Genetic Control of Disease Expression in Stem Rust of Wheat

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ABSTRACT

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In stem rust of wheat, susceptibility as measured by infection type may be genetically determined by the genotype of either the host or the pathogen. The absence of a locus, due to aneuploidy, is the equivalent of an allele for susceptibility. Thus, it may be assumed that in the euploid the allele for susceptibility may be either a nonfunctional DNA sequence or, if functional, the gene product does not interact with the gene product of the corresponding definitive gene in the host. It was also confirmed that in some cases high temperature may change a definitive phenotype to nondefinitive.

Additional key words: susceptibility, telocentric chromosomes.

When a given plant genotype is damaged by a pathogen we call the plant susceptible. Often this is interpreted to mean that susceptibility is determined by the host genotype. It may or may not be. Interorganismal genetics tells us that in the gene-for-gene relationship the definitive (D) phenotype (low infection type in stem rust of wheat) of the association (aegricorpus) of pathogen and host is the product of definitive corresponding genotypes of both symbionts. If either symbiont carries the corresponding nondefinitive genotype, the nondefinitive (N) phenotype (high infection type in stem rust of wheat) occurs (4). Previous cytogenetic studies of wheat involving genes for reaction to several pathogens made the assumption that absence (due to aneuploidy) of a locus was the same as an N allele in the euploid. This assumption was based on older genetic concepts and if true (as it appears to be) helps us understand the contribution of the host to the genetic control of plant disease development. Genetic studies (2) of two radiation-induced mutant cultures of *Melampsora lini* (Ehrenb.) Lev. indicated that the mutations were due to a deletion in one of the nuclei of the dicaryon. This suggests that in the pathogen the absence of the locus of a given gene also is the equivalent of an N allele.

The recent availability of telocentric aneuploids of wheat (7) permitted us to test the hypothesis that absence of a locus in the host is equivalent to an N allele, and to demonstrate that in the presence of the D allele in the host, other factors may determine susceptibility. Pathological, cytogenetic and genetic methods involving these telocentric aneuploids of wheat and *Puccinia graminis* Pers. *tritici* Ericksss. and Henn. were used to make the tests.

MATERIALS AND METHODS

Three cultures of *P. graminis tritici* and eight lines of *Triticum aestivum* L. em Thell were used in the study. The three cultures, 11-52D, 32B-67A, and 36-51A, will be referred to as 11, 32B, and 36, respectively. The eight wheat lines consisted of four euploid lines monogenic and homozygous for the dominant and definitive *Sr6, -8, -9a,* and *-11* alleles for low reaction (5) and four ditelosomic lines lacking and chromosome arms carrying the respective genes (6). All eight lines are in the Chinese Spring background. The phenotypic expression of the combinations of the cultures and the wheat lines are given in Table 1. In the study reported here the infection type (IT) produced on wheat seedlings was used as the measure of reaction. IT 3+ or higher was considered to indicate susceptibility.

Each of the four euploid (21″) lines was crossed with the corresponding ditelosomic (20″+t″) line. Four monotelodisomic (20″+t1″) F_1 plants of each cross were grown in a general-use greenhouse. Two groups of 36 F_2 seeds of the crosses involving *Sr8, -9a,* and *-11* and 50 involving *Sr6* were planted. Not all seeds grew; thus, the number of plants varied in each F_2 population. Each group was inoculated in the seedling stage with one of two cultures of *P. graminis tritici,* one of which (culture 11) had the D genotype and the other (culture 32B or 36) the N genotype corresponding to the respective D genotypes of the monogenic lines (Table 1). Half of the inoculated plants of each group involving the *Sr6* gene were grown at 20 C or below and the other half at 25 C or above to observe the effect on the temperature sensitivity of Psr6/ Rsr6 (3). The IT was recorded for each plant and the infected leaf was photographed.

Based on the phenotype of the aegricorpi developing on the population inoculated with culture 11 (and at 20 C for *Sr6*), predictions were made as to whether or not the plant was ditelosomic (20″+t″—completely lacking the definitive arm), monotelodisomic (20″+tl″—with one dose of the arm), or euploid (21″—with two doses of the arm) (Fig. 1). If IT 3+ or higher developed on a plant, that plant was predicted to be ditelosomic. If the IT was lower, it was predicted that the plant was

TABLE 1. Infection types[a] resulting from inoculation of eight lines of wheat inoculated with three cultures of *Puccinia graminis tritici*

	Cultures			
			11-52D	
Wheat lines	32B-67A	36-51A	20 C	25 C
Monogenic lines				
ISr6-Ra, CI 14163	3+	···	0;1	3+
ISr8-Ra, CI 14167	3+	···	3-c	···
ISr9a-Ra, CI 14169	···	3+	3-c	···
ISrll-Ra, CI 14171	3+	···	2≡	···
Aneuploid lines				
Ditelo 2DL	3+	3+	3+	3+
Ditelo 6AL	3+	3+	3+	···
Ditelo 2BS	3+	3+	3+	···
Ditelo 6BS	3+	3+	3+	···

[a] Infection types as described by Stakman et al (8).

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monotelodisomic or euploid. In the populations involving *Sr6* and *Sr11* variation in the lower ITs permitted prediction of which plants were monotelodisomic and which were euploid. The populations inoculated with cultures 32B and 36 could not be classified as to gene dosage on the basis of IT, as IT 3+ developed on all plants.

Each F_2 plant was transplanted to a 15-cm-diameter pot and grown in a general-use greenhouse; many were examined cytologically at meiosis. Nearly all plants that had been inoculated with culture 11 and had been classified as to gene dosage on the basis of IT were examined. Only random examination was made among other populations.

Seed from all the F_2 plants of all four crosses was harvested

TABLE 2. Reaction to cultures 11-52D and 32B-67A of *Puccinia graminis tritici* at 20 and 25 C, predicted and observed aneuploidy of F_2 plants, and segregation for reaction to culture 11-52D in F_3 families of the cross ISr6-Ra × Ditelo-2DL

		F_2				F_3
				Constitution		
Culture	Temp.[a]	Infection type	No. plants	Predicted from IT[b]	Observed cytologically	Segregation to culture 11-52D
11-52D	20 C	0;1	7	E[c]	21″	All D[d]
		3+CN	4	M	20″+tl″	All D
		3+CN	9	M	20″+tl″	Seg D:N
		0;1	1	E	···	All D
		3+CN	1	M	19″+tl″+l′	All D
		3+CN	1	M	20″+1′	Seg D:N
	25 C	3+	2	···	21″	All D
		3+	1	···	20″+tl″	Seg D:N
		3+	13	···	···	All D
		3+	5	···	···	Seg D:N
		3+	1	···	···	All N
32B-67A	20 C	3+	1	···	20″+tl″	All D
		3+	16	···	···	All D
		3+	5	···	···	Seg D:N
		3+	2	···	···	All N
	25 C	3+	1	···	21″	All D
		3+	11	···	···	All D
		3+	13	···	···	Seg D:N

[a] Each major block is divided by a slight separation. Above the gap observations on IT, cytology, and F_3 segregation were complete and cytology indicated a normal ditelosomic, monotelodisomic, or euploid condition. Below the gap the data did not meet the above criteria.
[b] IT = infection type.
[c] E = euploid, M = monotelodisomic.
[d] D = definitive phenotype, and N = nondefinitive phenotype.

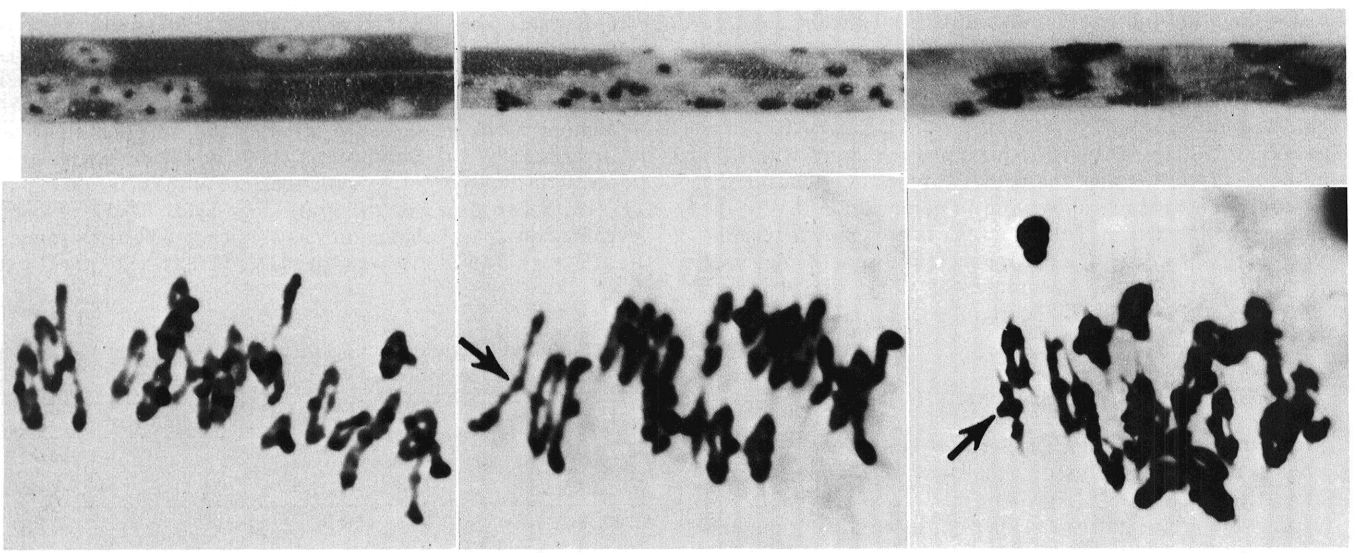

Fig. 1. Pathological and cytogenetic characteristics of aneuploids of wheat involving the short arm of chromosome 6B and the *Sr11* locus. Left—euploid, center—monotelodisomic, and right—ditelosomic. Top: infection types on leaves inoculated with *Puccinia graminis tritici,* culture 11-52D, which has the D genotype corresponding to *Sr11*. Bottom: meiotic chromosome complements at first metaphase of the plants shown at the top. The bivalent indicated by the arrow in the ditelosomic (right) consists of two short-arm telocentrics of chromosome 6B, both thus deficient for the *Sr11* locus. The terminal centromeres of the telocentric are being pulled toward the poles of the cell, but the interstitial chiasma near the centromere retards the bivalent from elongating. The bivalent indicated by the arrow in the monotelodisomic (center) is heteromorphic. It consists of a complete 6B chromosome (lower part of bivalent) and a chromosome telocentric for the short arm of chromosome 6B (upper part of bivalent) which is deficient for the *Sr11* locus. The chiasma in this bivalent is almost terminal, allowing the two centromeres to pull farther apart than in the ditelocentric bivalent. In the eupoloid (left) the 6B bivalent is not identifiable, but all 21 bivalents, including 6B, consist of complete chromosomes.

and about 40 (20–60) offspring of each plant were inoculated with culture 11 to determine segregation. Due to restricted transmission of some telocentric chromosomes, many of the relatively small F_3 families from suspected monotelodisomic plants did not show segregation.

RESULTS

All data are given in Tables 2–5. Each table has two sections (four for *Sr6*), one of which gives the data on the plants inoculated with culture 11 and the other the data on plants inoculated with culture 32B or 36. Each section is divided into two parts. The upper part contains data on plants for which observations on IT, cytology, and segregation in F_3 were complete, and cytology indicated a normal ditelosomic, monotelodisomic, or euploid condition. In the lower part data are given on plants that did not meet the above criteria.

Sr6. Of the 100 F_2 seed from the cross ISr6-Ra × Ditelo 2DL, 94 produced plants (Table 2). Of these, 45 were inoculated with culture 11, and 23 were grown at 20 C and 22 at 25 C. Of the 23 grown at 20 C, eight were classified as euploid (IT 0;1), seven of which had 21″ and one was not studied cytologically. All eight proved to be homozygous D in F_3. Fifteen plants were classified as monotelodisomic (IT 3+ CN) of which 12 were 20″+tl″, one was 20″+1′, and one was 19″+tl″+1′. In F_3, 10 of the 15 segregated D:N. Since a limited number of plants from each F_2 plant were tested in F_3, we may assume that the four plants with 20″+tl″ and the one with 19″+tl″+1′ which did not segregate would have done so had large enough populations been tested. The critical observation was that none of the eight plants classified as euploid segregated in F_3.

The 22 F_2 plants inoculated with culture 11 and exposed to 25 C, as well as the two populations of 24 and 25 plants inoculated with culture 32B and exposed to 20 and 25 C, resepectively, all showed the N phenotype (3+). The segregation in F_3 of the plants in these three groups to culture 11 was similar to that seen in the group inoculated in F_2 with culture 11 and exposed to 20 C.

If transmission of 2DL were equal to that of complete 2D, 25% (23) would have been expected to be ditelosomic. However, only three plants of the 94 studied were classified as ditelosomic; thus, male transmission of telo-2DL versus complete 2D was evidently quite poor.

Sr11. Of 72 seeds from the cross ISr11-Ra × Ditelo 6BS, 59 produced plants (Table 3). On the basis of IT, the 28 plants inoculated with culture 11 were classified as 14 euploid (IT-2≡2−), 10 monotelodisomic (IT 2−), and four ditelosomic (IT 3+) (Fig. 1). Cytology of the plants classified as euploid showed that 13 were 21″ and one was 20″+t2″ ′. Inoculation of the F_3 of these plants indicated that all were homozygous for the *Sr11* allele for low reaction. Of the 10 plants classified as monotelodisomic, one proved to be 20″+1′ and one was not studied cytologically. The remaining eight plants were monotelodisomic; six segregated in F_3 and two did not. The latter result presumably is due to the relatively small populations tested. The four plants predicted to be ditelosomic on the basis of IT were shown to be 20″+t″ cytologically. This was confirmed in F_3 where IT 3+ developed on

TABLE 3. Reaction to cultures 11-52D and 32-67A of *Puccinia graminis tritici*, predicted and observed aneuploidy of F_2 plants, and segregation for reaction to culture 11-52D in F_3 of the cross ISr11-Ra × Ditelo-6BS

	F_2				F_3
			Constitution		
Culture[a]	Infection type	No. of plants	Predicted from IT[b]	Observed cytologically	Segregation to culture 11-52D
11-52D	2=2−	13	E[c]	21″	All D[d]
	2−	2	M	20″+tl″	All D
	2−	6	M	20″+tl″	Seg D:N
	3+	4	Di	20″+t″	All N
	2=2−	1	E	20″+t2″′	All D
	2−	1	M	20″+1′	All D
	2−	1	M	···	All D
32B-67A	3+	1	···	20″+tl″	Seg D:N
	3+	1	···	20″+t″	All N
	3+	15	···	···	All D
	3+	12	···	···	Seg D:N
	3+	2	···	···	All N

[a]Each major block is divided by a slight separation. Above the gap observations on IT, cytology, and F_3 segregation were complete and cytology indicated a normal ditelosomic, monotelodisomic, or euploid condition. Below the gap the data did not meet the above criteria.
[b]IT = infection type.
[c]E = euploid, M = monotelodisomic, and Di = ditelosomic.
[d]D = definitive phenotype, and N = nondefinitive phenotype.

TABLE 4. Reaction to cultures 11-52D and 32B-67A of *Puccinia graminis tritici*, predicted and observed aneuploidy of F_2 plants, and segregation for reaction to culture 11-52D in F_3 in the cross ISr8-Ra × Ditelo-6AL

	F_2				F_3
			Constitution		
Culture[a]	Infection type	No. of plants	Predicted from IT[b]	Observed cytologically	Segregation to culture 11-52D
11-52D	3-c	10	E/M[c]	21″	All D[d]
	3-c	12	E/M	20″+tl″	All D
	3-c	6	E/M	20″+tl″	Seg D:N
	3-c	1	E/M	20″+1′	Seg D:N
	3-c	1	E/M	···	Seg D:N
	3+	1	Di	19″+tl″+t″	All N
32B-67A	3+	1	···	21″	All D
	3+	3	···	20″+tl″	All D
	3+	1	···	20″+tl″	Seg D:N
	3+	20	···	···	All D
	3+	2	···	···	Seg D:N

[a]Each major block is divided by a slight separation. Above the gap observations on IT, cytology, and F_3 segregation were complete and cytology indicated a normal ditelosomic, monotelodisomic, or euploid condition. Below the gap the data did not meet the above criteria.
[b]IT = infection type.
[c]E/M = euploid or monotelodisomic, and Di = ditelosomic.
[d]D = definitive phenotype, and N = nondefinitive phenotype.

TABLE 5. Reaction to culture 11-52D and 36-51A of *Puccinia graminis tritici*, predicted and observed aneuploidy of F_2 plants, and segregation for reaction to culture 11-52D in F_3 of the cross ISr9a-Ra × Ditelo-2BS

	F_2				F_3
			Constitution		
Culture[a]	Infection type	No. of plants	Predicted from IT[b]	Observed cytologically	Segregation to culture 11-52D
11-52D	3-c	4	E/M[c]	21″	All D[d]
	3-c	2	E/M	20″+tl″	All D
	3-c	2	E/M	20″+tl″	Seg D:N
	3-c	2	E/M	20″+1′	All D
	3-c	1	E/M	19″+1″′+tl″	Seg D:N
	3-c	15	E/M	···	All D
	3-c	6	E/M	···	Seg D:N
36-51A	3+	1	···	21″	All D
	3+	1	···	20″+tl″	All D
	3+	2	···	20″+tl″	Seg D:N
	3+	21	···	···	All D
	3+	8	···	···	Seg D:N

[a]Each major block is divided by a slight separation. Above the gap observations on IT, cytology, and F_3 segregation were complete and cytology indicated a normal ditelosomic, monotelodisomic, or euploid condition. Below the gap the data did not meet the above criteria.
[b]IT = infection type.
[c]E/M = eupoloid or monotelodisomic.
[d]D = definitive phenotype, and N = nondefinitive phenotype.

all plants tested. IT 3+ developed on all 31 F_2 plants inoculated with culture 32B and segregation in F_3 to culture 11 indicated that this population was similar in genetic constitution to the F_2 population inoculated with culture 11. The indicated seven ditelosomic plants constituted 11.9% of the population of 59, which indicates that male transmission of telo-6BS in 20″+tl″ plants was about 30% of the transmission of normal 6B.

Sr8. Of the 72 seeds from the cross ISr8-Ra × Ditelo-6AL, 58 produced plants (Table 4). Only one of 31 plants inoculated with culture 11 showed IT 3+. Cytologically, it was ditelosomic for one pair of chromosomes and monotelodisomic for another. The F_3 family of this plant was homozygous for the N phenotype; thus the ditelosomic pair was likely of 6AL. Among the 58 F_3 families from F_2 plants inoculated with either culture 11 or 32B, only one was homozygous for the N phenotype and only 11 showed segregation (29 expected), and one of the latter was from a monosomic plant. Thus either transmission of telo-6AL was restricted or aneuploid seeds had poor viability. Sears and Sears (7) suggested little restriction on transmission of telo-6AL versus complete 6A from indirect evidence.

Sr9A. Of the 72 seeds of the cross ISr9a-Ra × Ditelo-2BS, 65 produced plants (Table 5). No ditelosomic plants were identified by IT, cytology, or segregation in F_3. Only 19 (33 expected) of the 65 plants showed segregation in F_3. Male transmission of telo-2BS from 20″+tl″ was evidiently low.

DISCUSSION

All plants on which IT 3+ developed would be called susceptible; however, it should be noted that IT 3+ was the result of three different phenomena. When ditelosomic plants are inoculated with culture 11, which carries the D genotype, the N phenotype (IT 3+) develops as a result of the absence of the corresponding locus in the host. Thus the absence of the locus behaves like an "allele" for susceptibility. This suggests that alleles for "susceptibility" may, in some cases, be the result of a nonfunctional DNA sequence in euploids or, if functional, the gene product does not interact with the gene product of the corresponding D gene in the host. A second situation which results in "susceptibility" is when the culture has the N genotype even though the host has the D genotype. Here "susceptibility" is not due to the genotype of the host, but to the genotype of the pathogen. Finally, the temperature sensitivity of the D phenotype of Psr6/ Rsr6 is a third phenomenon resulting in "susceptibility." These three reasons for "susceptibility" as measured by IT (genotype of the host, genotype of the pathogen, and temperature acting on the D phenotype) are difficult to consider as a single biological phenomenon other than causing a reduction in the yield of the host. In an economic sense they are all the same, but they differ biologically, and probably the biochemical events which result in IT 3+ in these three cases are likewise different. All three block expression of the D phenotype, thus permitting the expression of the basic compatibility (1) of *P. graminis tritici* and wheat.

In the case of Victoria blight of oats, susceptibility is conditioned only when the host and pathogen have the corresponding D genotypes (4), thus representing a fourth determinant of "susceptibility."

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