant interaction occurred. The cross of Gabo C.I. 12795 (1/30) x Idaed 59 might be similar because additive resistance was easily recovered in an F_2 of only 25 plants.

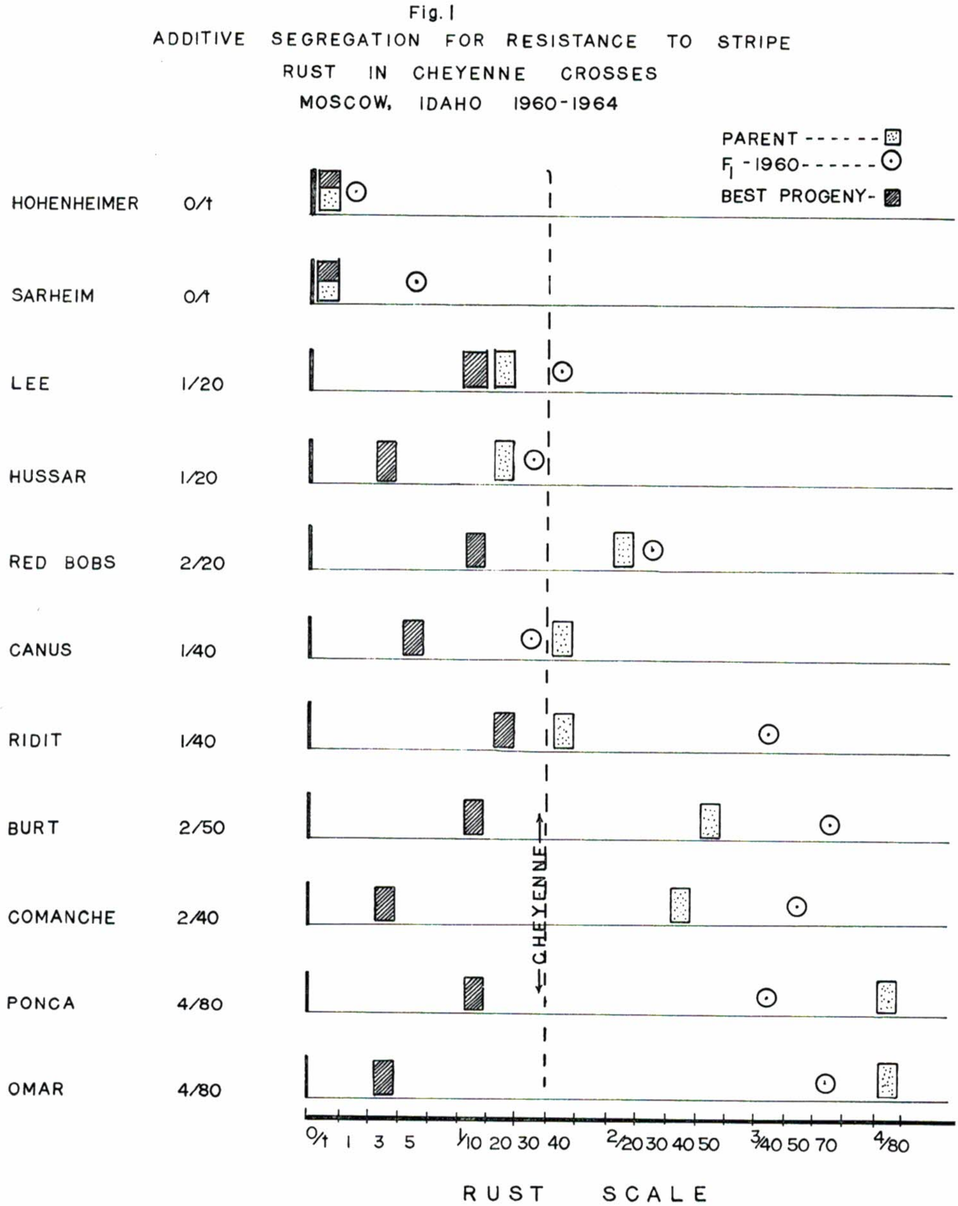

FIG. 1. Additive segregation for resistance to stripe rust in Cheyenne crosses at Moscow, Idaho, 1960-1964. Rust classified as pustule type (0-4) and percentage of plant leaf area covered.

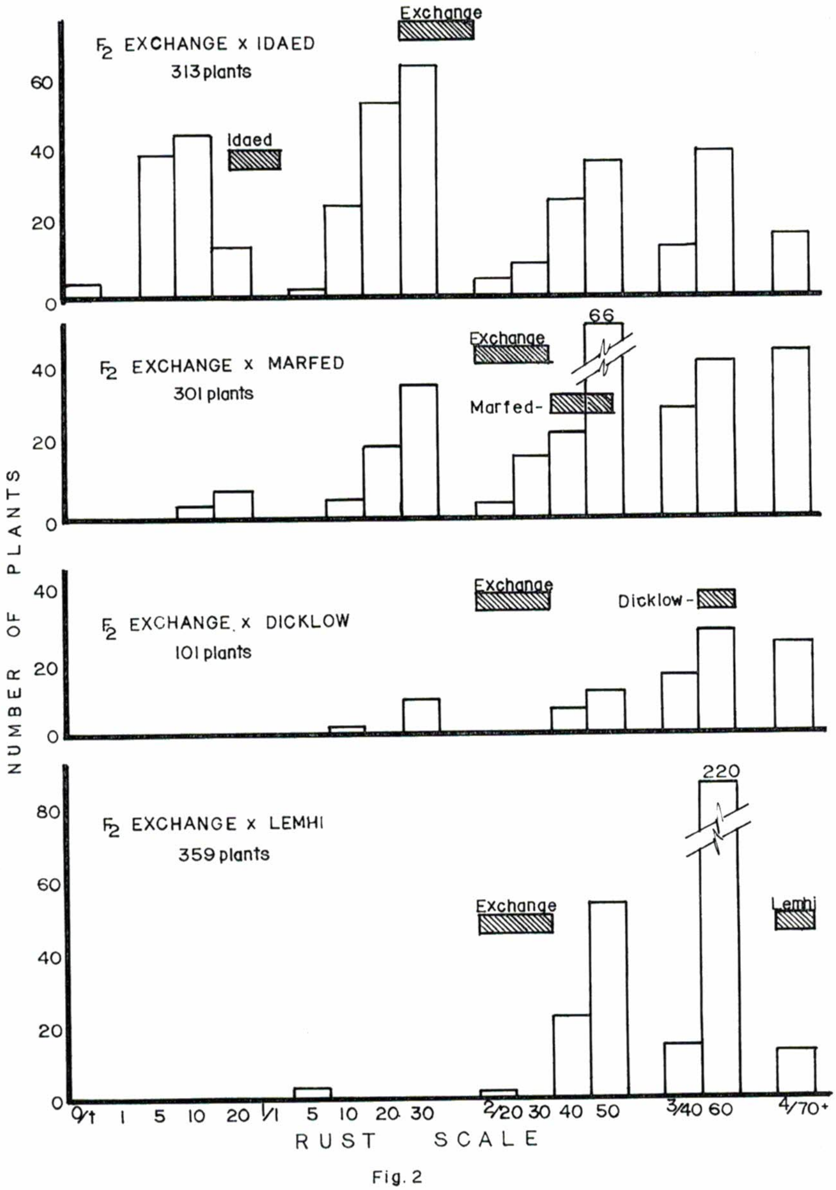

FIG. 2. F_2 segregation patterns for resistance to stripe rust in crosses with Exchange. Rust classified as pustule type (0-4) and percentage of plant leaf area covered.

Multigenic Segregations

Crosses of Idaed with Gaines C.I. 13448 and Wasatch C.I. 11925 produced F_2 distribution curves strongly humped in the middle of the resistance spectrum as would be expected from dosage effect from numerous small genes with at least two genes coming from Idaed.

Evidence for Gene Number

A minimum of 5 different genes is implied from the additive interaction in all combinations of Idaed, Cheyenne, Hussar, Comanche and Omar or Awned Elgin (POPE, 1965) (Table 1). The Omar contribution is part of the genotype

TABLE 1. Selected wheat variety combinations showing transgressive segregation for additive levels of resistance to stripe rust.

	Rust class[2]	Cheyenne 1/20	Idaed 1/20	Club[1] 4/80	Lemhi 62 4/80	Triplet 3/60	Federation 4/70	Itana 4/80	Hussar 1/30
Idaed	1/20	*	—	*	*	—	*	*	—
Comanche	2/40	*	*	*	—	—	—	—	*
Burt	3/50	*	*	—	*	—	—	*	
Hussar	1/30	*	*	*	—	—	*		
Ridit	2/20	*	*	—	*	*			
Canus	1/50	*	*	*	—				
Golden	4/20	—	*	C	*				
Gaines	1/30	—	*						
Wasatch	3/50	—	*						
C.I. 12632	1/20	*							

[1] Omar and Awned Elgin.
[2] Rust classified as pustule type (0-4) and percentage of leaf area covered.
C-Golden has the Omar resistance plus more.

of the related Golden which must have at least one other gene (No. 6). Lemhi 62 (gene 7) was additive with Idaed, Golden, Ridit and Burt. Burt (gene 8) had a characteristic large necrotic relatively non-sporulating rust lesion and was additive with Cheyenne, with Idaed in the variety Adams C.I. 13722 and with susceptible Itana in the varieties Wanser C.I. 13844 and McCall C.I. 13842. A similar gene plus something additional (gene 9) must be in the spring wheat Canus C.I. 11673 (1/70) which segregated for the Burt phenotype and was additive with Cheyenne, Idaed, and the susceptible Awned Elgin. Ridit (2/20) (gene 10), with a more resistant phenotype, also segregated for a Burt-like phenotype and was additive in crosses with Idaed, Cheyenne, Triplet C.I. 5408 and Lemhi 62.

Extending this list with two weak genes in Exchange additive with Marfed and Idaed, two genes in the susceptible Federation that was additive with Idaed and Hussar (HENRIKSEN and POPE, 1968), a gene in Gabo, additive with Idaed in a unique pattern, more than one gene in Eureka that was additive with both Idaed and Marfed, and multiple genes with small effect in Gaines and Wasatch, implies an extensive list of minor genes interacting for increased resistance to stripe rust without even considering multigenic combinations which are highly resistant or dominant major genes.

Interaction of Major and Minor Genes

There has been little phenotypic distinction, at Moscow, Idaho, between resistant varieties with multigenic non-dominant genes and varieties with very dominant genes. Both are highly resistant as varieties and in F_1 hybrids. Comparison by varieties is not valid because varieties with effective monogenic dominant resistance also have minor genes which add to the resistance as noted by LEWELLEN *et al.* (1967) for P.I. 178383 and Chinese 66. The highly resistant McMurachy C.I. 11876 must have at least 5 genes for resistance because in a cross with Lemhi no plants were fully susceptible in 250 F_2 plants. This differs only in the increased number of genes recognized from the situation of a complex of major and minor genes noted by KNIGHT and HUTCHINSON (1950) for resistance to bacterial blight (*Xanthomonas malvacearum*) in cotton in which an effective resistance required two major and indistinguishable minor genes, or as described by VAN DER PLANK (1966) for vertical and horizontal resistance to potato blight (*Phytophthora infestans*).

In resistant types showing some rust, dominance such as seen in Lee or C.I. 12632 was recognized in segregation patterns but was irrelevant to the expression of additive interactions with Cheyenne.

In controlled environment studies LEWELLEN *et al.* (1967) demonstrated that minor genes in P.I. 178383 were additive alone and with a dominant heterozygous major gene at warm temperature profiles. SHARP (1965) demonstrated a different temperature specificity for genes in Rego from the minor genes in P.I. 178383, and LEWELLEN and SHARP (1968) combined these for an additive increase in resistance.

Similar interactions were seen in resistant phenotypes in the field at Moscow in 1967 in lines taken from the variety Burt x P.I. 178383 (C.I. 13837), presumably indicating the presence of different numbers of additive minor genes in addition to the major dominant gene for resistance from P.I. 178383. Further F_1 crosses to these lines could be distinguished according to the resistance contributions of the second parent.

Genes From More Than Two Sources of Resistance

F_2 bulks in 1967 from double F_1 combinations with Cheyenne, Hussar, Comanche, and additive Omar-Cheyenne components, segregated for high levels of resistance thought to be better than the best two-way combinations.

In 1967 F_1 hybrids, Golden-Lemhi 62 (0/t) raised the resistance level of the additive Omar-Idaed 59 (0/10) to (0/t) and moderately resistant Gaines (1/30) to (0/10), patterns typical of multigenic combinations.

Genes having functions in sequential effects would explain the spectacular complementary interaction as seen in the Golden-Lemhi 62. Combinations of non-allelic genes having related or duplicate function might show from none to large additive interactions according to the virtue of increase in such activity.

In this situation the methodology of examining genes singly is not applicable.

These are not "genes for resistance" but genes controlling functions in a gene complex that confers resistance. Their functions can be more effectively analysed by addition and subtraction techniques in relation to well-known resistant genes or gene complexes.

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