

C. R. Riede · N. D. Williams · J. D. Miller

Wheat lines monogenic for resistance to stem rust from the wheat cultivar 'Waldron'

Received: 9 June 1994 / Accepted: 18 July 1994

Abstract The *Triticum aestivum* L. cultivar 'Waldron' has long lasting resistance to most North American stem rust (*Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. and E. Henn.) isolates. The objective of this research was to develop wheat lines monogenic for resistance to stem rust from 'Waldron' using allelism tests and tests for reaction to a series of ten stem rust cultures having a range of virulences. Twelve lines homozygous for single resistance genes were selected as parents of a diallel cross to test for allelism among genes for resistance. We identified 6 lines or groups of lines (WDR-A1, the WDR-B1 and WDR-B2 group, the WDR-C1 and WDR-C2 group, WDR-D1, the WDR-E1, WDR-E2, WDR-E3, and WDR-E4 group, and WDR-F1) that carried different single genes for resistance from 'Waldron'. A seventh line (WDR-G1) probably has two genes for resistance, one in common with WDR-C1 and WDR-C2. The gene in the WDR-E group is probably the same as *SrWld*1, and the one in WDR-F1 the same as *Sr11*. 'Waldron' probably has two or more genes for resistance to stem rust that previous genetic studies did not detect.

Key words *Triticum aestivum* · *Puccinia graminis* · Allelism · Inheritance · Segregation

Introduction

The wheat (*Triticum aestivum* L.) cultivar 'Waldron' (WDR) (C.I. 13958) was selected from a cross of 'Justin' with ND 81 and released in 1969 (Smith et al. 1969). It was a leading hard red spring wheat cultivar in North Dakota in the 1970s (Smith 1978). For many years, 'Waldron' has exhibited a very stable resistance against the prevalent races of stem rust in North America. Previous inheritance studies indicated that WDR possesses 1, 2, or 4 effective genes for resistance to stem rust (*Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. and E. Henn.), depending upon the culture of stem rust used (Williams and Miller 1982a). McVey and Roelfs (1978) determined that WDR was mixed for reaction to certain rust cultures. Based on reactions to stem rust cultures, they indicated that about 50% of the 'Waldron' plants possessed *Sr11*, and 20–25% possessed *Sr5*. They found a dominant gene, tentatively designated $SrWld_1$ which appeared to give resistance to most or all North American isolates of stem rust. Another gene, tentatively designated $SrWld_2$, gave resistance to certain rust isolates. Roelfs et al. (1983) surveyed the occurrence of stem rust in the United States and Mexico in 1981 and found no virulence for seedlings with $SrWld_1$, in bulked urediospore collections.

The development of wheat lines, each carrying a single gene for resistance to stem rust, has considerable potential value. These lines are useful in confirming results of genetic studies to determine the number of genes in a resistant parent, in tests for allelism and linkage, as genetic tester stocks in studying the inheritance of resistance in other cultivars, in inheritance studies of pathogenicity, in genetic differentiation and selection of stem rust cultures, in physiological studies of resistance, and as sources of specific genes for resistance, as indicated by Knott (1958) and Williams (1973). Numerous hexaploid and tetraploid wheat lines having single genes for stem rust resistance have been selected and utilized in genetic studies (Anderson et al. 1971; Gough and Williams 1969; Weeraratne and Williams 1971; Williams 1973; Williams et al. 1966; Williams and Kaveh 1976; Williams and Miller 1982b).

The objectives of this research were to: (1) select lines having a single gene for stem rust resistance derived from WDR, (2) determine allelic relations among the lines, and (3) develop a line containing a single gene for each of the genes for resistance in WDR.

Communicated by G. E. Hart

C. R. Riede (✉)
Instituto Agronômico do Paraná -IAPAR/CNPq, Cx. Postal 1331, 86001-Londrina-PR, Brazil

N. D. Williams · J. D. Miller
Agricultural Research Service, USDA,
and North Dakota State University, Fargo, N. D., USA

This paper is a contribution of the North Dakota Agricultural Experiment Station, Agricultural Research Service, U.S. Department of Agriculture, Journal series No. 2164

Table 1 Infection types[a] on 12 selected potential monogenic lines inoculated with ten different tester cultures of *Puccinia graminis* f. sp. *tritici*

WDR-line	Culture, standard race[a], and cereal rust laboratory code[b]									
	111-SS2 111 LCBB	Or11c 151 QBCN	GB121 121 DCML	370 C 151 QFLN	72-415 p1 15 B TLMQ	72.00 11-32-113 RTQQ	72-14-5 11-32-113 PRQQ	A-15 17 L HNQL	A-5 56 MBCT	A-14NW 29 HNHN
A1	;1^{-}	34^{-}	34	34	43	4	4	3^{-}	4	4
B1	3c	34^{-}	34	4	4	4	4	34	4^{-}	4
B2	;$1^{=}$	34^{-}	4	4	4	4	4	4	4^{-}	4
C1	13	3^{-}	31	3	43	34	3	3	4	4
C2	13	3^{-}	31	3	33^{+}	34	3^{-}	3	4	4
D1	2	34^{-}	34^{-}	4	4	4	4	4	4	4
E1	2^{-}	2	2^{-}	2	2	23	23	23	23	2
E2	1^{-} $2^{=}$	2	2	2	23	2	23	23^{-}	32	2
E3	;$1^{=}$	2	2^{-}	2	23	23	23	23	23	2
E4	2	2	2^{-} 1^{-}	23	32	23	23	32	23	2
F1	;$1^{=}$	11^{-}	;$1^{=}$	1^{-} $2^{=}$	4	34^{-}	4	34^{-}, 12^{-}	1^{-} $2^{=}$	4
G1	;$1^{=}$	3^{-}	31	32	34	34	3	3	4^{-}	4

[a] Stakman et al. (1962)
[b] Roelfs and McVey (1974)

Materials and methods

Lines having single genes for resistance to stem rust were selected from progenies of WDR-sel./'Little Club' (LC). Thirty-five F_2 families that produced monogenic ratios for reaction to stem rust in the F_3 were selected in a previous genetic study by Williams and Miller (1982a). When possible, selection was based on infection types (IT) (Stakman, et al. 1962) of the resistant segregants to obtain lines possessing each of the genes for resistance segregating in the cross. Ten seeds from each of the selected families were planted in pots, grown to maturity, and harvested individually. Seed of each line was subdivided into ten lots for testing with each of ten cultures (Table 1) of stem rust. Thirty-five lines homozygous for resistance were selected in the F_4 for further study. The selected lines were crossed with the susceptible tester LC, and the F_2s were tested for reaction to stem rust. A monogenic F_2 ratio confirmed the monogenic condition of the resistant parental line.

Twelve lines were selected from the different IT groups, and a diallel cross, without reciprocals, was made among them to differentiate parental lines having the same gene for resistance from those having different genes. Culture 111-SS2, or a spore mixture of culture 111-SS2 having reddish-brown urediospores, and culture Or11c, having orange urediospores, were used to inoculate F_2 seedlings from the diallel cross. The objective of the double inoculations was to obtain twice the amount of information from the same seedling. The inoculation and classification procedure was the same as that described by Riede et al. (1985).

Genetic ratios were tested for goodness of fit by application of Chi-square tests (Mather 1963; Snedecor 1946).

Results and discussion

The reactions to ten cultures of stem rust of the 35 lines, selected as possible single gene lines, and the segregation ratios of the F_2 from each line crossed with LC were used to select 12 lines for further study. The remaining 23 lines were not studied further, either because their reactions were similar to 1 or more of the 12 lines selected or because the F_2 segregation ratios were not distinctly monogenic. The 12 selected lines representing seven letter groups based on differences of ITs were designated WDR-A, WDR-B, WDR-C, WDR-D, WDR-E, WDR-F, and WDR-G. The separation in numerical order within letter groups was done to identify lines having similar ITs (Table 1). The crosses of these 12 lines had monogenic F_2 segregations of 3 resistant seedlings: 1 susceptible (Table 2). The 3:1 ratios confirmed that the lines had single genes for resistance to the stem rust cultures used.

Tests of F_2 seedlings from the diallel cross among the 12 selected lines were used to differentiate parents having the same single gene for resistance from those that differ. Absence of segregation in certain crosses showed that the parents had the same gene (Table 3).

Segregation in the F_2 of certain crosses indicated that the parental lines had different single genes for resistance. Crosses of WDR-A1 with each of 9 WDR-lines produced susceptible segregants in the F_2 of tests with either one or both of cultures 111-SS2 and Or11c (Table 4). Although the F_2 of WDR-A1/WDR-F1 was not obtained, ITs with cultures Or11c, GB121, and 370C were high on WDR-A1 but low on WDR-F1 (Table 1). These results indicated that WDR-A1 and WDR-F1 had different genes for resistance. The single gene for resistance in WDR-A1 appeared to be different from those in the other WDR lines.

Crosses of WDR-B1 and WDR-B2 with other lines produced some susceptible or nearly susceptible segregants in the F_2 when tested with cultures 111-SS2, Or11c, or both (Table 4). Thus, the gene for resistance in WDR-B1 and WDR-B2 was not allelic to those in the other 9 lines. Likewise, crosses of the WDR-C1, WDR-C2, WDR-D1, and WDR-E group with other lines produced susceptible F_2 segregants when tested with cultures 111-SS2, Or11c, or both. These results indicated that WDR-A1, the WDR-B1

Table 2 Reactions of F_2 wheat seedlings from crosses of potential monogenic lines (WDR) with the susceptible tester 'Little Club' to cultures of *Puccinia graminis* f. sp. *tritici*

WDR-lines	Culture	Number of F_2 seedlings		*P* value (3:1) between
		Resistant	: Susceptible	
A1	Or11c	56	17	0.50 – 0.75
B1	111-SS2	38	15	0.50 – 0.75
B2	111-SS2	30	9	0.75 – 0.90
C1	Or11c	37	14	0.50 – 0.75
C2	Or11c	56	16	0.50 – 0.75
D1	111-SS2	60	14	0.10 – 0.25
E1	Or11c	55	17	0.75 – 0.90
E2	Or11c	54	21	0.50 – 0.75
E3	Or11c	69	24	0.75 – 0.90
E4	Or11c	60	16	0.25 – 0.50
F1	Or11c	53	14	0.25 – 0.50
G1	Or11c	50	12	0.25 – 0.50

Table 3 Reactions of F_2 wheat seedlings from crosses among lines (WDR) having single genes for stem rust resistance from 'Waldron' that did not produce susceptible F_2 segregants to cultures of *Puccinia graminis* f. sp. *tritici*

Cross[a]	Number of F_2 seedlings		Culture
	Resistant	Susceptible	
B1/B2	139	0	111-SS2
C1/C2	137	0	111-SS2
E1/E2	148	0	111-SS2, Or11c
E1/E3	76	0	111-SS2, Or11c
E1/E4	142	0	111-SS2, Or11c
E2/E3	150	0	111-SS2, Or11c
E2/E4	138	0	111-SS2, Or11c
E2/E4	148	0	111-SS2, Or11c

[a] The parental line shown first in a cross was not necessarily the female parent

and WDR-B2 group, the WDR-C1 and WDR-C2 group, WDR-D1, the WDR-E group, and WDR-F1 have different single genes for resistance.

Progeny of crosses of 2 parental lines that had different independent, single genes for resistance should have segregated in a F_2 ratio of 15 resistant seedlings: 1 susceptible in tests with a culture such as 111-SS2, which was avirulent on both resistance genes. The numbers of crosses with significant deviations from expected ratios (40% of the crosses, tested with cultures 111-SS2 and Or11c, Tables 4 and 5) was greater than expected due to chance alone. The cause of the large number of significant deviations was not determined, but deficiencies in the number of susceptible seedlings in some crosses could have been caused by weak repulsion phase genetic linkage or preferential transmission of one or both resistance genes. The excess of susceptible seedlings in some crosses could have been caused by preferential transmission of alleles for susceptibility. The crosses involving each of the 12 lines showed both deficiencies and excess of susceptible seedlings in the segre-

Table 4 Segregation for reaction to cultures of stem rust (*Puccinia graminis* f. sp. *tritici*) of F_2 seedlings from crosses among wheat lines (WDR-) having single genes for resistance from the cultivar 'Waldron'

Cross[a] (WDR-line)	Cultures and reaction[b] (no. of F_2 seedlings)						
	111-SS2			Or11c			
	R	S	P (χ^2-15:1)	R	S	Ratio	*P*
	(Crosses with WDR-A1)						
A1/B1	138	3	<0.02	–	–		
A1/B2	135	6	>0.30	–	–		
A1/C1	132	7	>0.50	–	–		
A1/C2	132	5	>0.20	–	–		
A1/D1	130	9	>0.90	–	–		
A1/E1	144	3	<0.05	105	17	3:1	<0.01
A1/E2	147	0	<0.01	125	22	3:1	<0.01
A1/E3	140	1	<0.01	97	15	3:1	<0.01
A1/E4	121	17	<0.01	90	22	3:1	>0.01
	(Crosses with WDR-B1 and WDR-B2)						
B1/C1	141	3	<0.05	–	–		
B2/C1	129	8	>0.80	–	–		
B1/C2	134	9	>0.98	–	–		
B2/C2	113	27	<0.01	–	–		
B1/D1	121	21	<0.01	–	–		
B2/D1	109	26	<0.01	–	–		
B1/E1	104	35	<0.01	104	36	3:1	>0.80
B2/E1	117	29	<0.01	105	41	3:1	>0.30
B1/E2	138	2	<0.02	103	37	3:1	>0.50
B2/E2	138	6	>0.30	107	42	3:1	>0.30
B1/E3	140	6	>0.20	96	45	3:1	>0.05
B2/E3	140	7	>0.30	114	36	3:1	>0.70
B1/E4	133	11	>0.30	128	14	3:1	<0.01
B2/E4	109	37	<0.01	141	7	3:1	<0.01
B1/F1	130	14	>0.05	69	28	3:1	>0.30
B2/F1	125	20	<0.01	109	37	3:1	>0.90
	(Crosses with WDR-B2 and WDR-C2)						
C1/D1	120	11	>0.30	–	–		
C2/D1	135	1	<0.01	–	–		
C1/E1	126	1	<0.02	101	11	15:1	>0.10
C2/E1	134	11	>0.50	126	18	15:1	<0.01
C1/E2	140	1	<0.01	121	20	15:1	<0.01
C2/E2	144	3	<0.05	135	12	15:1	>0.30
C1/E3	142	2	<0.02	127	10	15:1	>0.50
C2/E3	150	2	<0.02	132	15	15:1	<0.05
C1/E4	131	13	<0.01	105	17	15:1	<0.01
C2/E4	134	4	<0.10	131	10	15:1	>0.50
C1/F1	136	14	>0.01	125	21	15:1	<0.01
C2/F1	139	5	>0.10	134	11	15:1	<0.50
	(Crosses with WDR-D1)						
D1/E1	128	9	>0.80	125	24	3:1	<0.02
D1/E3	139	2	<0.01	103	41	3:1	>0.30
D1/E4	140	4	>0.05	131	14	3:1	<0.01
D1/F1	140	8	>0.50	118	29	3:1	>0.10
	(Crosses with WDR-D1, WDR-E2, WDR-E3, WDR-E4)						
E1/F1	137	12	>0.30	137	12	15:1	>0.30
E3/F1	150	2	<0.02	135	15	15:1	>0.05
E4/F1	144	4	>0.05	144	4	15:1	>0.05

[a] The parental lines shown first in a cross was not necessarily the female parent
[b] R, resistant; S, susceptible

Table 5 Segregation for reaction to cultures of stem rust (*Puccinia graminis* f. sp. *tritici*) of F_2 seedlings from crosses of wheat lines WDR-G1 with other WDR-lines having single genes for resistance from the cultivar 'Waldron'

Cross[a] (WDR-G1/ WDR-line)	Cultures and reaction[b] (no. of F_2 seedlings)							
	111-SS2					Or11c		
	R	I	S	Ratio	P	R	S	P (χ^2 15:1)
A1	139	3	0	63:1	>0.50	–	–	
B1	148	2	0	63:1	>0.80	–	–	
B2	125	0	0	63:1	>0.01	–	–	
C1	111	28	0	3:1	>0.10	–	–	
C2	100	35	0	3:1	>0.80	–	–	
D1	108	5	0	63:1	<0.05	–	–	
				15:1	>0.30	–	–	
E1	115	1	0	63:1	<0.50	105	10	>0.20
E2	144	0	0	63:1	<0.10	136	8	>0.70
E3	148	0	0	63:1	>0.10	137	11	>0.50
E4	135	7	0	63:1	<0.01	115	8	>0.90
				15:1	>0.50			
F1	124	0	1	63:1	<0.30	98	1	>0.05

[a] WDR-G1 was not necessarily the female parent
[b] R, resistant; I, intermediate; S, susceptible

gating classes. No difficulties were noticed in the classification of segregating seedlings. Differential transmission of male and female gametes carrying a gene for resistance in the wheat cvs 'Gabo', 'Charter', and 'Yalta' was shown by Luig (1960). Nyquist (1962) reported the results of an extensive study of the inheritance of stem rust resistance of a common wheat strain derived from *Triticum timopheevi*. Observed F_2 ratios ranged from to 7.1% to 26.6% percent of susceptible plants. Differential fertilization of different degrees for the various hybrids was proposed as a major cause of the different ratios observed. The gene(s) causing differential fertilization was the same as, or was completely linked with each of the one or two genes proposed as controlling stem rust resistance of C.I. 12633. The case of preferential transmission or preferential genetic segregation has been addressed by Serra (1965) and Grant (1975), and classic examples in maize and drosophila were cited.

The F_2 data from the WDR-G1 crosses were difficult to interpret and inconclusive (Table 5). Only one cross, WDR-G1/WDR-F1, produced a susceptible segregant, but several crosses produced segregants having lower levels of resistance (intermediate) than those of the resistant class. The F_2 of crosses of WDR-G1 with WDR-C1 and WDR-C2 appeared to segregate for two levels of resistance in a ratio of 3 resistant seedlings: 1 intermediate. These 2 crosses indicated that WDR-G1 may have two genes for resistance, one in common with the gene in WDR-C1 and WDR-C2. Although sample sizes were too small to differentiate accurately between two-factor and three (or more)-factor segregations, the phenotypic ratios in the F_2 of crosses of WDR-G1 with the other 6 WDR-line groups indicated segregation for more than two genes for resistance in tests with culture 111-SS2. These data supported the hypothesis that WDR-G1 has more than one gene for resistance.

Phenotypic ratios in tests with culture Or11c on F_2 seedlings of WDR-G1/WDR-E lines fit a 15 resistant: 1 susceptible ratio; Or11c may have been virulent on one of the three genes segregating for resistance. Infection type data (Table 1) indicated that WDR-G1 did not have a gene in common with those in WDR-D1, the WDR-E group, and WDR-F1. WDR-G1 may have had a gene for resistance not represented in the other WDR-lines, although the IT data (Table 1) and the F_2 segregation ratios (Table 5) did not conclusively eliminate the possibility of a gene in common with WDR-A1 or with one in WDR-B1 and WDR-B2. The 3:1 segregation observed in the F_2 of WDR-G1/LC, when tested with culture Or11c (Table 2), indicated only one gene for resistance in WDR-G1. If WDR-G1 had two resistance genes, culture Or11c probably was virulent on one of the two.

Allelism tests (Tables 3, 4, and 5) and comparisons of ITs in tests with several stem rust cultures (Table 1) identified six lines or groups of lines having different single genes for stem rust resistance and a seventh line probably having two genes for resistance. WDR-A1, the WDR-B1 and WDR-B2 group, and WDR-D1 each had different single genes conditioning resistance (IT;$1^=$) only to culture 111-SS2 of the ten test cultures. WDR-C1 and WDR-C2 had a fourth single gene conditioning moderate resistance (IT 13^- to 3) to 111-SS2, Or11c, and several other test cultures. The WDR-E group of lines had a fifth single gene conditioning resistance (IT 2^- to 32) to ten test cultures. This gene is probably the one designated $SrWld_1$ by McVey and Roelfs (1978). WDR-F1 had a sixth single gene that conditioned resistance (IT;$1^=$ to $1^-2^=$) to culture 111-SS2, Or11c, and several other test cultures. Comparisons of ITs (J. D. Miller, unpublished) indicated that this gene may be the *Sr11* found in part of the WDR population by McVey and Roelfs (1978). WDR-G1 probably had two genes for resistance, one of which appeared to be the same as one in WDR-C1 and WDR-C2; the allelism relationship of the second gene was not determined.

Inheritance studies by Williams and Miller (1982a) indicated from one to four genes for resistance to stem rust in WDR-selection, depending upon the rust culture used. The present study, through selection of lines monogenic for resistance, showed that the WDR-selection had at least six genes for resistance and indicated that conventional inheritance studies are not always adequate to accurately analyze the genetics of resistance as complex as that of WDR.

References

Anderson MK, Williams ND, Maan SS (1971) Monosomic analysis of genes for stem rust resistance derived from Marquis and Reliance wheats. Crop Sci 11:556–558

Gough FJ, Williams ND (1969) Interaction of genes for pathogenicity in *Puccinia graminis* f. sp. *tritici* and for resistance in a selection of *Triticum durum* 'Acme'. Phytopathology 59:1868–1871

Grant V (1975) Genetics of flowering plants. Columbia University Press, New York

Knott DR (1958) The inheritance of stem rust resistance in wheat. In: Jenkins BC (ed) Proc lst Int Wheat Genet Symp, University of Manitoba, Winnipeg, Canada, pp 32–38

Luig NH (1960) Differential transmission of gametes in wheat. Nature 185:636–637

Mather K (1963) The measurement of linkage in heredity. Methuen & Co, London

McVey DV, Roelfs AP (1978) Stem rust resistance of the cultivar 'Waldron'. In: Ramanujam S (ed) Proc 5th Int Wheat Genet Symp. Indian Soc Genet Plant Breed, New Delhi, India, pp 1061–1065

Nyquist WE (1962) Differential fertilization in the inheritance of stem rust resistance in hybrids involving a common wheat strain derived from *Triticum timopheevi*. Genetics 47:1109–1124

Riede CR, Williams ND, Miller JD (1985) Inheritance of resistance to stem rust in the wheat cultivar 'Estanzuela Dakuru'. Crop Sci 25:623–626

Roelfs AP, Long DL, Casper DH (1983) Races of *Puccinia graminis* f. sp. *tritici* in the United States and Mexico in 1981. Plant Dis 67:82–84

Roelfs AP, McVey DV (1974) Races of *Puccinia graminis* f. sp. *tritici* in the U.S.A. during 1973. Plant Dis Rep 58: 608–611

Serra JA (1965) Modern genetics, vol 1. Academic Press, London

Snedecor GW (1946) Statistical methods, 4th edn. Iowa State College Press, Ames, Iowa

Smith GS (1978) Changes in North Dakota hard red spring wheat varieties, 1900–1977. N D Farm Res, No. 5 35:16–21

Smith GS, Frohberg RC, Sibbit LD, Ebeltoft DC (1969) 'Waldron' – A new high-yielding HRS wheat. N D Farm Res, No. 3 26:4–9

Stakman EC, Stewart DM, Loegering WQ (1962) Identification of physiologic races of *Puccinia graminis* var. *tritici*. USDA-ARS E617 Rev. (Scientific Journal Series Paper no. 4691). Minn. Agric Exp Stn, St. Paul, Minn.

Weeraratne H, Williams ND (1971) Inheritance of resistance to stem rust in six durum wheats. Crop Sci 11:915–918

Williams ND (1973) Development and use of wheat lines monogenic for resistance to stem rust. Agron Abstr 1973 Annu Meet, Am Soc Agron, p 17

Williams ND, Kaveh H (1976) Relationships of genes for reaction to stem rust from 'Marquis' and 'Reliance' wheat to other *Sr* genes. Crop Sci 16:561–564

Williams ND, Miller JD (1982a) Inheritance of resistance to stem rust in a selection of the wheat cultivar 'Waldron'. Crop Sci 22:1175–1179

Williams ND, Miller JD (1982b) Allelic and linkage relations among genes for stem rust resistance from *Triticum turgidum*, 'Mindum', 'Acme' selection, 'Palestine', and 'Khapli'. Crop Sci 22:1293–1297

Williams ND, Gough FJ, Rondon M (1966) Interaction of pathogenicity genes in *Puccinia graminis* f. sp. *tritici* and reaction genes in *Triticum aestivum* ssp. *vulgare* 'Marquis' and 'Reliance'. Crop Sci 6:245–248