

Genetics

**Transfer from *Tripsacum dactyloides* to Corn
of a Major Gene Locus Conditioning Resistance to *Puccinia sorghi***

R. R. Bergquist

Plant pathologist, Pfister Hybrid Corn Company, El Paso, IL 61738.

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ABSTRACT

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A dominant gene for resistance to common rust of corn (which is caused by *Puccinia sorghi*) was found among progeny of *Zea mays* × *Tripsacum dactyloides*-BC⁸-[S]. After four additional backcrosses to susceptible Corn Belt inbred lines, selected populations were selfed and testcrossed to a rust-susceptible recurrent parent to establish F₂ and testcross populations for genetic study. In greenhouse and field tests, F₂ generations segregated 3 resistant:one susceptible. Backcross generations to a susceptible parent segregated 1:1. The new gene, designated *Rp*₁^{Td}, occurs within 0.3 map units

of *Rp*₁^d on chromosome 10. In a testcross of F₁ progeny to a susceptible tester, five of 3,763 testcross progeny were susceptible (ie, lacked both *Rp*₁^d and *Rp*₁^{Td}). Plants with genes *Rp*₁^d and *Rp*₁^{Td} in repulsion were exposed in Hawaii to natural inoculum of *P. sorghi* that is virulent to plants with *Rp*₁^b, *Rp*₁^d, or *Rp*₁^k. The resistance provided by the *Rp*₁^d/*Rp*₁^{Td} combination was effective, although some small uredia appeared on the lower leaves of mature plants.

Additional key words: maize, race-specific resistance.

Common rust, caused by *Puccinia sorghi* Schw., is one of the major diseases of corn (*Zea mays* L.) in the cooler regions of the tropics (8) and is a major factor affecting quality and yield of sweet corn in north central USA (5). Grain yield losses as high as 25% are not uncommon in these areas (1). Utilization of a monogenic fleck-type resistance is an effective and economical means of

control (3). Malm and Beckett (11) observed a chlorotic fleck reaction on *Tripsacum dactyloides* (L.) L. (eastern gama grass) and suggested that it might be a source of rust resistance for corn. Bergquist (2) subsequently observed a qualitatively inherited dominant resistance to *P. sorghi* in *T. dactyloides*. Numerous sources of rust resistance to *P. sorghi* in corn are known (6,7). This resistance is race-specific and has been shown to be due to single dominant genes on chromosomes 3, 4, and 10 (7).

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In seeking new sources of corn rust resistance an exotic grass, *T. dactyloides*, was investigated. The current study was initiated to evaluate the potential of *T. dactyloides* as a source of resistance to common rust of corn and to assess the feasibility of transferring rust resistance from *T. dactyloides* to *Z. mays*.

Results of genetic and disease incidence studies of maize lines derived from *T. dactyloides* under artificial *P. sorghi* epiphytotics in greenhouse seedling and field tests in central Illinois and under severe natural infection in Hawaii are presented in this article.

MATERIALS AND METHODS

The *Z. mays* × *T. dactyloides*-BC⁸-[S] derivative was obtained from J. M. J. de Wet and J. Harlan (University of Illinois, Urbana) and was sown in 1975 in the Pfister Hybrid Corn Company disease nursery at El Paso, IL. In its original form, this source was variable for rust reaction and exhibited tripsacoid morphology, both characters poorly suited for commercial use in the seed corn production. The original tripsacoid derivative was crossed four additional generations with susceptible Corn Belt inbreds, A632, B37, Oh43, and W64A, to produce populations from which adapted lines, homozygous for rust resistance, were obtained by backcrossing and selfing with selection for resistance.

All disease ratings were made on 2- to 3-wk-old seedlings in the field and greenhouse. Techniques of inoculation, incubation, and disease rating were those conventionally employed for rusts of corn and other crops (4,9). A single culture (culture 75-01) of *P. sorghi* (collected in the field at El Paso, IL, in 1975) was utilized in the tests in Illinois. It has been clonally propagated in the growth chamber for many vegetative generations at weekly intervals. Naturally occurring biotypes that were virulent to plants with genes *Rp1^b*, *Rp1^d*, and *Rp1^k* were used in field studies in Hawaii (J. L. Brewbaker, personal communication).

All seed stocks were produced in the field by making appropriate controlled cross- and self-pollinations.

Chi-square tests were used to compare observed and expected ratios for goodness of fit.

RESULTS

Tripsacum derivatives and F₁ progenies. The *Tripsacum* derivatives, *Z. mays* × *T. dactyloides*-BC⁸-[S], expressed a chlorotic fleck under field conditions when inoculated with culture 75-01 of *P. sorghi*. The susceptible inbreds developed well-developed pustules. Progeny from crosses of the resistant *Tripsacum* derivatives with susceptible corn inbreds also were resistant to culture 75-01, which revealed that the resistance is dominant. Resistant plants were tripsacoid in appearance. Repeated backcrossings to Corn Belt inbreds A632, B37, Oh43, and W64A were made in attempts to transfer resistance into agronomically useful inbred families.

F₂ and backcross progenies. After four additional backcrosses, selected populations were selfed and testcrossed to a rust susceptible recurrent parent to establish F₂ and testcross populations for the current genetic study. Seedlings of F₂ populations derived from crosses between the susceptible cultivars and *Tripsacum* derivatives were tested in the greenhouse for reaction to culture 75-01 and in the field to natural infection by *P. sorghi*. Chi-square tests for 3:1 segregation of resistant and susceptible plants provided evidence for the hypothesis that *T. dactyloides* carries a single dominant gene for resistance (Table 1). Backcross generations to the susceptible parent segregated 1:1. All observed ratios closely approximated expected ratios.

Recombination tests with *Rp1^d*. The homozygous tripsacoid derivative was crossed with monogenic rust-resistant inbred B14A *Rp1^d/Rp1^d*. The single cross was advanced to the F₂ generation in addition to being testcrossed to a susceptible recurrent parent Oh43. Both the F₂ and testcross progeny were tested against culture 75-01, which is avirulent to both the tripsacoid parent and B14A *Rp1^d/Rp1^d*. All 277 F₂ progeny were resistant. This suggests that the genes in the two parents could be identical, allelic, or very closely linked. The testcross of F₁ progeny to rust-susceptible inbred Oh43 provided a more critical test to determine close linkage. In this test,

five of 3,763 testcross progeny were susceptible to culture 75-01. These data indicate that the gene in the tripsacoid derivative is either a part of the *Rp1* complex locus or very closely linked (within 0.3 map units) to it. *Rp1* is a complex region with several genes located within a segment of about 0.4 map units. It is located near the end of the short arm of chromosome 10 and is flanked by rust resistance loci *Rp5* and *Rp6*, which are 1.1 and 2.1 map units, respectively, from it (12).

Resistance of *Tripsacum* derivatives to naturally occurring biotypes of *Puccinia sorghi* in Hawaii. Different races of *P. sorghi* that occur naturally in Hawaii are virulent to plants with the alleles *Rp1^b*, *Rp1^d*, and *Rp1^k*. In Hawaii, plants with *Rp1^d* and *Rp1^{Td}* in combination or with *Rp1^s* were resistant to all naturally occurring Hawaiian biotypes from seedling to anthesis (J. L. Brewbaker, personal communication). As the plants containing dominant genes *Rp1^d* and *Rp1^{Td}* together or *Rp1^s* alone approached maturity following anthesis, minor uredial infections were observed on the lower leaves, whereas B14A (with genes *Rp1^d/Rp1^d-rp1^{td}/rp1^{td}*) was susceptible at all stages of plant growth. Data for host reactions to common rust from this test suggest that *Rp1^{Td}* is distinct from the *Rp1^b*, *Rp1^d*, and *Rp1^k* alleles in current use in Hawaii and very much like *Rp1^s*.

DISCUSSION

The search for source of rust resistance in *T. dactyloides* resulted in discovery of the gene *Rp1^{Td}*, which is located at or near the complex *Rp1* locus and which conditions resistance to rust races virulent to plants with *Rp1^b*, *Rp1^d*, and *Rp1^k*. In Hawaii, as in Illinois, the gene *Rp1^{Td}* from the tripsacoid derivative and *Rp1^s* conditioned a necrotic fleck type of resistance, but in Hawaii some small uredia were observed after anthesis on the lower leaves of plants with *Rp1^d/Rp1^{Td}* and *Rp1^s*.

The depletion of reserve germ plasm for resistance to new races of *P. sorghi* during the past 5 yr in Hawaii demands a new approach to breeding rust resistant corn hybrids for tropical and temperate areas where rust is a major concern. In each instance that a hybrid has succumbed, its resistance has been conditioned by a single gene. The new races virulent to the hybrid have differed from the

TABLE 1. Number of corn (*Zea mays*) × *Tripsacum dactyloides* hybrid seedlings resistant (R) and susceptible (S) to *Puccinia sorghi*^a among F₂ progeny from resistant × susceptible crosses and among progeny from testcrosses of the F₁ to a susceptible tester

Cross ^{b,c}	Expected		P value (3:1 or 1:1)
	R	S	
F ₂ [(II Tripsacoid-1)BC ⁵ Oh ⁴³]-1-5⊗	50	12	3:1
Oh43[(II Tripsacoid-1)BC ⁵ Oh ⁴³]-1-5	91	97	1:1
F ₂ [(II Tripsacoid-1)BC ⁵ Oh ⁴³]-1-8⊗	49	18	3:1
Oh43[(II Tripsacoid-1)BC ⁵ Oh ⁴³]-1-8	60	69	1:1
F ₂ [(II Tripsacoid-1)BC ⁴ Oh ⁴³]-14-2⊗	45	19	3:1
Oh43[(II Tripsacoid-1)BC ⁴ Oh ⁴³]-14-2	109	106	1:1
F ₂ [(II Tripsacoid-1)BC ⁴ Oh ⁴³]-14-3⊗	58	28	3:1
Oh43[(II Tripsacoid-1)BC ⁴ Oh ⁴³]-14-3	89	99	1:1
F ₂ [(II Tripsacoid-1)BC ⁴ Oh ⁴³]-14-7⊗	84	30	3:1
Oh43[(II Tripsacoid-1)BC ⁴ Oh ⁴³]-14-7	86	86	1:1
F ₂ [(IV Tripsacoid-10)BC ⁵ W64A]-4-4⊗	139	44	3:1
W64A[(IV Tripsacoid-10)BC ⁵ W64A]-4-4	180	187	1:1
F ₂ [(IV Tripsacoid-10)BC ⁵ W64A]-4-5⊗	187	64	3:1
W64A[(IV Tripsacoid-10)BC ⁵ W64A]-4-5	54	60	1:1
F ₂ [(IV Tripsacoid-10)BC ⁵ W64A]-4-7⊗	262	88	3:1
W64A[(IV Tripsacoid-10)BC ⁵ W64A]-4-7	144	137	1:1
F ₂ [(IV Tripsacoid-10)BC ⁵ W64A]-4-8⊗	179	57	3:1
W64A[(IV Tripsacoid-10)BC ⁵ W64A]-4-8	108	118	1:1

^aCulture 75-01.

^bTripsacoid = *Z. mays* × *T. dactyloides*-[S]. BC⁸ designates eight backcrosses followed by sib-mating.

^cThe notation, 5⊗, designates that plant number five and variously numbered plants on succeeding lines were selfed and concurrently backcrossed to the susceptible recurrent parent to make up the testcross.

previously predominant races only by virulence to overcome the new hybrid's resistance gene. This would be expected of a single-gene mutation or genetic recombination for increased virulence when selection pressure is placed on the pathogen population through the deployment of a single gene for resistance. During the period of 1978 to 1979, common rust was perpetuated on Oahu primarily on hybrids with Rp_1^d . Consequently, the natural rust population was virulent to plants with Rp_1^d . In 1980, monogenic resistant corn hybrids with Rp_1^b , Rp_1^d , and Rp_1^k succumbed to virulent races (J. L. Brewbaker, *personal communication*). The corresponding virulence genes have become established in the rust pathogen population, so it is unlikely that combinations of Rp_1^b , Rp_1^d , and Rp_1^k will be effective in cultivars multigenic for resistance.

As an alternative to single gene deployment, a pyramid of two or more genes, such as Rp_1^d/Rp_1^{Td} at the Rp_1 locus would result in a buffering effect by Rp_1^{Td} on Rp_1^d . Thus, the two genes in a single genetic background may contribute to or confer a kind of polygenic resistance that may result in a longer term of usefulness for the Rp_1 locus in the Corn Belt of the USA. While Rp_1^d now conditions an adequate level of disease control in the Corn Belt, hybrids having both Rp_1^d and Rp_1^{Td} should have a more durable resistance when both alleles are employed.

The backcross method would be a useful procedure to incorporate gene Rp_1^{Td} into parental inbred lines of a commercial breeding program. In hybrid production, the objective would be to incorporate gene Rp_1^d into one inbred and gene Rp_1^{Td} into the other inbred that constitutes the inbred parents of a single-cross hybrid. The ultimate objective would be to have both parents homozygous for genes Rp_1^d and Rp_1^{Td} . However, because of the very close linkage of Rp_1^d and Rp_1^{Td} , this combination could not be achieved easily without the use of rust races that could identify the double-dominant recombinant in coupling phase. Thus, one stage of seed production could use Rp_1^d in the seed parent and gene Rp_1^{Td} in the pollen parent. This would result in a hybrid that, in addition to protection from the two-gene combination, would have the more limited protection obtained from the single parental genes during seed production.

In this study, inconsistencies between the Illinois and Hawaii observations were apparent. In Illinois, the Rp_1^d and Rp_1^{Td} genes both conditioned a chlorotic fleck type of resistance in seedlings and in mature plants. On the contrary, in Hawaii genes Rp_1^d/Rp_1^{Td} expressed a chlorotic fleck type of resistance in plants from the seedling stage through anthesis. Near plant maturity, minor uredial infections were observed on the lower leaves. This might mean that a new virulent race is developing or that the Rp_1^{Td} gene conditions

seedling resistance accompanied by mature-plant susceptibility under Hawaiian conditions. Older plants with Rp_1^d/Rp_1^{Td} had fewer uredia than did plants with Rp_1^d , which is ineffective in Hawaii.

The discovery of a major gene locus, Rp_1^{Td} , that conditions resistance to *P. sorghi* in *T. dactyloides*, raises the question whether *Tripsacum* may have been an ancestral contributor toward the origin of corn (10). The evidence suggests that the Rp_1 locus of *Z. mays* has an ancestral origin in *Tripsacum*. Rp_1^{Td} appears very closely linked to Rp_1 locus chromosome 10 of *Z. mays*. The existence of rust resistance genes in *T. dactyloides* that recombine with the region of complex locus Rp_1 provides evidence for possible evolution of rust resistance genes that occur in region of Rp_1 on chromosome 10 from *Tripsacum*.

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