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Inheritance of Stem Rust Resistance of Tetraploid Wheats*

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The inheritance of seedling reaction of the standard stem rust differential varieties, and of certain other varieties known to have genes for resistance not represented in the standard differentials, has been under study for a number of years. A widely avirulent, single-spore culture (designated 111-SS2) of *Puccinia graminis* (Pers.) f. sp. *tritici* Ericks. & E. Henn. was selected as the test culture because it presumably would differentiate more genes for reaction than widely virulent ones. The hexaploid differentials Marquis, Reliance, and Kota in crosses with Little Club were shown to have three genes each for reaction to culture 111-SS2 (BERG *et al.*, 1963; and RONDON *et al.*, 1966). The tetraploid wheats Mindum and an Acme selection were shown to have three genes each, and the variety P.I. 94701, two genes for reaction to culture 111-SS2 (GOUGH and WILLIAMS, 1963; RONDON *et al.*, 1966). Khapli emmer had three genes for reaction to culture 111-SS2, and a fourth gene for reaction to a culture of race 56 (WILLIAMS and GOUGH, 1965). This report summarizes inheritance studies of reaction to culture 111-SS2 of three additional tetraploid differential varieties and four tetraploid wheats thought to have genes for reaction not represented in the standard differentials.

MATERIALS AND METHODS

The inheritance of reaction to culture 111-SS2 of *P. graminis* f. sp. *tritici* was studied in the F_2, F_3, BC-F_1 (backcross-F_1), and BC-F_2 (backcross-F_2) of crosses of *Triticum turgidum* L. 'Spelmar' (C.I. 6236), 'Kubanka' (C.I. 2094), 'Vernal' (C.I. 3686), 'Camadi Abdu Tipo' (P.I. 192168), 'St. 464' (C.I. 13160), C.I. 8155, and 'Iumillo' (C.I. 1736) with the susceptible variety 'Marrocos 9623' (P.I. 192334). F_1 plants from the crosses were backcrossed to Marrocos 9623 and allowed to self pollinate. The first foliage leaves of the F_2 and F_3 from

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crosses, and the F_1 and F_2 from backcrosses were inoculated with culture 111-SS2 and scored for rust reaction. Methods of inoculation and scoring have been described previously (GOUGH and WILLIAMS, 1963). Chi-square tests were used for analyzing the data.

RESULTS

Results from testing the F_3 and BC-F_2 of all crosses are summarized in Table 1. Data from the F_2 and BC-F_1 usually supported those of the F_3 and BC-F_2, and are not shown in this paper. The F_2 and BC-F_1 data from a few crosses were unclear. Small sample sizes in the F_3 and BC-F_2 precluded separation of lines segregating for two or more genes for resistance. Lines segregating for two or more genes, or for two or more levels of resistance, were pooled into a single class.

TABLE 1. Inheritance of reaction to culture 111-SS2 of *Puccinia graminis* f. sp. *tritici* in crosses of durum wheat.

Generation	No. of lines	Ratio	P(χ^2)	Number of genes
		(Spelmar × Marrocos 9623)		
F_3	375	46:10:1:4:2:1	>0.10	3
BC-F_2	93	4:3:1	>0.30	3
		(Kubanka × Marrocos 9623)		
F_3	385	1:2:1	>0.50	1
BC-F_2	61	1:1	>0.05	1
		(Vernal × Marrocos 9623)		
F_3	249	12:38:4:1:1:1:7	>0.70	3
BC-F_2	48	3:4:1	>0.50	3
		(Camadi Abdu Tipo × Marrocos 9623)		
F_3	365	48:7:1:1:2:2:2:1	>0.95	3
BC-F_2	70	4:1:1:1:1	>0.95	3
		(St. 464 × Marrocos 9623)		
F_3	250	39:16:1:1:2:2:2:1	>0.30	3
BC-F_2	154	4:1:1:1:1	>0.05	3
		(C.I. 8155 × Marrocos 9623)		
F_3	349	48:7:1:1:2:2:2:1	>0.30	3
BC-F_2	107	1:2:1	>0.50	2
		(Iumillo × Marrocos 9623)		
F_3	324	46:7:2:1:1:2:2:2:1	>0.50	3
BC-F_2	131	4:1:1:1:1	>0.30	3

Spelmar x Marrocos 9623—About 1/64 of the F_3 lines from Spelmar x Marrocos 9623 were homozygous susceptible, 2/64 segregated 3 moderately resistant seedlings (necrosis around large pustules) : 1 susceptible (infection type 4), 4/64 segregated 3 resistant seedlings (infection type 0; to 3-) : 1 susceptible, 1/64 were homozygous moderately resistant (necrosis around large pustules), 10/64 were homozygous highly resistant (infection type 0;), and 46/64 were grouped in a class of phenotypically inseparable lines. The BC-F_2 was classified

1/8 homozygous susceptible, 3/8 segregating 3:1 for resistance and susceptibility, and 4/8 inseparable.

These data indicated that three dominant genes conditioned the resistance of Spelmar to culture 111-SS2, and that the combination of any two of the three genes conditioned infection type 0;. Singly, two of the genes conditioned a similar range of infection types, from 0; to 3-, which could not be separated. The third gene conditioned necrosis around pustules.

Kubanka x Marrocos 9623—Tests of the F_3 and BC-F_2 from Kubanka x Marrocos 9623 were difficult to interpret because of difficulty in identifying parental phenotypes. Indications of transgressive segregation were observed, but parental variability precluded a determination of whether the transgressive variability was caused by environmental factors, genetic segregation of minor modifying factors, or segregation for major genes for resistance.

The F_3 lines were separated into three groups. One group included lines that appeared homozygous for reactions similar to that of Marrocos 9623 (infection type 3-4-c); a second group included lines that segregated for infection types ranging from near the Kubanka type (0; 1-1) to near the Marrocos 9623 type; and a third group included lines homozygous for reactions similar to the Kubanka type. The BC-F_2 lines were separated into two groups, a segregating class and one homozygous for reactions similar to that of Marrocos 9623. Results of the classification indicated that the resistance of Kubanka was conditioned by one major gene.

Vernal x Marrocos 9623—The F_3 and BC-F_2 from Vernal x Marrocos 9623 were separated into homozygous lines and lines that segregated for resistance and susceptibility. Gradations of infection types within a line, and small sample sizes, precluded recognition of genetic ratios within segregating lines. About 7/64, 1/64, 1/64, 1/64, and 4/64 of the F_3 lines were homozygous for infection types 3-4-c (susceptible), 0; 3-cn, 0; + 1-, 0; 1-, and 0;, respectively. The class segregating for resistance and susceptibility included about 38/64 of the lines. The remaining 12/64 of the lines segregated for various levels of resistance. The BC-F_2 were separated into three classes. About 1/8 of the lines were homozygous susceptible, 4/8 segregated 3 resistant seedlings : 1 susceptible, and 3/8 segregated but were phenotypically inseparable.

The F_3 and BC-F_2 results were not completely clear, but were interpreted as indicating that Vernal has three genes conditioning resistance to culture 111-SS2. Singly, one of the genes may condition a moderate level of resistance (infection type 0; + to 3-n). Singly, the other two genes may condition reactions that are closely similar to, or identical with, the reaction of Marrocos 9623. These two genes may condition moderate resistance when combined together, and may add to the effectiveness of the third gene when combined with it.

Camadi Abdu Tipo x Marrocos 9623—Approximately 1/64 of the F_3 lines from Camadi Abdu Tipo x Marrocos 9623 were homozygous susceptible (infection type 4-c). Lines showing monogenic segregations for resistance vs.

susceptibility were divided into three classes based on the phenotype of resistant seedlings. Each of the three classes occurred in a proportion approximating 2/64. The most resistant seedlings in the three classes had infection types 2-, 1, and 0;, respectively. Lines homozygous for infection types 2-, 1, and 0; were observed in proportions of about 1/64, 1/64, and 7/64 respectively. About 48/64 were classed as inseparable. In the BC-F_2, about 1/8 of the lines were homozygous susceptible. Three classes of lines, each constituting proportions of about 1/8, showed monogenic ratios for resistance vs. susceptibility. The most resistant seedlings in the three classes produced 2-, 1, and 0; infection types. About 4/8 of the lines were classed as inseparable.

The data indicated that Camadi Abdu Tipo and Marrocos 9623 differ by three, independent, incompletely dominant genes for reaction to culture 111-SS2. Individually, the three genes conditioned 2-, 1, and 0; infection types.

St. 464 x Marrocos 9623—The homozygous susceptible class in the F_3 from St. 464 x Marrocos 9623 constituted about 1/64 of the lines. Three classes of lines showed monogenic segregations for resistance vs. susceptibility. The proportion of each class was about 2/64. The most resistant seedlings in the three classes had infection types 0; 13 =, 0; + 12 =, and 0;, respectively. Lines homozygous for infection types 0; 13 =, 0; + 12 =, and 0; occurred in proportions of about 1/64, 1/64, and 16/64, respectively. About 39/64 of the lines were classed as inseparable. About 1/8 of the lines in the BC-F_2 were homozygous susceptible. Three classes of lines showed monogenic ratios for resistance vs. susceptibility. Each class occurred in a proportion approximating 1/8. The most resistant seedlings in the three classes produced infection types 0; 13 =, 0; + 12 =, and 0;. About 4/8 of the lines were classed as inseparable.

The data indicated that three independent genes conditioned the resistance of St. 464 to culture 111-SS2. One gene, when homozygous, conditioned a high level of resistance (infection type 0;) that masked lower levels of resistance conditioned by other gene pairs. The other two genes, when homozygous, conditioned infection types 0; + 12 =, and 0; 13 =. Variability in resistant classes of lines segregating 3 resistant seedlings : 1 susceptible indicated that resistance may be incompletely dominant.

C.I. 8155 x Marrocos 9623—About 1/64 of the F_3 lines from C.I. 8155 x Marrocos 9623 were homozygous susceptible. Three classes of lines showed monogenic segregations for resistance vs. susceptibility. The proportion of each class was approximately 2/64. The most resistant seedlings in the three classes had infection types 2-3-, 0; + 13 =, and 0; 1, respectively. Lines homozygous for infection types 2-3-, 0; + 13 =, and 0; occurred in proportions of about 1/64, 1/64, and 7/64, respectively. About 48/64 were classed as inseparable. About 1/4 of the BC-F_2 were homozygous susceptible, 2/4 were segregating 3 resistant : 1 susceptible, and 1/4 were classed as inseparable.

The F_3 data indicated that three incompletely dominant genes conditioned the resistance of C.I. 8155. One gene conditioned infection type 2-3-, one

infection type 0; 13 =, and one infection type 0; + 1. However, the data from the BC-F_2 indicated only two incompletely dominant genes for resistance.

Iumillo x Marrocos 9623—Approximately 1/64 of F_3 lines from Iumillo x Marrocos 9623 were homozygous susceptible. Three classes of lines showed monogenic segregations for resistance vs. susceptibility. Each of the three classes occurred in a proportion approximating 2/64. The most resistant seedlings in the three classes had infection types 2-3-, 0; 12 =, and 0; 13 =, respectively. Lines homozygous for infection types 2-3-, 0; 12 =, 0; 13 =, and 0; were observed in proportions of about 1/64, 1/64, 2/64, and 7/64, respectively. About 46/64 were classed as inseparable. About 1/8 of the lines in the BC-F_2 were homozygous susceptible. Three classes of lines showed monogenic ratios for resistance vs. susceptibility. Each class was observed in a proportion of about 1/8. Phenotypes of the most resistant seedlings in each class were similar to those observed in corresponding classes showing monogenic segregations in the F_3. About 4/8 were classed as inseparable.

The data indicate that three genes conditioned the resistance of Iumillo. Singly, one of the genes conditioned infection type 2-3-, one conditioned infection type 0; 12 =, and one conditioned infection type 0; 13 =. Apparently, two of the genes in combination conditioned infection type 0; 13 =, and other combinations of two or more genes conditioned infection type 0;.

DISCUSSION

The results indicate that Spelmar, Vernal, Camadi Abdu Tipo, St. 464, and Iumillo each have three genes for resistance to culture 111-SS2. C.I. 8155 may have either two or three genes for resistance, and Kubanka probably has one. Inheritance studies of the reaction of the tetraploid wheats to culture 111-SS2 generally have been more difficult to interpret than similar studies with hexaploid wheats. Marrocos 9623 is not an ideal variety for a susceptible parent because it often shows partial resistance. In segregating generations, variability of infection types on the same leaf and gradations of reactions among seedlings in the same line have made classification difficult in certain crosses. We plan to develop lines homozygous for single genes for resistance with respect to each gene indicated by the inheritance studies. This procedure could give positive confirmation that a variety has at least as many genes for resistance as indicated by the genetic studies, but it would not necessarily show that a variety had either more or less genes for resistance than indicated. Eventually, we plan to transfer each of the single genes to a uniform genetic background by backcrossing to a susceptible variety.

KNOTT (1966) has listed five potential uses for wheat lines with single genes for resistance. We have developed and used monogenic lines, and find they are useful in tests for allelism or linkage with genes for resistance from different varieties. Single genes for resistance may be useful as genetic markers.

We (WILLIAMS *et al.*, 1966) have shown the value of monogenic lines for studies of host-parasite relations by demonstrating a gene-for-gene relationship between genes for reaction of wheat and genes for pathogenicity of *Puccinia graminis* f. sp. *tritici*. Monogenic lines should provide a genetic basis for differentiation of stem rust cultures. Conversely, cultures of stem rust could be developed, through tests on monogenic lines, for directly analyzing wheat lines for genes for resistance. Genetically similar lines of wheat, each carrying single genes for resistance, should provide excellent materials for studies of the physiological nature of stem-rust resistance.

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Erratum: The correct spelling of "Camadi Abdu Tipo" is Gamadi Abdu Tipo, followed by a number, and of "Marrocos 9623" is Marruecos 9623.