

Partial Rust Resistance in Sweet Corn Hybrid Seedlings

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ABSTRACT

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Partial resistance in corn (*Zea mays*) to *Puccinia sorghi*, causal agent of common rust, was evaluated in seedlings in greenhouse experiments. In preliminary experiments, 11 sweet corn hybrids and two dent corn inbreds were differentiated on the basis of the number of sporulating uredinia per plant when inoculation techniques and replications were adequate. The components of the infection cycle through which partial resistance was expressed were evaluated further using five sweet corn hybrids: Miracle (moderately resistant), Gold Cup (intermediate), and Sweet Sue, Florida Staysweet, and Stylepak (susceptible). No differences were observed among the five hybrids for time-related components (latent period, infectious period, and rate of occurrence of sporulating uredinia in time). Latent period was about 6 days and infectious period was about 28 days. The maximum number of sporulating uredinia occurred about 20 days after inoculation. Components of partial resistance related to *P. sorghi* reproduction (number of lesions, number of sporulating uredinia, number

of uredinia per lesion, size of uredinia, and urediniospore production) varied among the hybrids. The partial resistance of Miracle was expressed as a reduction in all reproduction-related components. Gold Cup also had fewer uredinia and urediniospores than the susceptible hybrids but was not as resistant as Miracle owing to an increased number of chlorotic lesions per leaf. Florida Staysweet had fewer lesions than Sweet Sue and Stylepak but more uredinia per lesion. Size of uredinia and urediniospore production per uredinium were less on Sweet Sue than on Florida Staysweet and Stylepak. Consequently, partial rust resistance can be detected at the seedling stage and is expressed as reductions in various components of the infection cycle. Although screening for various components of resistance may be impractical in most breeding programs, detection of partial resistance at the seedling stage could be potentially beneficial if selections for resistance could be made before anthesis.

Additional key words: generalized resistance, maize, rate-reducing resistance, slow-rusting.

Severe epidemics of common rust (*Puccinia sorghi* Schw.) have occurred on sweet corn (*Zea mays* L.) in the midwestern United States during the past 10 years when weather conditions have been favorable. Yield reductions of up to nearly 50% have been observed on susceptible hybrids (4). Several of the most popular sweet corn hybrids are extremely susceptible to rust (3,11). In contrast, common rust has been of little economic importance in field corn production in the United States corn belt, primarily because of resistance (6).

Two types of resistance to common rust have been described: specific and generalized (6,7). Race-specific resistance is qualitatively expressed in the seedling and adult-plant stages. Resistant reactions are expressed as chlorotic or necrotic hypersensitive flecks with little or no sporulation. Specific resistance is controlled by single genes that occur at six or more loci. At least two of these loci are a complex of several very closely linked genes or pseudoalleles (13,14). A gene at one of these loci, Rp_1^d , conditioned resistance to all biotypes of *P. sorghi* that commonly occurred in the continental United States until a virulent biotype was reported in 1984 (1).

Generalized rust resistance has been effective against all biotypes of *P. sorghi* (6) and has been referred to as partial rust resistance (3). Partial resistance is controlled by many genes or perhaps as few as two (6-8,12). Dominant and additive gene effects have been important in inheritance of partial resistance (6-8,12).

Both specific and partial rust resistance are used by commercial sweet corn breeders (17). Sweet corn hybrids that possess specific rust resistance have been released recently, and several commercial breeders are incorporating Rp resistance into inbred lines. Even though specific resistance is effective at present, the stability of this

type of resistance is a cause for concern (17), especially since some races of *P. sorghi* are virulent on lines that carry Rp_1^d (1). Consequently, some sweet corn breeders select for high levels of partial resistance before beginning a backcross program for specific resistance (17). Several sweet corn inbreds and hybrids with levels of partial resistance adequate to prevent severe rust epidemics have been identified (3,11,12).

Quantitative, polygenically inherited resistance to foliar pathogens of several crops has been investigated (10). This slow-rusting, rate-reducing, partial, or generalized resistance has been characterized by the components of the infection cycle through which resistant reactions are expressed phenotypically. Partial resistance to *P. sorghi* generally has been observed to be expressed as fewer and smaller lesions, fewer uredinia, and reduced chlorosis surrounding uredinia (7,8,12); these components of partial resistance have not been documented quantitatively, however. In addition, partial rust resistance has been reported to be expressed only at the adult-plant stage (6,7).

The objective of this research was to determine if partial rust resistance could be distinguished in sweet corn genotypes inoculated at the seedling stage by evaluating differences in latent period, number of lesions, number of sporulating uredinia, size of uredinia, urediniospore production, and infectious period.

MATERIALS AND METHODS

Preliminary evaluations of seedling reactions. Four preliminary greenhouse evaluations were conducted for 11 sweet corn hybrids and two field corn inbreds that showed a range of reactions to *P. sorghi*. Ten seed of the 13 genotypes were planted in rows in 36 × 42 × 8 cm flats, with six or seven rows per flat. Each trial was conducted in a randomized complete block design with 3, 5, 5, and 10 replications in trials 1 to 4, respectively.

In all trials, plants were inoculated at the five- to six-leaf stage with a mixture of isolates of *P. sorghi* collected at several locations

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in Illinois. In trials 1 and 2, 2 mg of urediniospores were suspended in 400 ml of distilled water with five drops of Tween 80. The urediniospore suspensions were injected into leaf whorls with a hypodermic syringe until whorls were filled. In trials 3 and 4, suspensions were made from 2 and 4 mg of urediniospores, respectively, and sprayed onto plant leaves and into whorls with an atomizer (DeVilbiss Co., Somerset, PA 15501). In all four trials, plants were placed in a mist chamber for 6 hr after inoculation, then moved to a greenhouse bench.

Sporulating uredinia per plant were counted daily for 3 wk after inoculation in trials 1 and 2 and at 2- to 5-day intervals in trials 3 and 4. Data were analyzed by analysis of variance (ANOVA) ($P=0.05$) for each trial separately. Hybrids were compared by Waller-Duncan Bayesian least significant difference (BLSD) values, with $k=100$.

Components of partial resistance. Five sweet corn hybrids were selected for evaluation on the basis of previous greenhouse and field reactions to rust (11). Florida Staysweet, Stylepak, and Sweet Sue were considered susceptible, Gold Cup was intermediate in reaction, and Miracle possessed a high level of partial rust resistance.

Six trials of the experiment were conducted. Each trial included six replications, and each replication consisted of two plants of each hybrid grown in 11-cm pots in the greenhouse. For all trials, the youngest fully expanded leaf and the leaf just emerging from the whorl were inoculated when plants were at the five- to six-leaf stage. Thus, each experimental unit consisted of four inoculated leaves. In trials 1, 2, and 4, inoculations were made using a settling tower (2) and 2 mg of urediniospores per replication. In trials 3, 5, and 6, inoculations were made with an atomizer and suspensions of 1 mg of urediniospores in 50 ml of water with one drop of Tween 80 per replication. In all trials, plants were placed first in a mist chamber for 6 hr after inoculation, then on a greenhouse bench. Plants were subirrigated after inoculation to prevent leaves from becoming wet, which might have allowed secondary infection.

Data were collected on the four inoculated leaves 6, 8, 11, 13, 15, 18, 20, 22, 25, 27, and 29 days after inoculation. Length of uredinia, number of sporulating uredinia, number of lesions, and sporulation were measured. Since inoculation methods and greenhouse environments were not uniform for all six trials, each of the six replications in a trial was treated as a subsample and each trial was treated as a replication. Hybrids were compared by analysis of covariance ($P=0.05$) or by ANOVA and BLSD values. When variances were not homogeneous, data were transformed by common log transformations.

Uredinial lengths were measured from approximately 1,700 uredinia for each hybrid. All measurements were made immediately after urediniospores had been collected. For the first two trials, uredinia were measured at all sampling dates. For the last four trials, uredinia were measured two to five times, beginning 11 days after inoculation. At each sampling time, 10 sporulating uredinia per experimental unit were measured (five on the abaxial leaf surface and five on the adaxial) with a hand-held microcomparator (Finescale Co., Orange, CA 92668). Means of the 10 sub-samples for each experimental unit were analyzed by ANOVA and BLSD values to compare hybrids.

Sporulating uredinia on both the abaxial and the adaxial leaf surface were counted at each sampling date. Data were analyzed for both surfaces separately and for combined surfaces by analysis of covariance. Hybrids were treated as qualitative variables and time, as a quantitative variable. The number of sporulating uredinia was compared among hybrids over time by regressing sporulating uredinia on time. Occurrence of the maximum number of sporulating uredinia was determined for each hybrid by solving the first derivative of the regression equation describing uredinia occurrence in time. For example, sporulating uredinia as a function of time was described by the general equation

$$Y = a + bX - cX^2,$$

where Y equals sporulating uredinia, X equals days after inoculation, and a , b , and c are coefficients of the quadratic

equation. Thus, time of occurrence of maximum number of sporulating uredinia was solved from

$$b - 2cX = 0.$$

The maximum number of sporulating uredinia was then solved by substituting these values of time into the equation describing uredinia in time. The infectious period resulting from an inoculation was determined for each hybrid as the difference between the roots to the quadratic equations that described sporulating uredinia in time.

Chlorotic lesions per leaf were counted at the same sampling time as uredinia. The number of lesions per leaf and the number of sporulating uredinia per lesion were analyzed by covariance.

At each sampling date, urediniospores from all uredinia per experimental unit (four leaves per two plants) were collected in gelatin capsules using a small cyclone spore collector (ERI Machine Shop, Iowa State University, Ames 50011). Urediniospores were stored in a refrigerator for a maximum of 4 mo until all trials of the experiment were completed. Urediniospores from each capsule then were suspended in ethanol and collected on preweighed 1.6-cm² filter papers placed on a Hirsch funnel connected to a vacuum flask. Urediniospores on filter papers were dried and weighed. Daily average urediniospore weights were determined by dividing urediniospore weights by the number of days between each sampling time. Daily average urediniospore production was determined from a standardization curve developed from preweighed amounts of urediniospores (Fig. 1). The number of urediniospores per uredinium was determined by dividing the daily average number of urediniospores by the number of sporulating uredinia at each sampling time. Hybrids were compared at each sampling date by ANOVA and BLSD values.

RESULTS

Preliminary evaluations of seedling reactions. The ability to differentiate partial rust resistance on greenhouse-grown seedlings varied with inoculation technique, number of replications per experiment, and time of rust assessment. In trial 1, in which three replicates were inoculated by the injection technique, mean number of sporulating uredinia per plant was not significantly different among hybrids. In trial 2, in which five replicates were inoculated by the injection technique, significantly more sporulating uredinia were observed at most sampling dates on Cherokee, Earlibelle,

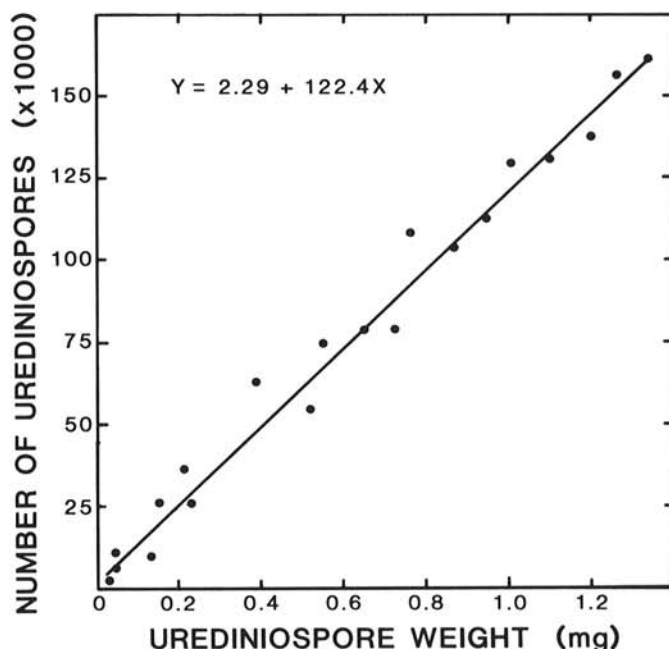


Fig. 1. Relationship between weight (mg) and number of urediniospores of *Puccinia sorghi*.

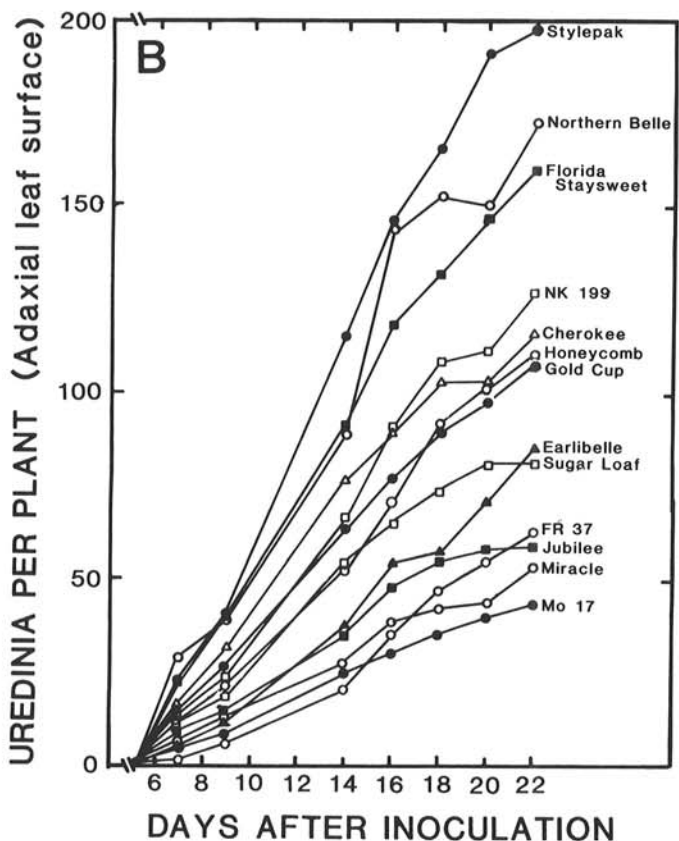
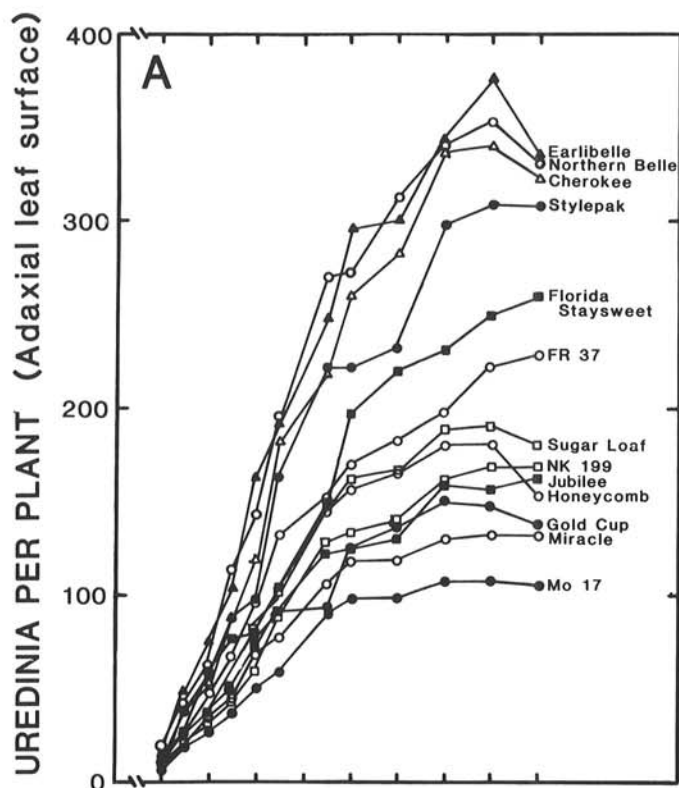


Fig. 2. Number of sporulating uredinia per plant on 11 sweet corn hybrids and two dent corn inbreds evaluated for partial rust resistance as seedlings in greenhouse trials. **A**, Trial 2, injection inoculation method: significantly more uredinia per plant on Earlibelle, Northern Belle, Cherokee, Stylepak, and Florida Staysweet than on Miracle and Mo 17 at 11 days after inoculation and thereafter. **B**, Trial 3, atomized mist inoculation: significantly more uredinia per plant on Stylepak, Northern Belle, and Florida Staysweet than on FR 37, Jubilee, Miracle, and Mo 17 at 14 days after inoculation and thereafter.

Florida Staysweet, Northern Belle, and Stylepak than on Mo 17 and Miracle (Fig. 2A). Differences were detectable 11 days after inoculation and thereafter. In trial 3, in which five replicates were inoculated with 2 mg of urediniospores, more uredinia per plant were observed 14 days after inoculation and thereafter on Florida Staysweet, Northern Belle, and Stylepak than on FR 37, Jubilee, Miracle, and Mo 17 (Fig. 2B). In trial 4, in which 10 replicates were inoculated with 4 mg of urediniospores, uredinia per plant were too numerous to count 10 days after inoculation and thereafter.

Components of partial resistance. At 6 days after inoculation, chlorotic flecks were observed on all hybrids in all six trials. By 8 days after inoculation, uredinia had erupted on all plants. A few telia and teliospores were observed on some plants of all hybrids 29 days after inoculation.

Uredinia were the same length on adaxial and abaxial leaf surfaces. Except for the eighth day after inoculation, uredinial length did not differ significantly among sampling times. Thus, comparisons of uredinial lengths among hybrids were made across all sampling times. Based on BLSD comparisons, uredinia on Stylepak were significantly longer than those on Gold Cup, Sweet Sue, and Miracle but not significantly longer than those on Florida Staysweet (Table 1). Means of the 10 sub-samples per experimental unit ranged from 0.28 to 1.31 mm.

The number of sporulating uredinia per leaf differed among hybrids. Sporulating uredinia as a function of time was described by quadratic regression equations where Y equaled the number of sporulating uredinia and X equaled days after inoculation (Fig. 3). Hybrids could be placed into four groups on the basis of analysis of covariance. The number of sporulating uredinia was highest on Stylepak and lowest on Miracle. Sweet Sue and Florida Staysweet did not differ significantly in number of sporulating uredinia, and Gold Cup had fewer sporulating uredinia than Stylepak, Sweet Sue, and Florida Staysweet.

The maximum number of sporulating uredinia occurred approximately 19–20 days after inoculation for all hybrids (Fig. 3). When data were extrapolated beyond 29 days after inoculation, a greater percentage of uredinia appeared to be sporulating 31 days after inoculation on Stylepak, Sweet Sue, and Florida Staysweet than on Gold Cup and Miracle; none of the uredinia would have been infectious by 34 days, however. The difference between the roots of the quadratic equations describing sporulating uredinia in time indicated that an infectious period from a single inoculation was approximately 27 days (Table 1).

Approximately 60% of the sporulating uredinia were on the abaxial leaf surface for Stylepak, Sweet Sue, and Florida Staysweet, and about 40% were on the adaxial leaf surface. For

TABLE 1. Length of uredinia of *Puccinia sorghi*, number of lesions per leaf, maximum number of sporulating uredinia per leaf, days after inoculation at which maximum number of sporulating uredinia occurred, and infectious period from a single inoculation for five sweet corn hybrids that differ in partial rust resistance

Hybrid	Uredinial length (mm) ^a	Number of lesions	Number of sporulating uredinia per leaf		
			U_{max}^b	DAI- U_{max}^c	IP ^d
Florida Staysweet	0.591	4.5	133	19.7	26.4
Gold Cup	0.573	4.9	95	19.0	25.5
Miracle	0.561	2.7	57	19.4	25.7
Stylepak	0.603	6.9	178	20.0	27.4
Sweet Sue	0.567	5.5	139	19.5	26.5
BLSD ($k = 100$)	0.030	0.52

^a Mean of approximately 1,700 uredial length measurements per hybrid.

^b U_{max} = maximum number of uredinia per leaf (U_{max}) determined from quadratic regression equations that described uredinia occurrence in time, where time equals DAI for U_{max} .

^c DAI- U_{max} = days after inoculation at which maximum number of uredinia occurred determined for each hybrid by solving the first derivative of the regression equations that described uredinia occurrence in time.

^d IP = infectious period from a single inoculation determined for each hybrid as the difference between the roots of the quadratic equations that described uredinia occurrence in time.

Gold Cup and Miracle, no differences were observed in the number of uredinia on adaxial and abaxial surfaces.

Chlorotic lesions, which usually have not been observed in field experiments, were observed 8 days after inoculation. Lesions enlarged with time, eventually becoming 1–3 cm long, although measurements were not taken. Individual lesions coalesced but usually were distinguishable until about 29 days after inoculation, when leaves began to senesce. The number of lesions per leaf did not differ significantly from 8 to 27 days after inoculation but did differ significantly among hybrids (Table 1).

The number of sporulating uredinia per lesion differed among hybrids (Fig. 4). Because the number of lesions per leaf was constant for a hybrid from 8 to 27 days after inoculation, the regression equations that described uredinia per lesion as a function of time were similar in shape to those that described uredinia in time, although hybrid rankings for this component were not the same as those for total number of sporulating uredinia. Florida Staysweet had the most sporulating uredinia per lesion approximately 21 days after inoculation, and Gold Cup and Miracle had the fewest.

Daily average urediniospore production was greatest about 13 days after inoculation, then decreased slowly until the 29th day (Fig. 5). Total urediniospore production and daily average urediniospore production differed among hybrids. Urediniospore production was greatest on Stylepak and did not differ on Florida Staysweet and Sweet Sue. Total and daily average urediniospore production was significantly lower on Gold Cup and Miracle than on Florida Staysweet and Stylepak.

Daily average urediniospore production per uredinium did not differ among hybrids from 8 to 13 days after inoculation (Fig. 6), then from 13 to 29 days was greatest for Stylepak and Florida Staysweet and lowest for Gold Cup, Miracle, and Sweet Sue.

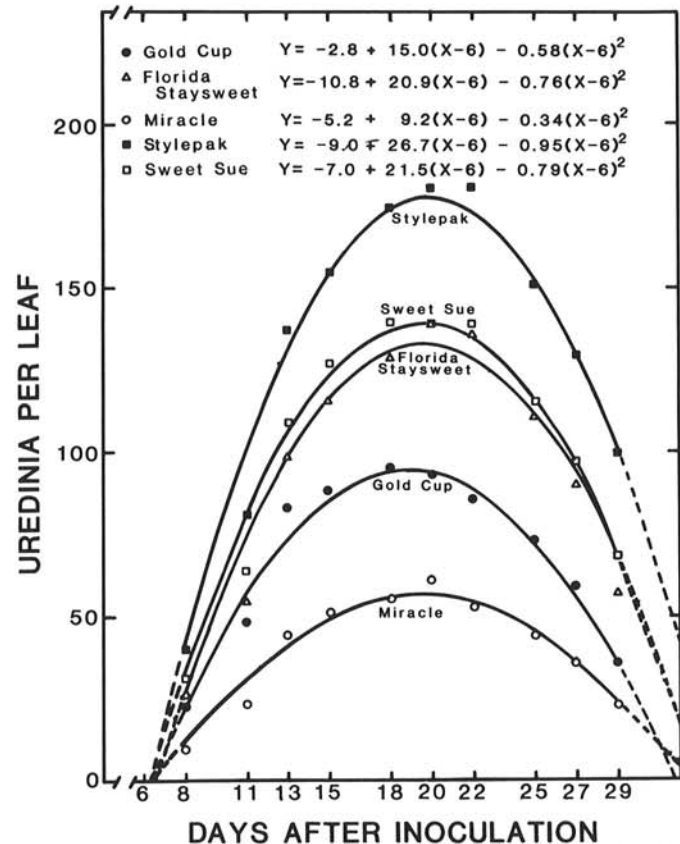


Fig. 3. Number of sporulating uredinia per leaf for five sweet corn hybrids evaluated for components of partial rust resistance as seedlings in greenhouse trials. Regressions differ significantly for all hybrids except Sweet Sue and Florida Staysweet.

DISCUSSION

Sweet corn hybrids evaluated as seedlings in greenhouse trials could be differentiated for partial resistance to *P. sorghi*. Partial resistance was expressed as reductions in components of the infection cycle related to *P. sorghi* reproduction (number of lesions, number of sporulating uredinia, size of uredinia, and urediniospore

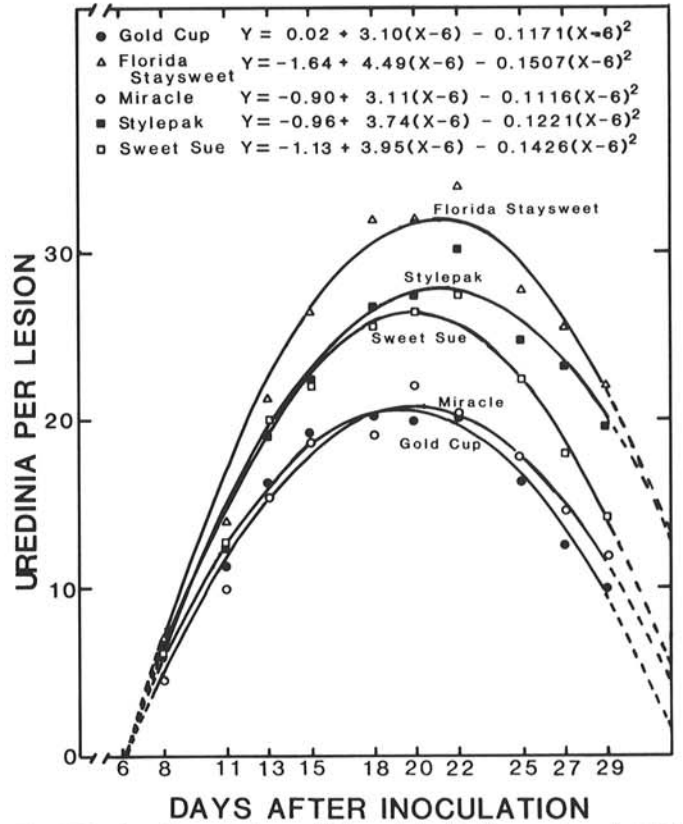


Fig. 4. Number of sporulating uredinia per lesion for five sweet corn hybrids evaluated for components of partial rust resistance as seedlings in greenhouse trials. Regressions do not differ significantly for Miracle and Gold Cup.

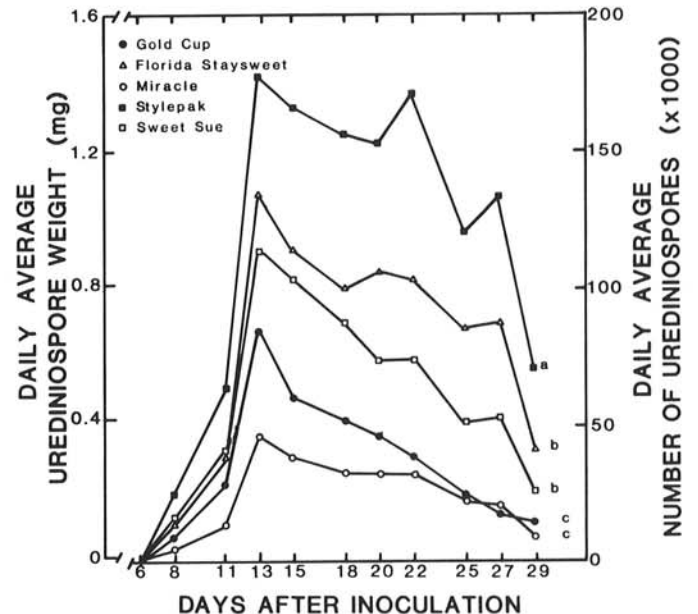


Fig. 5. Daily average weight (mg) of urediniospores collected from five sweet corn hybrids evaluated for components of partial rust resistance as seedlings in greenhouse trials. Letters indicate differences among hybrids for total sporulation per day from 13 days after inoculation, as determined by BLS comparisons.

production). Time-related components (latent period, infectious period, and sporulating uredinia occurrence in time) did not differ among genotypes. Consequently, partial rust resistance should reduce the rate at which rust epidemics develop at the seedling stage. Evaluation of sweet corn hybrids in field experiments has shown that differences in partial resistance to *P. sorghi* can be detected among genotypes at various plant growth stages (5).

Previous indications that generalized rust resistance was expressed only at the adult-plant stage may have resulted from three confounding effects. First, partial resistance is more difficult to detect at the seedling stage than specific resistance because specific resistance is expressed as qualitative reaction types at the seedling stage and partial resistance is expressed quantitatively. Second, the effects of partial resistance on *P. sorghi* reproduction are compounded by successive cycles of rust; differences in rust severity among partially resistant and susceptible genotypes are therefore maximized at the adult-plant stage even though differences among genotypes inoculated at various host growth stages are greatest at the seedling stage (5). Third, the resistance of *Z. mays* to *P. sorghi* increases with host maturity (5,16).

In this study, partial resistance or susceptibility of a hybrid was expressed through various components of the infection cycle. Partial resistance of Miracle was expressed as reductions in all reproduction-related components of the infection cycle. Gold Cup was not as resistant as Miracle but had fewer uredinia and urediniospores than Sweet Sue, Stylepak, and Florida Staysweet. The greater number of uredinia on Gold Cup than on Miracle resulted from a greater number of lesions per leaf rather than a greater number of uredinia per lesion. Urediniospore production per uredinium on Gold Cup was less than that on Miracle 22 days after inoculation and thereafter. Similarly, the number of chlorotic lesions that formed on Florida Staysweet was comparable to the number on Gold Cup, but Florida Staysweet had a higher number of uredinia per lesion and therefore was more susceptible. Likewise, uredinium size and urediniospore production per uredinium were generally lower for Sweet Sue than for the other susceptible hybrids.

At least two theoretical models have been proposed to demonstrate the effects of various combinations of resistance components on epidemic development (9,15). In evaluating the effects of components of resistance for many pathosystems,

including cereal rusts, Leonard and Mundt (9) indicated that for pathogens with high rates of reproduction and short latent periods, increases in latent period would result in greater decreases in the rate of population growth than changes of equal magnitude in other components of resistance. Shaner and Hess's (15) equations for integrating components of slow leaf-rusting resistance in wheat also can be used to identify the resistance components that are most effective in retarding epidemic development and to indicate the magnitude of change necessary for those components to be effective. Data from these monocyclic inoculation experiments with common rust suggest that variation exists among genotypes at the seedling stage for all reproduction-related components but not for time-related components. Ultimately, total urediniospore production is decreased on partially resistant genotypes. Consequently, partially resistant hybrids would perform substantially better in field situations than susceptible hybrids owing to several cycles of "autogenerated" inoculum.

Additional factors may affect the expression of partial resistance in adult plants. For leaf rusts of barley and wheat, length of latent period is associated with host age (10,15). If latent period of *P. sorghi* on *Z. mays* is related to plant age, differences in rust severity among resistant and susceptible genotypes may be increased further at the adult-plant stage. Based on Leonard and Mundt's (9) model, differences among genotypes for length of latent period would be of greater importance than reproduction-related components. Also, Headrick and Pataky (5) demonstrated that sweet corn hybrids became more resistant to *P. sorghi* after anthesis. Differences in rust severity approximately 3 wk after inoculation were smaller when partially resistant and susceptible genotypes were inoculated at adult-plant stages than when plants were inoculated at seedling stages.

For most breeding programs, screening for the various components of partial rust resistance probably would be impractical, since trials would be labor-intensive. In addition, detection of partial rust resistance in this study required precise inoculation techniques and substantial replication in the greenhouse. Nonetheless, identification of sources of partial resistance that are expressed through different components of the infection cycle may result in higher levels of resistance when these sources are crossed in hybrid combinations. Also, the ability to detect quantitative differences in rust severity among genotypes in the seedling stage would be of potential benefit to most breeding programs if selections for resistance could be made before anthesis. If plants were inoculated 3-4 wk after planting, most of the infectious period from the initial inoculation and several cycles of *P. sorghi* reproduction would be included in evaluations made just before anthesis.

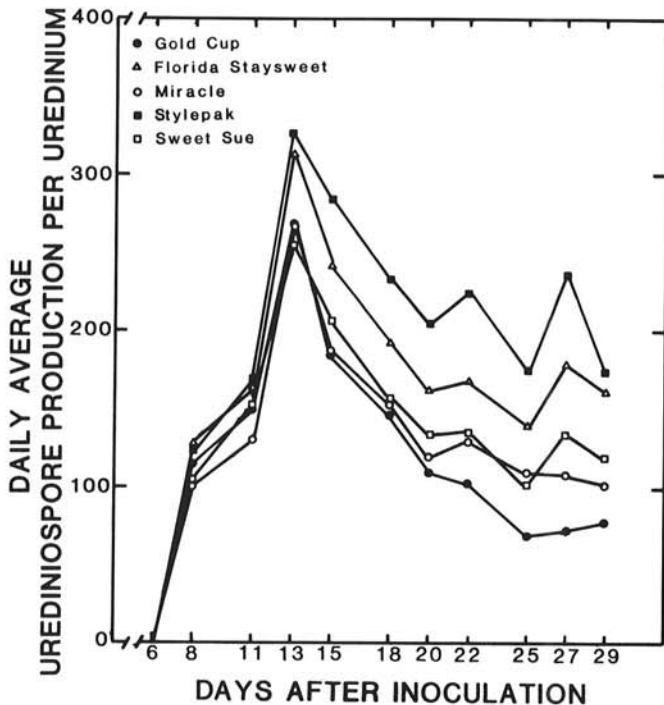


Fig. 6. Daily average number of urediniospores per uredinium for five sweet corn hybrids evaluated for components of partial rust resistance as seedlings in greenhouse trials.

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