Inheritance of Stem and Leaf Rust Resistance in Agent and Agrus Cultivars of Triticum aestivum

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ABSTRACT

Tests of F_3 and selected F_4 families from crosses of *Triticum aestivum* cultivars, Agent and Agrus with Little Club, indicated that both Agent and Agrus have at least four genes for resistance to culture 111-SS2 (race 111) of *Puccinia graminis* f. sp. *tritici*. In Agent, resistance to culture 111-SS2 was inherited independently of resistance to prevalent genotypes of *Puccinia recondita* f. sp. *tritici* in the field. But in Agrus, a gene for resistance to culture 111-SS2 was linked with the gene (presumably *Lr 19*) for resistance to leaf rust on the Agropyron chromosome substituted for wheat chromosome 7D. In F_4 families, infection types conditioned by two genes for resistance to 111-SS2 from Agent and two from Agrus, including the one on the Agropyron chromosome, were most effective at 20 C, moderately effective at 25 C, and ineffective at 30 C. The resistance conditioned by each of the remaining two genes from Agent and two from Agrus changed only slightly, or not at all, under the different incubation temperatures. Phytopathology 61: 1501-1505.

The inheritance of leaf and stem rust resistance was studied in crosses of *Triticum aestivum* L. 'Agent' (C.I. 13523) and 'Agrus' (C.I. 13228) with 'Little Club'. Agent and Agrus are used extensively in breeding programs because they represent combinations of acceptable wheat characters with leaf rust resistance derived from *Agropyron elongatum* (Host) Beauv.

Agent was developed by the Oklahoma Agricultural Experiment Station from a cross of a *Triticum* sp.-*Agropyron elongatum* derivative with *T. aestivum* 'Triumph'. A single dominant gene, believed to represent a natural translocation from *A. elongatum* to wheat chromosome 3D, conditions a high level of resistance to *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* Eriks. (11). The resistance is effective against all but one known strain of *P. recondita* f. sp. *tritici* in the United States.

Agrus, developed from (Trumbull X *A. elongatum*) X (Fultz X Trumbull-Hope-Hussar) at Purdue University Agricultural Experiment Station (2), has an *A. elongatum* chromosome substituted for wheat chromosome 7D (6, 7, 8, 10). The Agropyron chromosome carries a gene recently designated *Lr 19* (R. A. McIntosh, Dept. Agr. Botany, Univ. Sydney, New South Wales, Australia, *personal communication*) for resistance to several cultures of *P. recondita* f. sp. *tritici* (2). Data from the International Winter Wheat Rust Nursery, distributed by the USDA, indicate that cultures of the leaf and stem rust fungi capable of attacking Agrus occur worldwide.

Agent is resistant and Agrus is susceptible to most of the prevalent cultures of *P. graminis* (Pers.) f. sp. *tritici* Eriks. & E. Henn. in the United States. But information concerning the inheritance of resistance to stem rust is lacking for both cultivars. The purpose of this investigation was to determine the minimal number of genes for resistance in Agent and Agrus to a widely avirulent culture of *P. graminis* f. sp. *tritici*, and whether they were associated with the genes for leaf rust resistance from *A. elongatum*.

MATERIALS AND METHODS.—*Reaction to leaf rust.*—F_2 and backcross-F_1 plants from Agent X Little Club and Agrus X Little Club were scored for reactions to natural infection in the field at College Station, Texas, in 1968. In both years, Agent and Agrus were highly resistant to prevalent strains of *P. recondita* f. sp. *tritici*, and Little Club was highly susceptible.

Reaction to stem rust.—F_3, F_4, backcross-F_2, and backcross-F_3 families from Agent X Little Club and Agrus X Little Club were tested for their seedling reactions to single-spore culture 111-SS2 of *P. graminis* f. sp. *tritici*. Each tested family was derived from an F_2 or backcross-F_1 plant that had been scored for leaf rust reaction in the field. Culture 111-SS2 was used previously to study inheritance of resistance in nine durum, two emmer, and three common wheats (1, 4, 9, 13, 14).

The first foliage leaves of the plants were inoculated with urediospores suspended in a mixture of two parts mineral oil (N. F. light, labeled by Humco Laboratory, Texarkana, Ark.-Tex.) and five parts base oil B obtained from the Chevron Chemical Company, Ortho Division, San Francisco, Calif. Usually, 30 to 40 plants were tested in each family, but in some the number was as few as 15; in others, as many as 70. After inoculation, the plants were held in a humidity chamber at 20 ± 2 C for ca. 18 hr, dried slowly for 2 hr, then placed in a greenhouse at 25 ± 4 C under 800 ft-c of natural and supplemental fluorescent light.

The symbols proposed by Stakman et al. (12) were used to describe the infection types which characterized the phenotypic classes. All plants classed "susceptible" developed infection types as high as those in Little Club.

Gene symbols presented herein are provisional,

TABLE 1. Segregation in F_3 families from Agent X Little Club for reaction to culture 111-SS2 of *Puccinia graminis* f. sp. *tritici* and adult plant reactions of the parent F_2 plants to *Puccinia recondita* f. sp. *tritici*

Classification of F_3 families	*Puccinia graminis*, no. F_3 families[a]		*Puccinia recondita*, no. F_2 plants[b,c]	
	Expected	Observed	Resistant	Susceptible
Inseparable segregating and homozygous-resistant	318.63	317	247	70
Seg. 3:1 (0; to 3= and 4)	2.58	4	2	2
Seg. 3:1 (3= and 4)	2.58	3	2	1
Seg. 3:1 (3- and 4)	2.58	2	1	1
Seg. 3:1 (X and 4)	2.58	4	0	4
Homozygous-susceptible	1.29	0	0	0

[a] *P* between .5 and .7 for 247:2:2:2:2:1 ratio of families reacting as indicated.
[b] *P* between .5 and .7 for 3:1 ratio of leaf rust-resistant and -susceptible plants.
[c] Because Little Club was susceptible to both leaf rust and stem rust, the apparent association (*P* less than .01 as indicated by the χ^2 test for independence) between susceptibility to prevalent genotypes of *P. recondita* f. sp. *tritici* and the X infection type produced with culture 111-SS2 of *P. graminis* f. sp. *tritici* was attributed to chance deviation.

and are used only for reading clarity. The authors believe that genes for resistance should be assigned permanent symbols only after their relationship to previously designated genes in the *Sr* and *Lr* numerical series has been established.

RESULTS.—*Agent X Little Club.*—Three hundred and thirty F_2 plants, derived from five F_1 plants of Agent X Little Club segregated for resistance and susceptibility to leaf rust in the field in a ratio of 252:78, respectively. These numbers indicated that a single dominant gene conditioned the resistance of Agent to the prevalent strains of *P. recondita* f. sp. *tritici* (*P* between .50 and .70). A chi-square test for heterogeneity indicated that the population was homogeneous (*P* between .05 and .10). Further evidence that a single gene conditioned the observed resistance to leaf rust was indicated by the segregation ratio of 15 resistant plants:23 susceptible in a backcross-F_1 population (*P* between .10 and .20 for a 1:1 ratio).

Seedling resistance to culture 111-SS2 of *P. graminis* f. sp. *tritici* was controlled by four dominant genes in F_3 and backcross-F_2 families derived from the leaf rust tested F_2 and backcross-F_1 plants (Tables 1, 2). This conclusion was derived from the observed numbers of homozygous-susceptible families, and families that segregated in a 3:1 ratio for resistant and susceptible plants. The small size of some families, and an intergradation of infection types indicative of resistance, precluded separation of the remaining families into phenotypic classes.

Differences were noted among the low infection types of families that segregated for a single gene for resistance, but they were not sufficiently divergent to permit an accurate correlation of phenotypes with specific genes. Consequently, seedlings of F_4 and backcross-F_3 families, representing five plants from each F_3 and backcross-F_2 family that segregated three resistant seedlings to one susceptible, were inoculated with culture 111-SS2. Each family was subdivided and incubated in growth chambers at 20 ± 2, 25 ± 2, and 30 ± 2 C with 12 hr of light. Data from these tests were used to reinforce those obtained from testing the F_3 and backcross-F_2, and are reflected in the numbers of families classed as segregating for the four genes singly (Tables 1, 2).

The four genes were tentatively designated *Ag-1*, *Ag-2*, *Ag-3*, and *Ag-4*. *Ag-1* conditioned infection types 0;, 1, and 3=. Usually, the three infection types occurred on the same leaf, but varied in relative

TABLE 2. Segregation in backcross-F_2 families from Agent X Little Club for reaction to culture 111-SS2 of *Puccinia graminis* f. sp. *tritici* and adult plant reactions of the parent backcross-F_1 plants to *Puccinia recondita* f. sp. *tritici*

Classification of backcross-F_2 families	*Puccinia graminis*, no. backcross-F_2 families[a]		*Puccinia recondita*, no. backcross-F_1 plants[b,c]	
	Expected	Observed	Resistant	Susceptible
Inseparable segregating and homozygous-resistant	26.125	29	14	15
Seg. 3:1 (0; to 3= and 4)	2.375	1	0	1
Seg. 3:1 (3= and 4)	2.375	3	1	2
Seg. 3:1 (3- and 4)	2.375	2	0	2
Seg. 3:1 (X and 4)	2.375	2	0	2
Homozygous-susceptible	2.375	1	0	1

[a] *P* between .8 and .9 for 11:1:1:1:1:1 ratio of families reacting as indicated.
[b] *P* between .1 and .2 for 1:1 ratio of leaf rust-resistant and -susceptible plants.
[c] A χ^2 test for independence of the reaction to *P. recondita* f. sp. *tritici* from the reactions to *P. graminis* f. sp. *tritici* indicated no association (*P* between .3 and .5).

frequency at the three temperature levels. For example, infection type 3= was often absent at 20 C, but was the most prevalent one at 30 C. *Ag-2* conditioned a 3= infection type characterized by a small pustule in the center of a round chlorotic area. The 3= infection type remained unchanged regardless of the temperature. *Ag-3* conditioned a 3- infection type with a diamond-shaped chlorotic area. The infection type was stable at 20 and 25 C, but at 30 C it developed into an infection type 4. *Ag-4* conditioned 0; and 1 infection types at 20 C, an X infection type at 25 C, and a 4 infection type at 30 C.

The genes for resistance to leaf and stem rust were inherited independently. An association between *Ag-3* in the F_3 families and the gene for leaf rust resistance in the F_2 plants was indicated by the χ^2 test for independence (Table 1). All F_3 families classed as having *Ag-3* singly were progenies of F_2 plants that were susceptible to leaf rust. But as Little Club did not contribute resistance to either stem rust or leaf rust, the association was attributed to chance deviation. No association was indicated when the χ^2 test for independence was applied to the backcross data (Table 2).

Agrus X *Little Club*.—Johnson (5) showed that when an alien chromosome (A) substitutes for a wheat chromosome (W), and the 20'W + 1'A pollen functions as well as the euploid, a dominant marker on the alien chromosome and its recessive allele on the wheat chromosome would segregate in a 19:9 ratio. Segregation for resistance and susceptibility to prevalent strains of *P. recondita* f. sp. *tritici* among adult plants from Agrus X Little Club approached 19:9 ratios (Table 3) in four F_2 families. The χ^2 test for heterogeneity indicated that the four families were homogeneous (*P* between .20 and .30). In the backcross-F_1, the segregation of resistant and susceptible plants fitted a 1:1 ratio (*P* between .10 and .20) and indicated an equal, or nearly equal, distribution of wheat chromosome 7D and the substituted Agropyron chromosome among the male gametes.

Seedling resistance to culture 111-SS2 of *P. graminis* f. sp. *tritici* was controlled by four

TABLE 3. Segregation in F_3 families from Agrus X Little Club for reaction to culture 111-SS2 of *Puccinia graminis* f. sp. *tritici* and adult plant reactions of the parent F_2 plants to *Puccinia recondita* f. sp. *tritici*[a]

Classification of F_3 families	*Puccinia graminis*, no. F_3 families[b]		*Puccinia recondita*, no. F_2 plants[c,d]	
	Expected	Observed	Resistant	Susceptible
Inseparable segregating and homozygous-resistant	328.51	323	230	93
Seg. 3:1 (0; to 3= and 4)	5.32	11	3	8
Seg. 3:1 or 19:9 (3- and 4)[e]	2.66	2	2	0
Seg. 3:1 (2+ and 4)	2.66	3	0	3
Homozygous-susceptible	1.33	2	1	1

[a] F_2 plants and F_3 families were derived from four F_1 plants.
[b] *P* between .5 and .7 for 247:4:2:2:1 ratio of families reacting as indicated.
[c] *P* between .5 and .7 for 19:9 ratio of expected resistant and susceptible plants if the Agropyron chromosome substitutes for the missing wheat chromosome.
[d] The χ^2 test for independent indicated an association between the reaction *P. graminis* f. sp. *tritici* and *P. recondita* f. sp. *tritici* (*P* less than .01).
[e] The numbers of resistant and susceptible plants in each of the two F_3 families fitted both 19:9 and 3:1 ratios.

TABLE 4. Segregation in backcross-F_2 families from Agrus X Little Club for reaction to culture 111-SS2 of *Puccinia graminis* f. sp. *tritici* and adult plant reactions of the parent backcross-F_1 plants to *Puccinia recondita* f. sp. *tritici*

Classification of backcross-F_2 families	*Puccinia graminis*, no. backcross-F_2 families[a]		*Puccinia recondita*, no. backcross-F_1 plants[b,c]	
	Expected	Observed	Resistant	Susceptible
Inseparable segregating and homozygous-resistant	21.34	17	13	4
Seg. 3:1 (0; to 3= and 4)	3.88	7	4	3
Seg. 3:1 or 19:9 (3- and 4)[d]	1.94	2	2	0
Seg. 3:1 (2+ and 4)	1.94	3	1	2
Homozygous-susceptible	1.94	2	0	2

[a] *P* between .3 and .5 for 11:2:1:1:1 ratio of families reacting as indicated.
[b] *P* between .1 and .2 for 1:1 ratio of leaf rust-resistant and -susceptible plants.
[c] The χ^2 test for independence did not indicate an association between reactions to *P. recondita* f. sp. *tritici* and reactions to *P. graminis* f. sp. *tritici* (*P* between .1 and .2). However, other data indicated linkage between the gene conditioning 3= infection types to culture 111-SS2 and the one conditioning resistance to *P. recondita* f. sp. *tritici*.
[d] The numbers of resistant and susceptible plants in each of the two backcross-F_2 families fitted both 19:9 and 3:1 ratios.

independent dominant genes (Tables 3, 4) in F_3 and backcross-F_2 families derived from the leaf rust tested F_2 and backcross-F_1 plants. The genes were tentatively designated *Ars-1*, *Ars-2*, *Ars-3*, and *Ars-4*. *Ars-1* and *Ars-2* conditioned infection types ranging through 0;, 1, and 3=. In controlled temperature growth chambers, the relative numbers of 0; and 3= infection types in F_4 and backcross-F_3 families were greatest at 20 and 30 C, respectively. Pustules of the 3= infection type were larger at 30 C than at 20 or 25 C. At each temperature, similar infection types were conditioned by *Ars-1* and *Ars-2*. Consequently, the F_3 families which segregated in a 3:1 ratio of infection types attributed to *Ars-1* and *Ars-2* and infection type 4 were combined in a single class when the data were analyzed. *Ars-3* conditioned infection type 3- at 20 and 25 C, and infection type 4 at 30 C. *Ars-4* conditioned infection types 2=, 2+, and 4 at 20, 25, and 30 C, respectively.

The χ^2 test for independence indicated that one of the genes segregating for resistance to culture 111-SS2 in the F_3 was associated with the gene for resistance to leaf rust in the F_2 plants. No association was evident when the test was applied to the backcross data. However, the backcross populations were small, and failure to indicate an association apparently resulted from chance deviation. Supporting evidence of linkage was obtained by cytological examination of 82 seedling plants from a backcross-F_2 family that had segregated for infection types 3- and 4 when tested with culture 111-SS2. The backcross-F_1 parent had been free of leaf rust in the field. Chromosomes in cells of root tips of the 82 plants were stained in Feulgen and counted by Neal Tuleen, Cytogeneticist, Department of Soil and Crop Sciences, Texas A&M University. The plants were each inoculated with culture 111-SS2 of *P. graminis* f. sp. *tritici* and culture H-28 of *P. recondita* f. sp. *tritici* in the first and third leaf stages, respectively. The results (Table 5) clearly indicated irregularities in chromsome segregations, and that the gene, *Ars-3*, for resistance to culture 111-SS2 was linked with the gene for leaf rust resistance on the Agropyron chromosome.

TABLE 5. Segregation for chromosome number and reactions to cultures 111-SS2 of *Puccinia graminis* f. sp. *tritici* and H-28 of *Puccinia recondita* f. sp. *tritici* in seedlings of a backcross-F_2 family derived from a backcross-F_1 plant resistant to leaf rust in the field

No. of chromosomes	No. plants	Reaction to cultures	
		111-SS2	H-28
40	5	Susceptible	Susceptible
41	15	Susceptible	Susceptible
41	19	Resistant	Resistant
41 + telo [a]	1	Resistant	Resistant
42	10	Susceptible	Susceptible
42	22	Resistant	Resistant
42 + telo	3	Resistant	Resistant
43	5	Resistant	Resistant
43	1	Susceptible	Susceptible
44	1	Resistant	Resistant

[a] Telocentric chromosome.

DISCUSSION.—No genetic tests were made to relate the four genes in Agent for resistance to culture 111-SS2 with the four in Agrus. However, on the basis of the observed infection types, *Ag-1* may be the same as either *Ars-1* or *Ars-2*. Infection types attributed to these genes maintained a close similarity at 20, 25, and 30 C, and were slightly higher at 30 C than at 20 C. The infection type attributed to *Ag-2* was at the upper range of those attributed to *Ag-1*, *Ars-1*, and *Ars-2*, but differed from them by remaining constant regardless of the temperature. Both *Ag-3* and *Ars-3* conditioned a 3- infection type at 20 and 25 C, and a 4 infection type at 30 C. *Ars-3* was linked in coupling with the gene for leaf rust resistance on the Agropyron chromosome substituted for wheat chromosome 7D. One may postulate that *Ag-3* and *Ars-3* are the same gene by assuming that a segment of the Agropyron chromosome which substituted for wheat chromosome 7D in Agrus was translocated to a chromosome of Agent. This translocation would have been in addition to the one which transferred the gene for leaf rust resistance from Agropyron to wheat chromosome 3B. This hypothesis will be strengthened if future tests indicate that *Ag-3* is located on chromosome 7D. Infection types attributed to *Ag-4* and *Ars-4* were too unlike to have been conditioned by the same gene.

Evans et al. (3) screened seedlings of 38 wheat cultivars with seven cultures of *P. graminis* f. sp. *tritici* prevalent in East Africia. Except for cultivars Agatha and T4, adult plant reactions in field plots at Njoro, Kenya, were positively correlated with seedling reactions. Agatha and T4 were resistant to all cultures in the seedling tests, but highly susceptible in the field. Since Agatha's pedigree is Agrus X Thatcher[6], and T4 carries a translocation from *A. elongatum*, we suggest that the susceptibility of adult plants was induced by high temperature acting on *Ars-3* or *Ars-4*.

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