

Resistance

Erosion of Resistance to Common Leaf Rust in Exotic-Derived Maize During Selection for Other Traits

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ABSTRACT

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A tropical maize × Midwest-adapted sweet corn (*su*) composite (1R) was examined for changes in resistance to common leaf rust (*Puccinia sorghi*). Eighty-five randomly chosen S₁ families from each of three cycles (0, 5, and 10 yr) in the improvement of 1R were evaluated for susceptibility. To encourage recombination for all traits, four generations of random mating and efforts to reduce natural selection were undertaken in the establishment of 1R before cycle 0. Beginning with cycle 1, phenotypic recurrent selection with recombination was conducted each year for vari-

ous horticultural traits and for disease and insect resistance. No intentional selection was practiced for rust resistance. During the 10 cycles of selection, rust was found on the population each year but always at a low level. If resistance was selectively neutral in the absence of disease, recurrent selection would not have changed the level of resistance. However, mean rust resistance decreased from cycle 0 to cycle 10. This suggests that postponement of selection for rust resistance resulted in the loss of useful genes.

Additional keywords: disease resistance, plant breeding, *Zea mays*.

Leaf rust of maize (*Zea mays* L.), caused by *Puccinia sorghi* Schwein., has been documented as a problem of economic consequence on sweet corn (3,8,11,13,15). Various sources of resistance have been described (1,2,8,9,12,13), and various screening methods have been devised (1,5,6). Genes for resistance, useful in sweet corn breeding, are often found in genotypes having traits unde-

sirable in commercial sweet corn. These may be in dent corn or in tropical maize unadapted to temperate regions.

At the University of Minnesota, utilization of tropical maize in sweet corn improvement has been under way for 20 yr. Recently, after recognition of the economic importance of leaf rust, tropical-derived sugary germ plasm developed at the University was screened for resistance. Emphasis has been placed on partial resistance as a supplement to the hypersensitive form of rust resistance, as in the *Rp* series, to achieve a theoretically greater durability

of resistance. The purpose of this study was to determine the change in levels of partial resistance found in a tropical-derived composite (IR) at various stages during 10 yr of improvement for various traits and for adaptability to the Minnesota environment. No intentional selection for rust resistance was practiced during this 10-yr period.

MATERIALS AND METHODS

Establishment of composite IR. Composite IR was initiated in 1968 by hybridizing 17 land races and cultigens from Mexico and Peru with each of nine U.S. state agricultural experiment station sweet corn (*su*) inbreds and each of two proprietary inbreds (Table 1). These 11 inbreds were recognized for excellence in specific and/or general combining ability for yield but varied widely in earliness, quality, and type and were highly susceptible to leaf rust. Following self-pollination of the F_1 , four generations of random mating were conducted, beginning in 1970. Each year two fields were planted, one in isolation for open-pollination and the other for controlled crosses. Each field contained approximately 7,000 plants per year. Based on knowledge of variation in maturity, planting times within each field were staggered through the spring to reduce assortative mating for maturity. All the plants that set seed in the isolation field were harvested, and an equal amount of seed for the next generation was saved from each and bulked. In the crossing field, 400–500 crosses were handmade across the staggered planting dates to maintain variability, with all females contributing an equal amount of seed to the next generation. Seed from the two fields was bulked at the end of each year in proportion to the number of plants that contributed seed. This program was continued annually through 1973.

Improvement of composite IR. Beginning in 1974, recurrent mass selection for phenotype was performed each year on approximately 14,000 open-pollinated plants in an isolation field, with one in 10 plants selected for earliness, vigor, freedom from diseases and pests and for plant, ear, and kernel type. An equal amount of seed from each of these selected plants was bulked to provide seed for the next year.

Randomly chosen plants from remnant seeds of open-pollinated IR at cycle 0 (1972), cycle 5 (1977), and cycle 10 (1982) were self-pollinated in 1984 to produce S_1 families. Eighty-five S_1 families from each of these three cycles and a susceptible control hybrid, Jubilee, were evaluated in 1986 in a rust nursery. Single-row, 250-cm plots spaced in rows 90 cm apart were replicated three times in a randomized complete block design. Spacing within plots varied from 4 to 15 cm, as plots were planted heavily and not thinned. Planting was delayed until June 25 to increase the likelihood of development of an epidemic level of rust in the S_1 families, following artificial inoculation of susceptible maize

spreader strips in the nursery (16). The spreader strips consisted of mechanical mixtures of rust-susceptible hybrids and were planted 3 wk before the test plots. These spreader strips were inoculated when plants were at the classical two-leaf stage (15–20 cm high). Plot ratings for rust were obtained on September 5 by adapting the 0–9 visual scale described by Davis et al (1) for rating rust severity. The uppermost six leaves of the plant were emphasized in the evaluation. Plot ratings were estimated as a composite score rather than as an average of individual plants within each plot. The points on the scale used were as follows: 0 = immune response, no visible disease; 1 = immune response, hypersensitive flecks present; 2 = one to 10 single disease areas (pustules and groups of pustules) present; 3 = 10–20 single disease areas present plus evidence of a banding pattern; 4 = numerous

TABLE 2. Summary of variance analysis for leaf rust rating of cycles 0, 5, and 10 from the Minnesota IR maize composite

Source of variation	df	MS	F
Replication	2	0.255	9.11**
Cycle	2	0.430	15.36*
Error	4	0.028	

Waller-Duncan *K*-Ratio LSD = 0.38

** Indicates significant differences at $P = 0.05$.

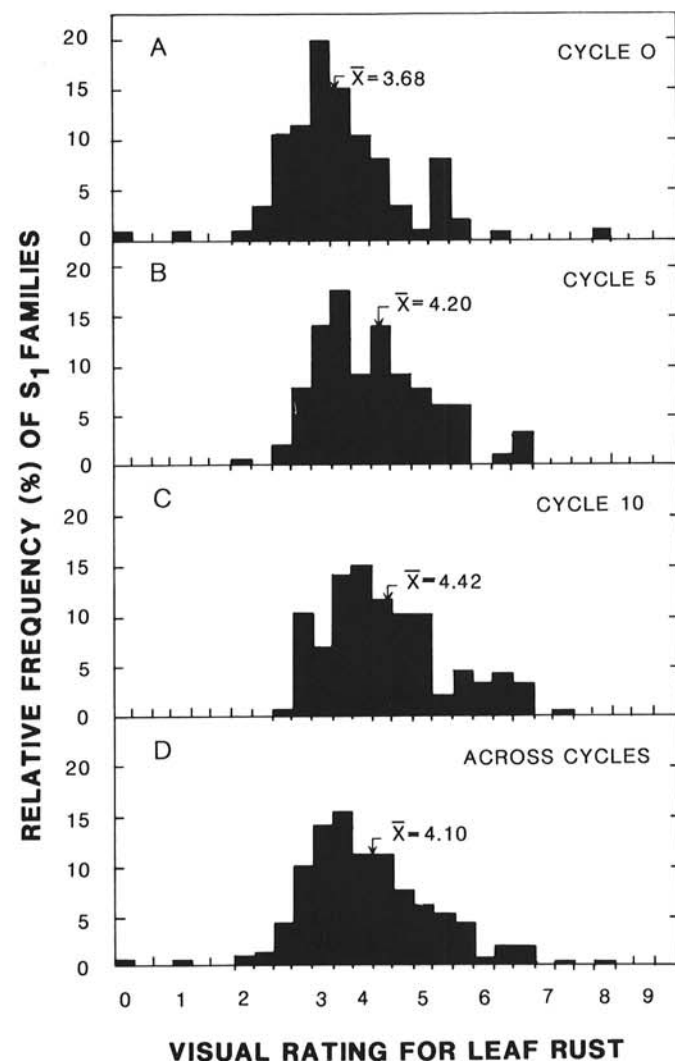


Fig. 1. Frequency of common leaf rust level in S_1 families during the development of the Minnesota IR maize composite: A–C from cycles 0, 5, and 10, respectively; and D, across cycles. Eighty-five randomly chosen S_1 families were evaluated from each cycle. See text for explanation of the rating scale.

TABLE 1. Parental sources of maize from which the IR composite was initiated at the University of Minnesota

Exotic parents and source	Adapted sugary (<i>su</i>) inbred parents
Paro (Peru)	I453
Chullpi (Peru)	I5125
Huayleno (Peru)	P39
Piscorunto (Peru)	P51
Comp. Dulce (Peru)	GG 22
Chapareno (Peru)	GG 62
Comp. Gto. Gpo. 13 #1382 (Mexico)	C6
Comp. Gto. Gpo. 14 #1382 (Mexico)	C13
Comp. Gro. Gpo. 15 #1396 (Mexico)	I11 18b
Comp. Pue. Gpo. 12 #5081 (Mexico)	I11 27a
Michoacan 4 #2134 (Mexico)	I01t (T36)
Maiz Dulce Gto. 93A (Mexico)	
Michoacan 15 #2124 (Mexico)	
Dulcilo do Sonora 57 #1568 (Mexico)	
Jalisco 188 #1453 Tep. 60-61 (Mexico)	
Gto. 98 #1352 Tep. 60-61 (Mexico)	
Chullpi 4096 (Mexico)	

single disease areas present plus a well-defined banding pattern; 5 = up to two well-defined banding patterns with numerous single disease areas present; 6 = leaf margins becoming necrotic with numerous single disease areas present plus up to two banding patterns; 7 = numerous single disease areas, banding patterns, and necrotic margins well defined; 8 = all leaf tissue necrotic except for center of leaf; 9 = all leaf tissue necrotic except midrib and some adjoining leaf tissue. Category 4 on the scale is considered to be a critical breakpoint where well-defined banding begins, indicating susceptibility.

Plot means were also obtained for degree of chlorotic flecking of the leaves, overall level of foliar disease, plant maturity, and plant height, either by rating or by measurement. Ratings were made on a scale of 1-3 as follows: leaf fleck (1 = none; 2 = few, scattered; 3 = many, prominent); total foliar symptoms (1 = none; 2 = scattered leaf lesions; 3 = numerous leaf lesions); plant maturity (1 = plants vegetative; 2 = tassel in boot or emerging; 3 = anthesis or beyond).

RESULTS

Epidemic development was sufficient to result in a rust level on Jubilee of 4-5, a level seen from time to time in commercial fields, and a level that, for this hybrid, has been shown to reduce yield and quality (3,14). Rust rating on the S_1 families ranged from 0 to 8 across the three cycles. Significant differences were found among cycle means (Table 2), with the highest mean rust level in cycle 10 and the lowest in cycle 0 (Fig. 1). Even more striking was the preponderance of resistant S_1 families from cycle 0 as compared to those of cycles 5 and 10. Fifteen of the 17 most resistant S_1 families were from cycle 0 (Table 3). Conversely, 11 of the most susceptible 17 were from cycle 10, and only two were from cycle 0. The combination of selection for various horticultural traits, genetic drift, and natural selection for adaptation, decreased mean rust resistance with increasing cycles. The reduced cycle means are caused by reduced frequency of families with high resistance.

As shown in Figure 1, extreme types (ratings 0, 1, and 8) were lost quickly (i.e., by cycle 5). However, aside from these few extreme families, the distribution was similar among cycles. Both cycles 5 and 10 had many families with more resistance than Jubilee.

TABLE 3. Cycle of origin from the Minnesota 1R maize composite of the 17 most resistant and the 17 most susceptible of 255 S_1 families evaluated for common leaf rust

Most resistant S_1 families		Most susceptible S_1 families	
Cycle of origin	Mean leaf rust rating ^a	Cycle of origin	Mean leaf rust rating ^a
0	0 a ^b	0	8.00 p ^b
0	1.00 ab	10	7.33 pp
0	2.00 bc	5	6.67 no
5	2.00 bc	5	6.67 no
0	2.33 cd	5	6.67 no
0	2.33 cd	10	6.67 no
0	2.33 cd	10	6.67 no
0	2.67 cde	10	6.67 no
0	2.67 cde	0	6.33 mno
0	2.67 cde	5	6.33 mno
0	2.67 cde	10	6.33 mno
0	2.67 cde	10	6.33 mno
0	2.67 cde	10	6.33 mno
0	2.67 cde	10	6.33 mno
0	2.67 cde	10	6.00 lmn
0	2.67 cde	10	6.00 lmn
5	2.67 cde	10	6.00 lmn

^a Leaf rust rated on a scale of 0-9, where 0 = none and 9 > 96% ($\pm 35-36\%$ actual area, based on a modified Cobb scale) of leaf area infected.

^b Means not followed by one or more letters in common are different as determined by the Waller-Duncan test ($K = 100$; $P \approx 0.05$).

Across cycles, susceptibility to leaf rust was correlated with a greater severity of chlorotic leaf flecking, less overall foliar disease, later plant maturity, and greater plant height, but the values for r were low (Table 4). The absolute value of r increased from cycle 0 to cycle 10, and the associations were all significant ($P \leq 0.05$) in cycle 10. Evaluation for total foliar disease included various symptoms other than rust pustules, such as northern corn leaf blight (*Exserohilum turcicum*), senescence, and tissue-browning in some S_1 families as a later symptom of leaf rust following the pustule stage. None of the trait associations suggested difficulty in utilizing resistance genes from this material.

Resistant S_1 families tended to show fewer and smaller pustules than susceptible families. Only one S_1 , 72-111, was found to be free of rust at the September evaluation (Table 3). However, by early October, a scattering of pustules was seen on some plants in this S_1 . Among selfed progenies from remnant seed of 72-111 examined in 1987, a wide range of resistance levels was found.

DISCUSSION

Only a few examples can be found in which changes in disease resistance have been monitored in synthesized, heterogeneous populations of crop plant species. In the best-documented of these, resistance to scald (*Rhynchosporium secalis* (Oudem.) J.J. Davis) in barley (*Hordeum vulgare* L.) composite populations was conserved or increased when disease pressure was present (7,19). Resistance to scald and to two other diseases, powdery mildew (*Erysiphe graminis* f. sp. *hordei*) and net blotch (*Drechslera teres*), increased in later generations of these populations, sometimes in an associated manner (18). It has been suggested that the highly variable *R. secalis* evolves with the host population when both are closed systems (10), and that less virulent races tend to be found on less resistant host populations. However, *P. sorghi* in the Upper Midwest is not a closed system, as it does not overwinter and as the populations are replenished each year from other host germ plasm in other regions.

Harlan (4) discussed examples of selection for maintenance in heterogeneous commercial crops of adequate levels of resistance to a prevalent disease. Increased levels of resistance to southern corn rust (*Puccinia polysora*) were naturally selected in open-pollinated maize in Africa following the accidental introduction of this pathogen onto the continent. During the several hundred years that maize had been grown in Africa, it apparently had lost most of its resistance to southern rust in the absence of selection pressure by the pathogen.

The present results do not agree with the general conclusions reached in the detailed studies of the scald-barley system that resistance is maintained in composite populations (18,19). Whether resistance erodes probably is dependent on details of the nature of the resistance as well as on linkage and on the construction and handling of the populations, including how plants are selected to represent the next generation. During the 10 cycles of selection in 1R, rust generally was present but not severe. If the criteria for selection had included rust level, one would have expected rust resistance to increase, rather than decrease, from cycle 0 to 10; however, no direct selection for resistance was knowingly made. Harlan (4) discussed the possibility

TABLE 4. Phenotypic correlations (r values) on a family-mean basis between common leaf rust rating and four traits for which the Minnesota 1R maize composite had undergone selection

Cycle	Leaf fleck ^a	Total foliar symptoms from all diseases ^a	Plant maturity ^a	Plant height
0	0.30** ^b	-0.04	0.01	0.03
5	0.49**	-0.10	0.14*	0.12
10	0.54**	-0.14*	0.17*	0.14*
Across cycles	0.45**	-0.09*	0.12**	0.11**

^a See text for description.

^b*, ** The value for r is significant at the 5 and 1% levels, respectively.

that resistance in a host species is maintained only at a cost of fitness, and that, under light selection pressure by the pathogen, resistance can be lost. This is one possible explanation for our findings, but it is not the only one.

We attribute the source of resistance in IR to the tropical component; the II adapted *su* inbreds are generally known to be very rust-susceptible. Furthermore, higher levels of resistance have not been found in a population developed by intercrossing these II inbreds. Some of the resistance in IR is race-specific, based on the observed hypersensitive reactions that are so typical of known race-specific resistance genes and on the extreme effectiveness of the resistance under epidemic conditions. Partial resistance is also present in these plants, but whether or to what extent such resistance is race-specific is not known. From these studies of resistance, and in the absence of differential corn lines or other markers to gauge the phenotypic diversity of the rust fungus, it is not yet possible to know exactly how the observed erosion is taking place; it could involve only a few genes of strong effect or many resistance genes of differing effect. It is possible that the midwestern rust populations have become adapted somewhat specifically to midwestern maize germ plasm, and that, through selection for desirable traits, the proportion of genes derived from the improved parents increased, resulting in a more rust-susceptible maize population in later cycles.

These results suggest that postponement of selection for a disease resistance trait following a wide cross may carry with it the risk of losing important genes for that trait. Other work with the IR composite, based on monitoring of isozyme marker loci, provides little indication that the exotic germ plasm was eliminated during three generations of random mating in the establishment of the composite before the initiation of selection in cycle 0 (17). This does not preclude, however, the possibility that the initiation of selection may have resulted in the loss of genes for partial resistance to rust through linkage or trait associations. During the 10 cycles, considerable natural and artificial selection pressure was placed on IR for adaptability, economically important traits (particularly ear and kernel traits), early maturity, and resistance to common smut (*Ustilago maydis*).

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