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TELOSOMIC MAPPING OF GENES FOR RESISTANCE TO STEM RUST OF WHEAT[1]

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SUMMARY

Telosomic mapping procedures were used in an attempt to localize genes for stem-rust resistance on specific chromosome arms and to determine the relative distance of each gene from the centromere. Sr18 was mapped near the centromere on the long arm of chromosome 1D, but tests for recombination on the short arm were not made because of unavailability of a telosome for 1DS. The location of Sr19 was not determined definitely, because apparent recombinants with both arms of chromosome 2B were recovered. The most probable location of Sr19 is on the short arm of 2B, about 7.7 crossover units from the centromere. Sr16 from Reliance was on the long arm of 2B, either independent of the centromere or loosely linked with it. Sr9d from Hope and Sr9a from Red Egyptian were mapped 10-13 units from the centromere on the long arm of 2B.

Three genes for resistance to wheat stem rust [*Puccinia graminis* Pers. var. *tritici* (Eriks. & E. Henn.) Guyot], derived from 'Marquis' and 'Reliance' wheat (*Triticum aestivum* L.), were located on specific chromosomes by monosomic analyses (ANDERSON, WILLIAMS, and MAAN, 1971). One of the genes was on chromosome 1D and appeared to be the same as a gene designated *Sr18* by BAKER *et al.* (1970). A second gene was on chromosome 2B (XIII) and appeared to be identical, allelic, or closely linked to *Sr16* (KAVEH, 1968). The third, *Sr19*, was on chromosome 2B but independent of *Sr16* (KAVEH, 1968). KAVEH (1968) showed that *Sr19* was linked with about 24% recombination with *Sr9a* from 'Red Egyptian' and a gene now designated *Sr9d* from 'Hope' (LOEGERING and SEARS, 1970; KNOTT, 1971; WILLIAMS and MILLER, 1973).

SEARS (1962, 1966) described a method for using telocentric chromosomes of wheat to locate genes on specific chromosome arms and map gene-to-centromere distance in terms of crossover units. Sears and Loegering (1968) used telocentrics to show that *Sr16* from 'Thatcher' and *Sr9a* from Red Egyptian were on the long arm of chromosome 2B. *Sr9a* and *Sr16* showed 10.6% and about 50% recombination with the

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centromere, respectively.

The present work was designed to determine the chromosomal location and the distance from the centromere of genes for stem-rust resistance in lines having monogenic resistance from Marquis and Reliance spring wheats.

MATERIALS AND METHODS

Wheat lines Mq-A, Mq-B, and Rl-B were from seedstocks maintained at the North Dakota Agricultural Experiment Station, Fargo. These lines have single genes for resistance, designated *Sr18*, *Sr19*, and *Sr16*, respectively. Seedstocks of wheat lines having *Sr9a* (CI14169) and *Sr9d* (CI14177) were obtained from Dr. W. Q. Loegering, University of Missouri. These two lines were designated ISr9a-Ra (LOEGERING and HARMON, 1969) and ISr9d-Ra (LOEGERING and SEARS, 1970). Seedstocks of ditelo-1DL, ditelo-2BL, ditelo-monotelosomic 2BS [20"+t"(2BS)+t'(2BL)], and 'Chinese Spring' were obtained from Dr. E. R. Sears, Curtis Hall, University of Missouri. Ditelo-1DS was unavailable.

The breeding scheme was similar to one diagrammed by SEARS and LOEGERING (1968). Mq-A was crossed as male with ditelo-1DL, and each of the lines Mq-B, Rl-B, ISr9a-Ra, and ISr9d-Ra was crossed with both ditelo-2BL and ditelo-2BS (monotelo-2BL). F_1 plants were used as male parents in testcrosses to Chinese Spring. The testcross progenies were tested for reaction to stem rust, and pollen-mother-cells were examined to determine the presence or absence of a telocentric chromosome and to determine chromosome pairing. The progenies of testcross plants from crosses of Mq-B, ISr9a-Ra, and ISr9d-Ra with the ditelo stocks were tested for rust reaction, to confirm the classifications of the testcross plants.

Cultures of race 111 (culture 111-SS2) and race 29 were used to inoculate seedlings of the testcrosses. Inoculum of the two rust strains was from cultures maintained at the North Dakota Agricultural Experiment Station, Fargo. Culture 111-SS2 was used to test progeny of crosses involving Mq-A, Mq-B, Rl-B, and ISr9d-Ra. The culture of race 29 was used to test progeny of crosses involving ISr9a-Ra. The methods of inoculation and scoring of reaction to rust were similar to those described earlier (WEERARATNE and WILLIAMS, 1971).

RESULTS AND DISCUSSION

Four classes of testcross plants should be possible if the gene in question is on the chromosome arm present in the ditelosomic parent. These classes are as follows: 1) rust-resistant with 21" of chromosomes (or equivalent), 2) rust-susceptible with 21" (or equivalent), 3) rust-resistant with 20"+t1" (or equivalent), and 4) rust-susceptible with 20"+t1" (or equivalent). The first and fourth classes are parental or non-crossover types, and the second and third classes are crossover types. Recovery of crossover types would not be expected if the gene is on the opposite chromosome arm. Certain of the cytological observations did not fit either of the two expected cytological types. Most of these aberrant types could be explained as resulting from chromosomal non-disjunction in the males (the F_1 plants). Cytological types for which it appeared that the male gamate carried either an allele for resistance on a telosome or an allele for susceptibility on an entire chromosome were classified as crossovers. All other aberrant cytological types were classified as non-crossovers. The rates of recombination and transmission of the telosome, and the observed and expected frequencies with respect to resistance vs. susceptibility and non-crossover type vs. crossover type, are summarized in Table 1.

Table 1. Summary of segregations for seedling reaction to wheat stem rust (*Puccinia graminis* var. *tritici*) and crossing over between *Sr* genes and the centromere in the progeny of Chinese Spring//monogenic resistant wheat lines/ditelosomics.

Wheat line (gene)	Telosome		No. testcross plants[1] R-n.c.o.	S-c.o.	R-c.o.	S-n.c.o.	Total	Recombination p ± S.E. (%)	Telo. trans. t ± S.E. (%)
		Exp.	(1-p)(1-t)n	p(1-t)n	ptn	(1-p)tn	n		
Mq-A (*Sr18*)	1DL	Obs.	90	2	0	75	167	1.2 ± 0.8	45.5 + 3.9
		Exp.	89.9	1.1	0.9	75.1	167.0		
Mq-B (*Sr19*)	2BL	Obs.	114	2	3	61	180	2.8 ± 1.2	36.1 ± 3.5
		Exp.	111.8	3.2	1.8	63.2	180.0		
Mq-B (*Sr19*)	2BS	Obs.	142	6	8	25	181	7.7 ± 2.0	20.4 ± 3.0
		Exp.	133.0	11.1	2.8	34.1	181.0		
ISr9d-Ra (*Sr9d*)	2BL	Obs.	105	15	3	49	172	10.5 ± 2.3	26.7 ± 3.4
		Exp.	112.8	13.2	4.8	41.1	171.9		
ISr9a-Ra (*Sr9d*)	2BS	Obs.	175	0	0	16	191	0.0	9.9 ± 2.2
		Exp.	172.1	0.0	0.0	18.9	191.0		
ISr9a-Ra (*Sr9a*)	2BL	Obs.	106	14	6	23	149	13.4 ± 2.8	20.1 ± 3.3
		Exp.	103.1	15.9	4.0	25.8	148.8		
Rl-B (*Sr16*)	2BL	Obs.	21	20	6	14	61	42.6 ± 6.3	29.5 ± 5.8
		Exp.	24.7	18.3	7.7	10.3	61.0		

[1]R = resistant; S = susceptible; n.c.o. = non-crossover type; c.o. = crossover type; p = recombination frequency; t = telosome-transmission frequency; and n = total no. plants. Theoretically, the n.c.o. types would be R with 21" and S with 20"+t1", and the c.o. types would be R with 20"+t1" and S with 21". Exceptions to the expected cytological types were classed as c.o. types if the configuration could be explained only through crossing over; otherwise, they were classed as n.c.o. types. Values for t were derived from the proportions of plants receiving a telosome from the male parent and cannot be obtained directly from figures in columns R-c.o. and S-n.c.o.

Mq-A (*Sr18*)

Two possible recombinants were observed among 167 testcross plants from the crosses involving ditelo-1DL. Both of these possible recombinants were of the susceptible type with 21". Since no resistant crossover plants with 20"+t1" were recorded, we could not conclusively exclude the possibility that the two susceptible plants with 21" were from an accidental selfing. Nineteen plants had unexpected cytological configurations (Table 2). All plants with unexpected cytological configurations were classified as non-crossover

Table 2. List of unexpected cytological types observed in telosomic mapping of genes for resistance to wheat stem rust, *Puccinia graminis* var. *tritici*.

Parent, gene, telosome	Cytological type (No. plants)[1]
Mq-A, Sr18, 1DL	(R-n.c.o.):21"+1' (4), 20"+1"' (3), 19"+2'+1'" (1), 19"+t1"+1' (1), 20"+1' (1). (S-n.c.o.): 20"+t1"+1' (6), 19"+t1"+1"' (3).
Mq-B, Sr19, 2BL	(R-n.c.o.): 20"+t2" (2), 20"+1"' (1), 20"+1' (1), 20"+t1" (small t) (1). (S-n.c.o.): 20"+1' (2), 19"+3' (1), 18"+1"'+t1"+1' (1).
Mq-B, Sr19, 2BS	(R-n.c.o.): 20"+1' (8), 21"+1' (3), 21"+t1" (1), 21"+t' (1), 21"+t1"+1' (1), 20"+t1"+1' (1), 20"+t1"+i' (1) 20"+t2"' (1), 20"+1'+i' (1), 20"+2' (1), 19"+2'+i' (1), 18"+1""+t1' (1). (R-c.o.): 19"+t1"+1' (1). (S-n.c.o.): 20"+1' (3), 19"+t1"+1' (2), 21"t' (1), 20"+t1"+2' (1), 19"+t1"+1"' (1), 18"+t1"+2' (1). (S-c.o.): 21"+1' (1), 20"+2" (1), 18"+1"'+3' (1).
ISr9d-Ra, Sr9d, 2BL	(R-n.c.o.): 20"+1' (6), 20"+1"' (2), 21"+1' (1) 20"+t2"' (1), 19"+3' (1). (S-c.o.): 19"+1"'+1' (1). (S-n.c.o.) 20"+1' (6), 18"+1"'+t'+t' (1).
ISr9d-Ra, Sr9d, 2BS	(R-n.c.o.): 20"'+1' (7), 20"+1'+i' (4), 20"+t2"' (2), 19"+1"" (1).
ISr9a-Ra, Sr9a, 2BL	(R-n.c.o.): 21"+t (2), 18"+t2"'+2"', 20"+t1"+t'+t' (1). (S-n.c.o.): 20"+1' (3).
R1-B, Sr16, 2BL	(R-n.c.o.):21"+1' (1), 20"+t1"+1' (1). (S-n.c.o.): 20"+1' (2), 19"+t1"+1' (2), 20"+1' (1).

[1]R-n.c.o. = resistant, non-crossover class
S-n.c.o. = susceptible, non-crossover class
R-c.o. = resistant, crossover class
S-c.o. = susceptible, crossover class

types. A ditelosomic for the short arm of 1D was not available for use. The available evidence indicates that the gene *Sr18* is located on the long arm of chromosome 1D.

Marquis-B (*Sr19*)

Two susceptible and three resistant crossover types were recorded among 180 testcross plants from Mq-B/ditelo-2BL. The observed percentage of recombination was 2.8 ± 1.2. Three of the five possible recombinants with the 2BL telosome were questionable because of imperfectly clear cytological configurations. The remaining two crossover-type plants had 20"+t1" and were resistant. Nine plants having unexpected cytological configurations (Table 2) were classified as non-crossover types.

Also, six susceptible and eight resistant crossover types were recorded among 181 testcross plants from Mq-B/ditelo-2BS. These data gave a recombination value of 7.7 ± 2.0. Only one of 14 possible recombinants with the 2BS telosome was questionable because of imperfectly clear cytological configurations. Thirty-five plants had unexpected cytological configurations (Table 2). These 35 plants had about the same percentage of crossover types as the entire sample.

The number of crossover types was larger and the cytological identification of the crossover types was more reliable in the testcross of Mq-B/ditelo-2BS than in the testcross of Mq-B/ditelo-2BL. These data indicated that *Sr19* is located on the short arm of chromosome 2B. *Sr19* is linked with about 24% recombination with the *Sr9* locus (KAVEH, 1968). If *Sr9* is 10.6 map units from the centromere on the long arm of 2B (SEARS and LOEGERING, 1968), *Sr19* should be either about 35 map units from the centromere on the long arm or about 13 map units from the centromere on the short arm. Our data indicated that *Sr19* is much closer than 35 map units from the centromere. If crossing over is restricted in heteromorphic pairs, the telosomic technique would underestimate map distances. Thus, the distance of 7.7 map units from the centromere on the short arm is a reasonable figure. If the telosomic technique greatly underestimates map distances, *Sr19* possibly could be near the centromere on the long arm of 2B.

If *Sr19* is on the short arm of 2B, the apparent recombinants in the cross with ditelo-2BL must have resulted from causes other than normal chromosome pairing and crossing over. They could have resulted from experimental mistakes and from abnormal pairing and disjunction of chromosomes caused by genetic differences between the parents. In certain cytological preparations from plants with 20"+t1", the telocentric was involved in a complex figure of four chromosomes, and this abnormality may have resulted in irregular disjunction of the crossover products.

ISr9d-Ra (*Sr9d*), ISr9a-Ra (*Sr9a*), and Rl-B (*Sr16*)

The data (Table 1) show clearly that *Sr9d* is on 2BL. Crossing over occurred in ISr9d-Ra/ditelo-2BL but not in ISr9d-Ra/ditelo-2BS. Testcrosses of ISr9d-Ra/ditelo-2BL indicated a crossover value of 10.5%. This value is close to the 10.6% obtained by SEARS and LOEGERING (1968) for *Sr9a*. A value of 13.4% was indicated in our tests for crossing over between *Sr9a* and the centromere. Limited numbers of testcross plants of Rl-B/ditelo-2BL indicated a crossover value of 42.6% (Table 1). This value does not differ significantly from results of SEARS and LOEGERING (1968), which indicated that *Sr16* was on the long arm of 2B, and 50 or more crossover units from the centromere. *Sr16* segregated independently of alleles at the *Sr9* locus (KAVEH,

1968), and we expected a gene-to-centromere map distance greater than 50 units for *Sr16*.

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