Allelism and Linkage of Three Genes in Chromosome 2B of Wheat for Reaction to Puccinia graminis tritici

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ABSTRACT

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The principles of interorganism genetics were used in selecting cultures of *Puccinia graminis* f. sp. *tritici* to study the allelism and linkage of the genes *Sr9d, Sr9e,* and *Srtt1* for low reaction in wheat. It was found that *Sr9d* and *Sr9e* are alleles or very closely linked. Linkage of *Srtt1* and *Sr9* was estimated to be 24 ± 7.8%.

Additional key words: stem rust of wheat.

The study of inheritance of reaction and pathogenicity is difficult when more than two corresponding gene pairs for low infection type (LIT) are involved in a single pathogen:plant host association. This is because of the category IV (5) "epistasis" of one corresponding gene pair for LIT over other corresponding gene pairs for higher infection types (HIT). Commonly this problem is overcome by inserting into the system cultures of the pathogen with genotypes for high pathogenicity (Hp) that "cover up" all but one of the genes for low reaction (Lr) in the host, or by inserting into the system host lines with genotypes for high reaction (Hr) which "cover up" all but one of the genes for low pathogencity (Lp) in the pathogen. Inheritance of reaction is studied by selecting cultures with proper genotypes for Lp and Hp corresponding to the genes for Lr being studied (2). Sometimes the ideal cultures or host lines are not available. Nevertheless the principles of "cover up" and Category IV "epistasis" permit development of experimental designs which give definitive results for studies on the inheritance of either reaction or pathogenicity in the associated organisms, even in the absence of ideal materials. By the use of these principles, the linkage and allelism relationships among the *Sr9d, Sr9e,* and *Srttl* genes of wheat (*Triticum aestivum* L. em Thell.) for reaction to *Puccinia graminis* Pers. f. sp. *tritici* Erickss. and E. Henn. were studied.

MATERIALS AND METHODS

Wheat lines monogenic for *Sr9d* (C.I. 14179), *Sr9e* (W3196), and *Srtt1* (W1656) and the digenic line *Sr9e Srtt1* (W3496) were used in the study (4, 7, 8). Allelism has been shown for *Sr9d* and *Sr9a* (7), and *Sr9e* and *Sr9b* (8) but the allelism of *Sr9d* and *Sr9e* has not been tested directly. Gene *Srtt1* is linked with *Sr9e* in W3496 with 19.6 ± 1.6% crossover (8). All three genes are in chromosome 2B, and the *Sr9* locus is on the long arm.

The eight possible kinds of cultures with respect to pathogenicity on the three monogenic lines are shown in Table 1. Cultures high (H) or low (L) (3) with all three lines would be of no use in the study. The ideal cultures to use would be the three that are H with two of the lines and L with the other (2); however, only one of these was available. Of the other three kinds of cultures, the one H with *Sr9e* and L with the other two was unavailable. A single culture was selected to represent each of the three groups (Table 1).

The cross C.I. 14179 (*Sr9d srtt1*) × W3496 (*Sr9e Srtt1*) was made. The F_2, F_3 families, and some F_4 families were inoculated with one or more of the three cultures and scored for infection types (IT) by standard procedures (9). The HIT phenotype was IT 3+ to 4. The three LIT phenotypes were; 00; for *Lpsrtt1/ Lrsrtt1,* 2 for *Lpsr9d/ Lrsr9d,* and 2− for *Lpsr9e/ Lrsr9e.* The latter two were very similar and often could not be differentiated with confidence. No category IV complementary interactions were noted.

The limitations imposed because of the missing cultures and the similarity of the *Sr9d* and *Sr9e* phenotypes in this three-gene system dictated the procedures used in the study.

RESULTS

The F_2 of the cross *Sr9d srtt1* × *Sr9e Srtt1* was inoculated with culture 38-51A, which gives HIT with *Sr9d* and *Srtt1* but LIT with Sr9e. The result was 185 L plants (2−) and 62 H plants (3+) ($P = 0.99$ for a 3:1 ratio). Assuming allelism of *Sr9d* and *Sr9e,* the 185 L plants should be homozygous *Sr9e* or heterozygous *Sr9e Sr9d* and will be referred to as the 38L group (low to culture 38-51A). The 62 H plants should be homozygous *Sr9d* and will be referred to as the 38H group. Two of the 38H plants died before producing seed; thus there were 60 F_3 families in the 38H group.

Linkage of genes Sr9 and Srtt1.—If crossing-over

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TABLE 1. Eight possible kinds of cultures of *Puccinia graminis* f. sp. *tritici* based on pathogenicity on three wheat lines monogenic for genes *Sr9d, Sr9e,* and *Srtt1*

Culture group	Infection type C.I. 14179 (*Sr9d*)	W3196 (*Sr9e*)	W1656 (*Srtt1*)	Representative culture
A	H[a]	H	H	[b]
B	H	H	L	...[c]
C	H	L	H	38-51A[d]
D	L	H	H	...
E	H	L	L	17-51A
F	L	L	H	139-52A
G	L	H	L	...
H	L	L	L	[b]

[a]Abbreviations: H = high infection type and L = low infection type.
[b]Available but not used.
[c]No cultures of this kind were available.
[d]Laboratory culture numbers. 38 = race number (9) and 51 = year of collection (1951).

occurred between *Sr9* and *Srtt1,* these would be evident in F_3 families of the 38H group when inoculated with culture 17-51A, which gives HIT with *Sr9d* and LIT with *Sr9e* and *Srtt1*. Twelve to 16 plants of each family were inoculated. Since none of the 38H plants should have *Sr9e,* only *Srtt1* would be detected and these would represent cross-over in F_2. The 60 38H-F_3 families segregated 4 homozygous L:21 heterozygous:35 homozygous H. Crossing over is estimated to be 24 ± 7.8% by Allard's formula 16 (1), which is reasonably close to the 19.6 ± 1.6% found by McIntosh and Luig (8). To determine crossing-over in the 38L group it would be necessary to inoculate the homozygous *Sr9e* F_3 families with a culture L on *Srtt1* and H with *Sr9e*. Such a culture was not available.

Allelism of genes Sr9d and Sr9e.—The best test for allelism of *Sr9d* and *Sr9e* would be to inoculate the 38L-F_3 families with two cultures that were H with *Srtt1,* one that was H with *Sr9d* and L with *Sr9e* and the other L with *Sr9d* and H with *Sr9e*. The latter culture was not available; therefore, a single culture was used that was H with *Srtt1* and L with both *Sr9d* and *Sr9e* (culture 139-52A), which permits expression of both *Sr9* alleles. If in reality these two genes are allelic, then all the 38L-F_3 families should show LIT 2– to 2. The occurrence of any plants with HIT would suggest crossing-over. None of 4,644 plants from the 38L-F_3 families had plants with HIT. Since one third of the F_3 families should be homozygous *Sr9e*, the test involved approximately 3,100 plants in about 123 segregating families. This indicates that *Sr9d* and *Sr9e* are allelic or very closely linked.

DISCUSSION

The two dominant genes *Sr9d* and *Sr9e* are for low reaction to *P. graminis* f. sp. *tritici.* No recessive allele (*sr9*) is known, although the absence of the locus behaves as a recessive in wheat plants aneuploid for chromosome 2BL. When the F_2 of the cross C.I. 14179 × W3496 is inoculated with culture 38-51A, the phenotype but not the genotype of *Sr9d* is "covered up" in the segregating population, and this dominant gene appears to be a recessive allele for H. Loegering and Sears (6) pointed out in a study of *Sr9a* and *Sr9b* that an apparent recessive allele for susceptibility may be the result of a gene for Hp in the pathogen corresponding to a dominant allele for Lr in the host.

The determination of allelism of *Sr9d* and *Sr9e* seemed difficult because of the similarity of LITs produced by their corresponding gene pairs. This was overcome, in the absence of ideal cultures, by inoculating with culture 139-52A and looking for plants with HIT in a defined portion of the segregating population. Both the alleles are dominant in this system. No plants with HIT were found; thus, we can consider the two genes to be allelic or very closely linked.

The study reported here is an example of the use of interorganismal genetic concepts in the design of experiments. The understanding of disease caused by biotic agents is dependent on the further use of these concepts.

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