CYTOGENETICAL STUDIES IN WHEAT

III.* STUDIES OF A GENE CONDITIONING RESISTANCE TO STEM RUST STRAINS WITH UNUSUAL GENES FOR AVIRULENCE

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Summary

A dominant gene conditioning resistance to certain stem rust strains each with unusual genes for avirulence was located on chromosome 1D. It was found to be widespread among bread wheats, and is present in many Australian cultivars, some of which possess no resistance to strains of wheat stem rust prevalent in the field. Pathogenic tests indicated that it was identical with a gene described previously by North American investigators. As it is different from any of the previously catalogued genes in wheat for stem rust resistance the designation *Sr18* is proposed.

I. Introduction

Somatic hybridization was shown to occur between wheat stem rust (*Puccinia graminis* var. *tritici* Eriks. & Henn.) and rye stem rust (*P. graminis* var. *secalis* Eriks. & Henn.) by Watson and Luig (1959) and Bridgmon and Wilcoxson (1959). Watson and Luig concluded that the pathogenicities of the two resultant hybrids were intermediate between those of the parental cultures. On the basis of infection types shown by the parental and hybrid cultures on various accessions of four *Triticum* species they considered that rye stem rust was an avirulent strain of *P. graminis* var. *tritici* rather than a different "forma specialis" as proposed by Eriksson (1894). However, these authors did not propose a revised taxonomic treatment of *P. graminis*.

The host–pathogen relationships of genes for avirulence in the abovementioned somatic hybrids on cultivars of bread wheat (*Triticum aestivum* L.) were investigated by Luig and Watson (1965). They reported that the Australian cultivars Gabo and Charter possessed the same factor conditioning resistance to strain 103-H-2. This gene, designated *SrG2*, was inherited independently of the factor *Sr11*, which, in both cultivars, confers resistance to certain field strains. More recently, studies at this institution showed that a gene, operative against 103-H-2 and designated *SrPp1*, was present in the cultivars Purple Straw, Mona, Pusa, and Mentana.

The present studies report the location by aneuploid analysis of both *SrG2* in Gabo and *SrPp1* in Purple Straw on chromosome 1D. Pathogenic tests to be

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§ This paper presents certain data contained in the thesis entitled "Studies on the genetic nature of resistance in common wheat to strains of stem rust possessing unusual genes for avirulence" submitted in 1968 by A. K. Sanghi to the University of Sydney in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

described employing different stem rust strains show that these genes are identical, and, moreover, indicate that they are the same as the factor reported in various cultivars by investigators in the United States of America.

II. Materials and Methods

To determine the chromosome bearing the gene *SrG2*, Gabo W1422* was used as the male parent in crosses with each of the 21 monosomic stocks of Chinese Spring. In a second experiment Purple Straw W1816, possessing *SrPp1*, was crossed with the available 18 monosomic stocks which had been developed in the wheat accession W2691, a line bred at Sydney University specifically for susceptibility to *P. graminis* var. *secalis* and to strains of *P. graminis* var. *tritici* with unusual genes for avirulence (Watson and Luig 1963; Luig and Watson 1967). F_2 families from monosomic F_1 plants were tested with stem rust strain 103-H-2 (culture 58-L-1) in the series of crosses involving Chinese Spring, and with strain 111-E-2 (culture 56-L-1) in the case of W2691 hybrids. The former culture originated as a somatic hybrid between wheat and rye stem rusts (Watson and Luig 1959) whilst 111-E-2 was introduced from the United States of America (Watson 1957). The latter could have arisen as a hybrid between *P. graminis* var. *tritici* and *P. graminis* var. *secalis* (Luig and Watson 1965). Although avirulent on nearly all of numerous wheat cultivars on which it has been tested, certain genes, including *Sr5* and *Sr11*, which condition resistance to various field strains of wheat stem rust are not operative against 111-E-2. However, *Sr5* is effective against 103-H-2.

A number of wheat stocks were tested with stem rust strains 103-H-2, 111-E-2, M10-b (culture 58-L-2) and H-42 (culture 64-L-1). M10-b arose from the same somatic cross as 103-H-2 (Watson and Luig 1959), whilst H-42 is a sexual hybrid between 111-E-2 and rye stem rust.

The wheat stocks included lines with single genes extracted from Purple Straw W1816, Mentana W1129, Mona W1168, and Pusa W801. Two lines with genes from Marquis and Reliance, respectively, were kindly supplied by Dr. N. D. Williams, Fargo, North Dakota. The material also included three substitution lines. Two of these involved the replacement of the 1D chromosome pair of Chinese Spring with the corresponding pair of Hope or Timstein (hereafter designated CS/Hope 1D and CS/Timstein 1D respectively) and in the third line (CS/Timstein 6B) chromosomes 6B of Timstein replaced the homologous Chinese Spring pair.

Finally, tests for allelism between the genes conditioning resistance in some stocks were conducted by observing the infection types exhibited in segregating generations of hybrid populations.

III. Results

(*a*) *Monosomic Analyses*

Table 1 presents the segregation in F_2 seedling populations from monosomic F_1 plants of crosses between Chinese Spring monosomics and Gabo tested with strain 103-H-2. Gabo and Chinese Spring exhibited "$;2\equiv2=$" and "2–2" infection types respectively. The semi-resistant reaction of Chinese Spring is controlled by a gene on chromosome 6B as later indicated. Segregation in F_2 populations occurred for the "$;2\equiv2=$" infection types characteristic of Gabo and for infection types ranging from "2–2" to "33+". This semi-resistant to moderately susceptible group was considered to represent the contrasting phenotype to Gabo. Within it no discrete categories were made as difficulties were experienced in making precise classifications based on single leaves, presumably due to the factor on Chinese Spring 6B being incompletely dominant. Segregation ratios in F_2 populations from crosses between W2691 monosomics and Purple Straw tested with strain 111-E-2 are included also in Table 1. The infection types shown by W2691 and Purple Straw were "3+" and "$;2\equiv2=$" respectively, and F_2 segregants exhibited one or other of these types.

* W numbers refer to the Sydney University Wheat Accession Register.

In both cases a single dominant gene conditioned resistance and the significant deficiencies of susceptible segregants in crosses involving monosomic 1D indicated that the gene in each resistant cultivar was located on this chromosome. The total (excluding chromosome 1D) for the cross W2691 × Purple Straw showed a significant deviation ($0{\cdot}05 > P > 0{\cdot}025$) for single factor pair segregation. The data were homogeneous (χ^2_{16} heterogeneity = 6·56, $P = 0{\cdot}99$–$0{\cdot}95$). Luig and Watson (1967) also found that crosses between W2691 and Vernstein showed a significant deviation from a 3 : 1 F_2 ratio for rust reaction.

TABLE 1

SEGREGATION FOR SEEDLING REACTION IN MONOSOMIC F_1 PROGENIES FROM CHINESE SPRING MONOSOMICS × GABO AND W2691 MONOSOMICS × PURPLE STRAW CROSSES WHEN TESTED WITH DIFFERENT STEM RUST CULTURES

Chromosome Involved	Reaction of Chinese Spring Monosomic × Gabo to 103-H-2		χ^2 Value* (3 : 1)	Reaction of W2691 Monosomic × Purple Straw to 111-E-2		χ^2 Value* (3 : 1)
	Resistant	Susceptible		Resistant	Susceptible	
1A	25	6	0·53	90	29	0·03
2A	92	19	3·68	34	9	0·38
3A	17	11	3·05	83	25	0·20
4A	22	11	1·22	92	28	0·18
5A	25	8	0·01	34	10	0·12
6A	31	8	0·42	Not tested		
7A	23	6	0·29	133	37	0·95
1B	98	23	2·32	56	15	0·57
2B	92	32	0·04	30	9	0·08
3B	21	8	0·10	56	15	0·57
4B	20	9	0·56	47	15	0·02
5B	Not tested			25	7	0·17
6B	128	41	0·49	Not tested		
7B	31	8	0·42	49	14	0·26
1D	258	12	60·84	93	12	10·31
2D	119	38	0·04	42	11	0·51
3D	77	33	1·47	44	9	1·82
4D	231	78	0·01	11	3	0·10
5D	15	7	0·55	Not tested		
6D	19	8	0·31	46	12	0·57
7D	115	42	0·26	66	23	0·03
Total†	1201	396	0·04	938	271	4·34

* Values for significance: 3·84 ($P = 0{\cdot}05$); 6·64 ($P = 0{\cdot}01$).

† Excluding monosomic 1D.

(*b*) *Pathogenic Tests*

The infection types exhibited by various wheat stocks to four rust strains are presented in Table 2. The infection types shown by lines possessing *SrPp1*, *SrMt1*, *SrMn1*, and *SrPs1*, isolated from Purple Straw, Mentana, Mona, and Pusa, respec-

tively, were identical, and indicate that the gene for resistance is the same in each line. Gabo and Timstein exhibited the same infection types as these lines, indicating that *SrG2* is also identical with *SrPp1*. This conclusion is supported by monosomic analyses which showed that *SrG2* and *SrPp1* are both located on chromosome 1D. The chromosome location of *SrG2* was confirmed by the behaviour of CS/Timstein 1D which showed similar infection types to Gabo and Timstein. Since CS/Hope 1D and lines possessing the genes *SrMq-A* or *SrRl-A* showed similar infection types to the stocks previously mentioned, it appears that Hope, Marquis, and Reliance possess this gene.

TABLE 2

INFECTION TYPES SHOWN BY VARIOUS WHEAT STOCKS WHEN TESTED WITH FOUR STEM RUST STRAINS

Stock	Stem Rust Strain			
	103-H-2	111-E-2	H-42	M10-b
Chinese Spring W1806	2–2	3=	2–	3+
Gabo W1422	;2≡2=	;	;	;*
Timstein	;2≡2=	;	;	;*
CS/Timstein 1D	;2≡	;2=	;	3+
CS/Timstein 6B	3+†	3=	2–	;2≡*
Purple Straw W1816	2=	;2≡2=	;2≡	3+
SrPp1 (from Purple Straw)	2=	;2≡2=	;2≡	3+
Mentana W1124	0	0	0	0;
SrMt1 (from Mentana)	2=	;2≡2=	;2≡	2++3c
Mona W1168	;	;	;	$2=^{n}$
SrMn1 (from Mona)	2=	;2≡2=	;2≡	2++3c
Pusa W801	0;	0;	0;	;1–2=
SrPs1 (from Pusa)	2=	;2≡2=	;2≡	2++3c
SrMq-A (from Marquis)	2=	;2≡2=	;2≡	2++3c
SrRl-A (from Reliance)	2=	;2≡2=	;2≡	2++3c
Hope W517	0;	0;	;	0;
CS/Hope 1D	;2≡	;2≡	;	3+
W2691	3+	3+	3+	2++3c

* *Sr11* operative.

† Susceptibility due to absence of factor for resistance on Chinese Spring 6B.

However, the gene is not operative against strain M10-b. CS/Timstein 1D was susceptible, but CS/Timstein 6B resistant, to this rust. Timstein 6B possesses *Sr11* (Sears and Rodenhiser 1948), which confers resistance to M10-b. Pusa, Mentana, and Mona owe their resistances to this strain to genes other than *SrPp1*. A comparable situation exists in Hope.

Mentana, Mona, and Pusa exhibit infection types which are significantly lower to 103-H-2, 111-E-2, and H-42 than those of lines carrying the single genes listed in Table 2. In each of these cultivars two or more additional genes are operative against these rusts.

A comparison of the behaviours of Chinese Spring and CS/Timstein 6B to 103-H-2 indicates that the resistance of Chinese Spring to this strain is controlled by

chromosome 6B. It has been shown that a single factor pair conditions the Chinese Spring "2–2" infection type.

(c) *Studies on Host Allelism*

Six hundred F_2 seedlings and seedlings in 268 F_3 lines of the cross Gabo × CS/Hope 1D were tested with culture 103-H-2. No segregation for susceptibility occurred in either generation although the infection types ranged from ";" to "2=2–", the highest exceeding those of the parents. However, no seedling exhibited infection types as high as the "2–2" category characteristic of Chinese Spring.

Segregation for infection types was not shown in the F_2 generation of a cross between Mona and Gabo when 185 seedlings were tested with 103-H-2 and 104 seedlings with 111-E-2, indicating that the genes conditioning rust resistance in these cultivars were allelic or closely linked.

IV. Discussion

These investigations demonstrate that a dominant gene conferring resistance to stem rust is present in many wheat cultivars, some of which have been bred in Australia. The conclusion that the same gene is involved was based partly on the parallel pathogenic behaviour of various stocks to certain rust strains. These stocks comprised either cultivars or monogenic lines in which the factor had been separated from other genes conditioning rust resistance. Confirmatory evidence came from aneuploid analyses in which in the two cases studied the gene was found to be located on chromosome 1D.

The gene is considered to be identical with that described in other cultivars by investigators in the United States of America. Sears, Loegering, and Rodenhiser (1957) found that CS/Hope 1D exhibited "0,0;" infection types to stem rust culture 111-54A. From studies of the inheritance of pathogenicity in a cross between races 111 and 36 of wheat stem rust, Loegering and Powers (1962) identified a gene for rust resistance in CS/Hope 1D, Marquis, Reliance, and Kota. Williams, Gough, and Rondon (1966), from studies of the interaction of pathogenicity in the fungus and reaction genes in the host plant, described a common gene for rust resistance in Marquis and Reliance. Kaveh, Williams, and Gough (1968) found that the gene designated *Mq-A* in Marquis was allelic or very closely linked with a gene for rust resistance on chromosome 1D of Hope. By aneuploid analyses Anderson and Williams (1968) placed *Mq-A* in Marquis and *Rl-A* in Reliance on chromosome 1D. Strain 111-E-2 in the current studies is probably similar to, although not identical with, various cultures of race 111 used in these investigations.

The gene is operative against certain rust strains possessing unusual genes for avirulence. These strains are known to have arisen, or are suspected to have arisen, following either sexual or asexual hybridization between cultures of *P. graminis* var. *tritici* and *P. graminis* var. *secalis*. Such hybrids are avirulent on many cultivars which are susceptible to strains of wheat stem rust occurring in the field. Purple Straw and Mona, for example, are of this type. Cultivars such as Mentana, Gabo, Hope, Marquis, and Reliance have additional factors operative against field strains of stem rust. Nevertheless, the gene described in this paper does not provide protection against

all intervarietal hybrid rust strains. In the current studies it was effective against 103-H-2 but not M10-b, although both originated as hybrids from the same somatic cross. It does, however, operate against H-42, produced by hybridization on the alternate host, *Berberis vulgaris* L.

The gene exhibited some variation in the infection types to the three rusts against which it operated. With 103-H-2 infection types were usually higher suggesting that this strain may be heterozygous for the corresponding avirulence gene. Infection types with H-42 were in some cases slightly lower than when 111-E-2 was used. These deviations may have been due to environmental differences during incubation or rust development or both. Nevertheless, when tests were conducted with the same rust strain in the same environment, some stocks possessing the gene described in this paper as the only major factor for resistance showed a range in infection types from ";" to ";2=" as, for example, with 111-E-2. These minor variations are best explained by differences in the genetic backgrounds in which the gene is present.

The gene is widespread among wheat cultivars and Loegering and Harmon (1969) state that it is known to be absent only in Little Club, Chinese, and Prelude. Our studies showed that it is not present in Brevit, Federation, Eureka, Gular, Kenya C6042 (used in the breeding of Yalta, Charter, and Kendee), Koala, Morocco, Norka, or Yalta, most of which have very dissimilar pedigrees.

Gabo was selected from the cross Bobin W39[2] × Gaza [*T. turgidum* L. (*durum* group)]. Its resistance to cultures employed in the present investigations was derived from Bobin W39 since no segregation for infection types was observed in F_2 populations of a cross between Bobin and Gabo to 103-H-2. Furthermore Gaza is semi-susceptible to this strain. This is to be expected since the gene conditioning resistance is located in the D genome. In the evolution of hexaploid wheat this genome was contributed by *T. tauschii* (Coss.) Schmal. [= *Aegilops squarrosa* L.]. A study of the infection types shown by accessions of this species would be of interest for this reason.

Certain cultivars such as Marquis, Gabo, and Purple Straw have been at one time important in wheat cultivation. Others, such as Hope, occur in the pedigrees of many cultivars of economic importance. The gene described in the current investigations may have been of value initially in providing resistance against some field strains of stem rust, but, as pointed out by Loegering and Powers (1962), selection pressure in populations of the fungus would favour the establishment of a population virulent on plants with this gene. However, the gene may still be important in regions where hybridization between wheat and rye stem rusts occurs naturally. For example, as pointed out in this paper, the factor *Sr11* in Gabo and other cultivars of economic importance is not effective in providing resistance to some strains produced in this manner.

As the gene described is different from any previously catalogued factor for stem rust resistance in wheat the designation *Sr18* is proposed.

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