Theor Appl Genet (1995) 90: 1158–1163

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Chromosomal location of genes for stem rust resistance derived from 'Waldron' wheat

Received: 9 June 1994 / Accepted: 18 June 1994

Abstract The chromosomal locations of genes for resistance to stem rust (*Puccinia graminis* Pers.: Pers. f. sp. *tritici* Eriks. & E. Henn.) in the wheat (*Triticum aestivum* L.) cultivar 'Waldron' (WDR) were determined by monosomic analyses. Wheat lines WDR-B1, -C2, -E4, and -F1,which have single genes for resistance to stem rust derived previously from WDR sel. 'Little Club', were crossed onto a complete set of 21 'Chinese Spring' monosomics. The F_2 and backcross-F_1 (BC_1F_1) seedlings from each of the 84 crosses were tested for reaction to culture 111-SS2 (CRL-LCBB) of stem rust, and a few selected segregants were analyzed cytologically for chromosome number. The F_2 from 2 crosses of WDR-C2, -E4 and -F1 and the BC_1F_1 from 2 crosses of WDR-F1 were tested also with culture Or11c (CRL-QBCN). Significant deviations from disomic ratios towards monosomic ratios in the F_2 and BC_1F_1 were used to determine which chromosomes carried the genes for resistance. Cytological analyses of certain BC_1F_1 and susceptible F_2 plants were used to help identify the location of the genes for rust resistance. WDR-B1 has a gene, herein designated *Sr41*, for resistance on chromosome 4D. WDR-C2 has a gene on chromosome 7A that may be the same as one previously designated *SrWld2*. WDR-E4 has a gene on chromosome 2A, possibly *SrWld1*, which is effective against most or all North American stem rust cultures. WDR-F1 has a gene on chromosome 6B that is the same as or similar to *Sr11*.

Communicated by G. E. Hart

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This paper is a contribution of the North Dakota Agricultural Experiment Station, Agricultural Research Service, U.S. Department of Agriculture, Journal series No. 2165

Key words *Triticum aestivum* · *Puccinia graminis* · Aneuploid · Cytogenetics · Monosomics

Introduction

Stem rust of wheat (*Triticum aestivum* L.) caused by *Puccinia graminis* Pers.: Pers. f. sp. *tritici* Eriks. and E. Henn is a serious disease that can severely reduce the yield and quality of a wheat crop. The epidemics caused by race 56 in 1935 and race 15B from 1950 to 1954 resulted in severe losses. The major method for control of stem rust has been through the breeding of resistant cultivars using race specific genes for resistance.

The hard red spring wheat cultivar 'Waldron' (WDR) was grown extensively in North Dakota for many years (Smith 1978). 'Waldron' has shown a high level of resistance to infections of the stem rust fungus. Resistance is exhibited in both seedling and adult plants and extends to both prevalent and nonprevalent races of the rust population in North America (Williams and Miller 1982). Inheritance studies indicated that WDR possesses one, two, or four effective genes for resistance to stem rust, depending upon the culture of stem rust used (Williams and Miller 1982). Through selection of wheat lines monogenic for resistance from WDR, Riede et al. (1995) showed that WDR has at least six genes for resistance to stem rust.

McVey and Roelfs (1978) determined that WDR was heterogeneous for reaction to certain rust cultures. Based on reactions to stem rust cultures, they indicated that about 50% of the WDR plants they tested possessed *Sr11*, and 20–25% possessed *Sr5*. Also, they found a dominant gene tentatively designated *SrWld1* that appeared to give resistance to most or all North American isolates of stem rust. Another gene tentatively designated *SrWld2* gave resistance to a limited number of rust isolates.

Roelfs et al. (1983) surveyed the occurrence of stem rust in the United States and Mexico in 1981. Their data indicated that there was no virulence in bulked urediospore collections from seedlings with *SrWld1*.

Aneuploid analyses have been advocated by several authors (Kuspira and Unrau 1959; Law and Worland 1972; Morris and Sears 1967; Sears 1954) and used to locate gene(s) on wheat chromosomes by many others (Anderson et al. 1971; Bedo et al. 1979; Dyck and Kerber 1977; Kosner and Bartos 1982). The segregation ratio for a trait conditioned by a gene on the monosome of a monosomic plant depends upon the transmission rate of the monosome in male and female gametes. For dominant, monogenic resistance, only the nullisomic progeny of a selfed critical monosomic plant would be susceptible, and the proportion of susceptible offspring would be lower than expected for a disomic ratio of non-critical monosomics. Thus, deviating segregation ratios can be used to locate genes to specific chromosomes. However, the procedure requires cytological examinations to identify the chromosomal constitution of plants, especially the parental and F_1 plants.

Six wheat lines having single genes for resistance to stem rust were selected from segregating generations from 'WDR' sel./'Little Club' (LC) (Riede et al. 1995). The location of WDR genes for stem rust resistance on specific chromosomes will provide valuable information that may be used by geneticists, pathologists, and plant breeders. Four of the six monogenic lines were used in crosses to the 'Chinese Spring' (CS) monosomics. The objective was to determine the chromosomal locations of genes for resistance to stem rust in the four lines.

Materials and methods

Wheat lines having single genes derived from 'WDR' for resistance to cultures of races 111 and 151 of the stem rust fungus (*P. graminis* f. sp. *tritici*) were studied by means of aneuploid analysis. The seeds of parental cultivars WDR (C.I. 13958), 'LC' (C.I. 4066), and 'CS' (C.I. 6322) were obtained from seedstocks at the North Dakota Agricultural Experiment Station, Fargo, N. D. The monosomic lines of 'CS', developed by E.R. Sears (1954), were obtained from L.R. Joppa, Fargo, N. D.

Four monogenic lines designated WDR-B1, WDR-C2, WDR-E4, and WDR-F1 that were developed from progenies of WDR sel./'LC' (Riede et al. 1995) were crossed as male parents to 21 lines, each monosomic for a different chromosome of 'CS'. Monosomic (2n = 20″ + 1′) and disomic (2n = 21″) F_1s were selfed and backcrossed onto euploid 'CS' (2n = 21″). Two other monogenic lines developed from 'WDR' sel./'LC', WDR-A1 and WDR-D1, will be evaluated later.

A root tip squash technique was used for initially determining the number of chromosomes of the female parents and BC_1F_1 seedlings. Root tips were treated in a saturated solution of 1-bromonaphthalene for 4–5 h, fixed in Farmer's solution overnight, hydrolyzed in 1 M HCl at 60–70°C for 10 min and stored in 70% ethanol. Chromosome counts were made on root tips stained in leuco-basic-fuchsin and aceto-carmine and squashed between a glass slide and a coverglass. Aceto-carmine smears of pollen mother cells (PMCs) (Belling 1921) were used to verify the chromosome number of the parents before their use in crosses.

The F_2 and BC_1F_1 seedlings were tested for their reaction to the stem rust fungus (*P. graminis* f. sp. *tritici*). The number of seedlings required for an accurate differentiation between a disomic and monosomic ratio was calculated by methods given by Hanson (1959). Approximately 150 F_2 and a minimum of 10 BC_1F_1 seedlings from each monosomic F_1 family were tested.

The stem rust inoculum was obtained from urediospore cultures of *P. graminis* f. sp. *tritici* maintained in liquid nitrogen at the North Dakota Agricultural Experiment Station, Fargo, N. D. Culture 111-SS2 (CRL-LCBB) (Roelfs and McVey 1974) had reddish-brown urediospores and culture Or11c (CRL-QBCN) had orange urediospores. The methods of inoculation and scoring of the stem rust reaction have been described previously (Riede et al. 1985). Phenotypes were recorded in terms of infection types as described by Stakman et al. (1962).

Significant deviations from disomic ratios toward monosomic ratios were used to identify the specific chromosomes that carried the genes for resistance. The exact monosomic ratio depends on the transmission rate of the univalent chromosome and varies with environment and among the 21 different monosomic lines (Khush 1973; Morris and Sears 1967). Chi-square tests were used for analyzing data from segregating populations. The chi-square test for heterogeneity was used to determine if the results of non critical crosses could be pooled (Mather 1963). Cytological analysis of PMCs or root tip cells in certain F_2 or backcross-F_1 plants was used along with reactions to stem rust to help identify the chromosomes bearing the genes for resistance.

Results and discussion

The infection types of the four monogenic lines and parental cultivars are presented on Table 1. The resistant donor cultivar 'Waldron' had infection type ;, when tested with both cultures 111-SS2 and Or11c, and the susceptible controls 'CS' and 'LC' had infection type 34. The four lines had distinctly resistant reactions to both cultures, with the exception of B_1, which was resistant only to culture 111-SS2. The results from monosomic analyses are presented as follows:

Monosomic analysis of WDR-B1

Significant deviations from disomic ratios toward monosomic ratios were observed in the progeny of CS mono-4D/WDR-B1. These results indicated that the gene for resistance in WDR-B1 was located on chromosome 4D. Data from the noncritical crosses were homogeneous and pooled. The F_2 and BC_1F_1 segregations of noncritical crosses fit 3:1 and 1:1 ratios, respectively (Table 2). Ten susceptible F_2 plants of CS mono-4D/WDR-B1 were cytologically verified as nullisomics (Table 3). These results fit the expectation that all susceptible (recessive) F_2 plants from the critical cross are nullisomics (Khush 1973). These cytological observations confirmed the conclusion that the location of the gene for resistance in WDR-B1 is chromosome 4D. WDR-B1 was resistant only to culture 111-SS2 among ten different stem rust cultures when tested by Riede et al. (1995). Genes for stem rust resistance located on chromosome 4D have not been reported previously. Thus, we propose the symbol *Sr41* for this gene.

Monosomic analysis of WDR-C2

Significant deviations from disomic ratios towards monosomic ratios were observed in both F_2 and BC_1F_1 of CS mono-5A/WDR-C2 and CS mono-7A/WDR-C2 when tested with culture 111-SS2 (Table 4). These results indicated that the gene in WDR-C2 was either on chromosome

Table 1 Infection types produced by two cultures of stem rust, *Puccinia graminis* f. sp. *tritici*, on the parental wheat cultivars and monogenic lines

Cultivar or line	Cultures and infection types[a]	
	111-SS2	Or11c
Waldron	;	;
WDR-B1	23	34
WDR-C2	12	21
WDR-E4	12^-	2
WDR-F1	$;1^=$	11^-
Little Club	34	34
Chinese Spring	34	34

[a] Necrotic flecks; 1, small, necrotic pustules; 2, small- to medium sized pustules with chlorosis; 3, medium-sized chlorotic pustules; 4, large pustules without chlorosis

Table 2 Segregation for seedling reaction to culture 111-SS2 of *Puccinia graminis* f. sp. *tritici* among F_2 and backcross-F_1 seedlings from crosses of monogenic wheat line WDR-B1 (*Sr 41*) with 'Chinese Spring' monosomics (*R* resistant, *S* susceptible)

Chromosome	Number of seedlings		Probability
	R	S	
F_2			(χ^2, 3R:1S)
Monosomic 4D	379	52	< 0.01
Disomic 4D	109	30	0.03–0.05
Pooled noncritical crosses	2327	726	0.10–0.20
BC_1F_1			(χ^2, 1R:1S)
Monosomic 4D	33	6	< 0.01
Disomic 4D	12	11	0.80–0.90
Pooled noncritical crosses	257	216	0.05–0.10

Table 3 Distributions among classes for meiotic chromosome number and pairing of susceptible F_2 plants derived from crosses of wheat lines WDR-B1, WDR-C2, and WDR-F1 with 'Chinese Spring' monosomics susceptible to *Puccinia graminis* f. sp. *tritici* culture 111-SS2

Cross	Chromosome number[a]		
	20″	20″ + 1′	21″
CS mono-4D/WDR-B1	10	0	0
CS mono-7A/WDR-C2	11	0	0
CS mono-4B/WDR-C2	0	3	0
CS mono-6B/WDR-F1	3	0	0

[a] 20″ = 20 bivalent chromosomes, 20″ + 1′ = 20 bivalents + 1 univalent, 21″ = 21 bivalent chromosomes

5A or on 7A. The segregation for reaction in the F_2 from disomic F_1 plants of these 2 crosses fit 3:1 ratios (Table 4). The pooled data from non critical crosses fit a 3:1 ratio for the F_2 and a 1:1 ratio for the BC_1F_1 (Table 4).

Seedlings from CS mono-5A/WDR-C2 and CS mono-7A/WDR-C2 were tested with culture Or11c that was used previously in the selection of this monogenic line from WDR-sel./'LC' (Riede et al. 1995). A significant deviation from a disomic ratio towards a monosomic ratio was observed only in the F_2 derived from CS mono-7A/WDR-C2 (Table 4). The F_2 segregation in CS mono-5A/WDR-C2 fits a 3:1 ratio. These results indicated that the gene for resistance in WDR-C2 was located on chromosome 7A.

Cytological observations showed that 11 susceptible (recessive) F_2 seedlings from CS mono-7A/WDR-C2 were nullisomics as expected for a critical cross (Table 3). Mitotic chromosome number and the reaction to stem rust observed in backcross-F_1, 'CS'//CS mono-5A/WDR-C2 seedlings showed that among plants with 42 and 41 chromosome were both resistant and susceptible seedlings and that the gene for resistance in WDR-C2 was not on chromosome 5A (Table 5). The expectations for the BC_1F_1 are that resistant plants should be disomics (42′) and susceptible ones monosomics (41′) (Khush 1973).

The gene in WDR-C2 located on chromosome 7A conditioned resistance to six of ten stem rust cultures when tested by Riede et al. (1995). The gene in WDR-C2 may be the same as the one designated *SrWld2* by McVey and Roelfs (1978), because they produce similar infection types when tested with stem rust test cultures.

Monosomic analysis of WDR-E4

Significant deviations from disomic ratios towards monosomic ratios were observed in both the F_2 and BC_1F_1 of CS mono-2A/WDR-E4 and CS mono-5B/WDR-E4 when tested with culture 111-SS2. These results indicated that the gene in WDR-E4 was either on chromosome 2A or 5B. The segregation of the F_2 from disomic F_1 plants of CS mono-5B/WDR-E4 also showed a significant deviation from a disomic ratio. The pooled data for non critical crosses fit a 3:1 for the F_2 and a 1:1 ratio for the backcross-F_1 (Table 6).

Seedlings from CS mono-2A/WDR-E4 and CS mono-5B/WDR-E4 were also tested with culture Or11c. A significant deviation from a disomic ratio towards a monosomic ratio was observed only in the F_2 derived from CS mono-2A/WDR-E4. The F_2 segregation in CS mono-5B/WDR-E4 fit a 3:1 ratio (Table 6). Cytological analysis of root tips of BC_1F_1 'CS'//CS mono-2A/WDR-E4 and 'CS'//CS mono-5B/WDR-E4 indicated that the gene in WDR-E4 was on chromosome 2A and not 5B (Table 5).

The gene in WDR-E4 located on chromosome 2A conditioned resistance to ten different cultures of stem rust when tested by Riede et al. (1995). This gene is probably the same as the one designated *SrWld1* by McVey and Roelfs (1978) that is effective against most North American isolates of stem rust and against stem rust cultures in other areas of the world (Australia, Brazil, India, Mexico, Pakistan, and Turkey).

Monosomic analysis of WDR-F1

Significant deviations from disomic ratios towards monosomic ratios were observed in both the F_2 and BC_1F_1 of

Table 4 Segregation for seedling reaction to cultures 111-SS2 and Or11c of *Puccinia graminis* f. sp. *tritici* among F_2 and BC_1F_1 seedlings from crosses of monogenic line WDR-C2 with 'Chinese Spring' monosomics (*R* resistant, *S* susceptible)

Chromosome	Number of seedlings		Probability	Test culture
	R	S		
F_2			(χ^2, 3R:1S)	
Monosomic 5A	261	26	< 0.01	111-SS2
Monosomic 7A	556	108	< 0.01	111-SS2
Disomic 5A	124	35	0.30–0.50	111-SS2
Disomic 7A	25	6	0.30–0.50	111-SS2
Pooled non-critical crosses	1575	537	0.50–0.70	111-SS2
Monosomic 5A	94	30	0.80–0.90	Or11c
Monosomic 7A	46	4	< 0.01	Or11c
BC_1F_1			(χ^2, 1R:1S)	
Monosomic 5A	48	6	< 0.01	111-SS2
Monosomic 7A	27	7	< 0.01	111-SS2
Disomic 7A	8	5	0.70–0.80	111-SS2
Pooled non-critical crosses	180	149	0.05–0.10	111-SS2

Table 5 Distribution among classes for mitotic chromosome number and reactions to *Puccinia graminis* f. sp. *tritici* of BC_1F_1 wheat seedlings derived from crosses of lines WDR-C2, WDR-E4, and WDR-F1 with 'Chinese Spring' monosomics (*R* resistant, *S* susceptible)

Cross	Chromosome number and reaction						Culture
	42′		41′		40′		
	R	S	R	S	R	S	
CS//CS mono-5A/WDR-C2	9	4	2	0	0	0	111-SS2
	3	2	0	1	0	0	Or11c
CS//CS mono-2A/WDR-E4	4	0	0	5	0	0	111-SS2
	11	0	0	5	0	1	111-SS2
	11	0	0	5	0	1	Or11c
CS//CS mono-5B/WDR-E4	6	4	0	0	0	0	111-SS2
	5	4	2	1	0	0	111-SS2
	4	5	2	1	0	0	Or11c
CS//CS mono-5B/WDR-F1	7	1	1	0	0	0	111-SS2
	4	5	0	1	0	0	Or11c
CS//CS mono-6B/WDR-F1	11	0	0	0	0	0	111-SS2

Table 6 Segregation for seedling reaction to cultures 111-SS2 and Or11c of *Puccinia graminis* f. sp. *tritici* among F_2 and BC_1F_1 wheat seedlings from crosses of monogenic line WDR-E4 with 'Chinese Spring' monosomics (*R* resistant, *S* susceptible)

Chromosome	Number of seedlings		Probability	Test culture
	R	S		
F_2			(χ^2, 3R:1S)	
Monosomic 2A	354	32	< 0.01	111-SS2
Monosomic 5B	274	23	< 0.01	111-SS2
Disomic 5B	112	14	< 0.01	111-SS2
Pooled non-critical crosses	1782	623	0.30–0.50	111-SS2
Monosomic 2A	238	51	< 0.01	Or11c
Monosomic 5B	223	75	0.95–0.98	Or11c
BC_1F_1			(χ^2, 1R:1S)	
Monosomic 2A	21	6	< 0.01	111-SS2
Monosomic 5B	17	5	0.01–0.02	111-SS2
Pooled non-critical crosses	138	121	0.20–0.30	111-SS2

CS mono-5B/WDR-F1 and CS mono-6B/WDR-F1 when tested with culture 111-SS2. These results indicated that the gene in WDR-F1 was either on chromosome 5B or 6B. The F_2 data from disomic F_1 plants of CS mono-5B/WDR-F1 deviated significantly from a 3:1 ratio, but was similar to a 15:1 ratio. Apparently, CS mono-5B/WDR-F1 may be transmitting the gene for resistance in WDR-F1 abnormally or the cross was segregating for a second gene for resistance. These results indicated that chromosome 6B probably carried the gene for resistance in WDR-F1. The

Table 7 Segregation for seedling reaction to cultures 111-SS2 and Or11c of *Puccinia graminis* f. sp. *tritici* among F_2 and BC_1F_1 wheat seedlings from crosses of monogenic line WDR-F1 with 'Chinese Spring' monosomics (R resistant, S susceptible)

Chromosome	Numbers of seedlings		Probability	Test culture
	R	S		
F_2			(χ^2, 3R:1S)	
Monosomic 5B	281	18	< 0.01	111-SS2
Monosomic 6B	372	23	< 0.01	111-SS2
Disomic 5B	136	10	< 0.01	111-SS2
Disomic 6B	62	23	0.50–0.70	111-SS2
Monosomic 5B	73	19	0.30–0.50	Or11c
Monosomic 6B	87	6	< 0.01	Or11c
BC_1F_1			(χ^2, 1R:1S)	
Monosomic 5B	33	7	< 0.01	111-SS2
Monosomic 6B	27	3	< 0.01	111-SS2
Pooled non-critical crosses	194	176	0.30–0.50	111-SS2
Monosomic 5B	9	3	0.05–0.10	Or11c
Monosomic 6B	12	0	< 0.01	Or11c

pooled data from non critical crosses did not fit a 3:1 ratio. The data from the non-critical crosses were homogenous but were deficient in the observed number of seedlings in the susceptible class when compared to a 3:1 ratio. The pooled BC_1F_1 data from the non critical crosses fit a 1:1 ratio (Table 7).

The F_2 and BC_1F_1 from CS mono-5B/WDR-F1 and CS mono-6B/WDR-F1 were tested with culture Or11c. A significant deviation from a disomic ratio towards a monosomic ratio was observed only in the cross with monosomic 6B. These results indicated that chromosome 6B carried the gene for resistance to stem rust present in WDR-F1. The segregating populations from crosses of WDR-F1 and WDR-E4 with CS mono-5B showed large deficiencies of susceptible plants (compared to a 3:1 ratio) when tested with culture 111-SS2 but fitted a 3:1 ratio when tested with culture Or11c. The same single plant of the CS mono-5B parental line was used for crosses with both WDR-F1 and WDR-E4. This plant of CS mono-5B may have carried a gene for resistance effective against culture 111-SS2 and ineffective against Or11c. Cytological observations showed that 3 susceptible (recessive) F2 seedlings from CS mono-6B/WDR-F1 were nullisomics (Table 3) and 11 disomic seedlings were resistant (Table 5), as expected for a critical cross.

WDR-F1 was resistant to five out of the ten cultures of stem rust used in tests by Riede et al. (1995). The gene present on chromosome 6B of WDR-F1 reacted similarly to *Sr11* located on chromosome 6B by Knott (1959) and is probably the same gene. About 50% of the 'Waldron' plants tested by McVey and Roelfs (1978) carried *Sr11*.

The chromosomal locations of four genes for stem rust resistance derived from the spring wheat cultivar 'Waldron' were determined by means of a monosomic analysis. Ratio analyses accompanied by cytological examinations of segregating populations showed that single genes for resistance to stem rust in wheat lines WDR-B1, WDR-C2, WDR-E4, and WDR-F1 were located on chromosomes 4D, 7A, 2A, and 6B, respectively. This knowledge of the chromosomal locations will enable geneticists, breeders, and pathologists to more easily relate the genes for resistance in 'Waldron' to other known genes for resistance and incorporate them into new cultivars.

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

Bedo Z, Sutka J, Bocsa E, Balla L (1979) Location of stem rust resistance in the wheat variety 'Arthur' using monosomic analysis. Cereal Res Commun 7:191–199

Belling J (1921) On counting chromosomes in pollen mother cells. Am Nat 55:573–574

Dyck PL, Kerber ER (1977) Chromosome location of gene *Sr29* for reaction to stem rust. Can J Genet Cytol 19:371–373

Hanson WD (1959) Minimum family sizes for the planning of genetic experiments. Agron J 51:711–715

Khush GS (1973) Cytogenetics of aneuploids. Academic Press, New York

Knott DR (1959) The inheritance of stem rust resistance. IV. Monosomic analysis of rust resistance and some other characters in six varieties of wheat including 'Gabo' and 'Kenya Farmer'. Can J Plant Sci 39:215–228

Kosner J, Bartos P (1982) Monosomic analysis and study of inheritance of resistance to stem rust in wheat cultivar 'Kavkaz'. Sbor UVTIZ – Genet a Slecht 18:101–108

Kuspira J, Unrau J (1959) Theoretical ratios and tables to facilitate genetic studies with aneuploids I. F_1 and F_2 analysis Can J Genet Cytol 1:267–312

Law CN, Worland AJ (1972) Aneuploidy in wheat and its use in genetic analysis. Plant Breeding Institute Annual Report, Cambridge, pp 25–65

Mather K (1963) Two class segregation. In: Mather K (ed) The measurement of linkage in heredity. Methuen & Co, London, pp 13–31

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

Morris R, Sears ER (1967) The cytogenetics of wheat and its relatives. In: Quisenberry KS, Reitz LP (ed) Wheat and wheat improvement. (Agronomy series, vol 13). 13: American Soc of Agronomy, Madison, Wisc., pp 19–87

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

Riede CR, Williams ND, Miller JD (1995) Wheat lines monogenic for resistance to stem rust from wheat cultivar 'Waldron'. Theor Appl Genet 90:1164–1168

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

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

Sears ER (1954) The aneuploids of common wheat. Mo Agric Exp Stn Res Bull, p 572

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

Stakman EC, Stewart DM, Loegering WQ (1962) Identification of physiologic races of *Puccinia graminis* var. 'tritici'. USDA, ARS E617

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