Expression of Partial Resistance to Common Rust in Sweet Corn Hybrids at Various Host Growth Stages

J. M. Headrick and J. K. Pataky

Graduate research assistant and assistant professor, Department of Plant Pathology, University of Illinois, Urbana 61801.

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ABSTRACT

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Six sweet corn hybrids varying in levels of partial resistance to *Puccinia sorghi*, causal agent of common maize rust, were inoculated simultaneously in the field at eight stages of growth. Both partial resistance and an adult plant resistant reaction were observed. Differences in partial resistance were measurable at all growth stages. Miracle and Sugar Loaf displayed high levels of partial resistance, whereas Stylepak and Florida Staysweet were highly susceptible. All hybrids were most resistant to rust when inoculated at the late silk stage and most susceptible when inoculated at the five- to six-leaf stage. As plant age increased, rust severity decreased. This adult plant resistant reaction was most apparent after the onset of reproductive growth of the host. Regressions of rust severity on plant age were fit best by a quadratic model for five of the six hybrids. In general, the rate at which hybrids with high levels of partial resistance displayed the adult plant resistant reaction was slower than that for hybrids with low levels of partial resistance. The adult plant resistant reaction is apparently a universal property of sweet corn and is a function of plant age, whereas partial resistance is a genotype-specific trait and functions at all growth stages. Partial resistance and the adult plant resistant reaction were similar in that both reduced the number of uredinia per leaf area. Both should be more durable than race-specific resistance.

Common maize rust, caused by *Puccinia sorghi* Schwein., is an economically important disease of sweet corn (*Zea mays* L.) in the midwestern United States. It is especially severe during cool, wet seasons and may cause yield losses as great as 50% in susceptible sweet corn hybrids (5).

Resistance to common rust is of two types: race-specific resistance and generalized or partial resistance (10–13,22). Race-specific resistance is characterized by chlorotic or necrotic flecks, is based on host plant hypersensitivity, and is qualitative in expression. It is frequently dominant and monogenic in inheritance although at least two loci are actually a complex of closely linked genes (11,12,24). Alleles for race-specific resistance occur at six or more loci (11,12).

Partial resistance, also referred to as slow-rusting, rate-reducing, or generalized resistance, is quantitative in expression and controlled by several or as few as two genes (11–13,15,22). Partial resistance can affect a number of components of the infection cycle, including number of lesions, number of uredinia, uredinium size, and sporulation (19,22). It is usually most discernable in mature plants and has been referred to as adult plant resistance (9–13); however, it also is detectable in seedlings (19).

Most commercial dent corn hybrids in the United States possess high levels of partial resistance and are not economically damaged by rust (11–13,18). Considerable variation exists among commercial sweet corn hybrids for levels of partial resistance (4,20). Many popular sweet corn hybrids are highly susceptible to rust.

Adult plant resistance has been described in several pathosystems (1,6,8,16,25). Many investigators have stressed the practical importance of this type of resistance because of its apparent effectiveness against all races of the pathogen and its durability compared with race-specific resistance (1,2,6,11, 15,22,24,25). The components of adult plant resistance, plant organs affected, and growth stage of initial expression have varied among host species and cultivars (9).

The objective of this study was to investigate the effect of host plant growth stage on the expression of partial resistance to common rust in sweet corn.

MATERIALS AND METHODS

The experiment was done in 1984 and 1985 at two locations in Urbana and Champaign, IL, with 10 replicates in each of the four trials. The experimental design was a split-plot, randomized complete block with an 8 × 6 factorial treatment design. Eight plant growth stages (plant ages) were main plots and six hybrids were subplots. Each subplot consisted of three two-plant hill-plot subsamples spaced 30 cm apart in rows 76 cm wide.

Hybrids Florida Staysweet, Gold Cup, Jubilee, Miracle, Stylepak, and Sugar Loaf were selected on the basis of known differences in rust reaction, differences in endosperm mutations, and similarity of maturity (Table 1). The hybrids were planted once a week for 8 wk from 31 May to 19 July 1984 and 8 May to 1 July 1985, so that eight distinct plant growth stages, ranging from five-leaved seedlings to late silk, occurred at the time of inoculation.

All plots were sprayed weekly from 8 July to 28 July 1984 and 3

TABLE 1. Seed sources, endosperm mutations, and days to maturity for hybrids evaluated for expression of partial rust resistance at various host growth stages

Hybrid	Source	Endosperm[a]	Days to maturity
Florida Staysweet	Ill. Foundation Seeds, Inc.	*sh2*	87
Gold Cup	Harris Moran Seed Co.	*su*	80
Jubilee	Rogers Brothers Seed Co.	*su*	81
Miracle	Crookham Co.	*se*	84
Stylepak	Stokes Seeds, Ltd.	*su*	85
Sugar Loaf	Sunseeds, Inc.	*sush2*	83

[a] *sh2* = Shrunken-2, *su* = sugary, *se* = sugary enhancer, and *sush2* = heterozygous shrunken-2.

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July to 10 July 1985 with mancozeb (Dithane M-45) at a rate of 1.3 kg/ha to prevent naturally occurring rust infection before inoculations. Plants were inoculated on 10 and 20 August 1984 and 19 July 1985. Whole plants were sprayed to leaf wetness with an inoculum solution of 500 mg of urediniospores in 7.5 L of water and 5 ml of Tween 80 (ICN Nutritional Biochemicals, Cleveland, OH), using a compressed-air sprayer (Sears, Roebuck and Co., Chicago, IL). Thus, the initial inoculum concentration per leaf area was about equal for all plants. Inoculations were made at dusk to avoid rapid evaporation and to aid in urediniospore germination.

Rust severity was measured as relative percent leaf area infected for each hill-plot using a modified Peterson scale (21). Ratings were made on 28 August and 4, 11, and 18 September 1984 and 3, 10, 17, and 26 August 1985. The data from the 4 September 1984 and 10 August 1985 ratings (25 and 22 days after inoculation, respectively) were used for analysis because the infections were well developed by these dates and none of the hybrids had begun to senesce. Ratings were on a whole-plant basis with equal weight given to all leaves because age effects within plants were not evident. The ratings were based principally on primary infection and therefore were relative for all ages of plants.

Data were analyzed by analysis of covariance with genotype as a qualitative independent variable. Regressions of rust severity on plant age (growth stage) were done by hybrid for each trial (by location and year) and for trial means. *F*-statistics were examined to determine the overall significance of each model and the significance of polynomial terms ($P < 0.05$). Residuals were analyzed for homogeneity: $\log_{10}$ and arc sine transformations of the data in 1984 did not improve variance stability. In 1985, the data points appeared to be normally distributed and were not transformed. In both years, plant age in days was significantly correlated ($r = 0.99$) with accumulated heat units and was used as the independent variable. Slopes of lines tangent to the regression equation describing mean rust severity (2 yr, two locations) as a function of plant age were derived and plotted over plant age as a method of comparing the adult plant reactions of the hybrids without using transformations.

RESULTS

Environmental conditions were more favorable and rust was about twice as severe in 1985 as in 1984. Mean rust severity at about 3 wk after inoculation ranged from 1.4% at the late silk stage to 13.9% at the five- to six-leaf stage in 1984 and from 3.7% at the late silk stage to 20.7% at the five- to six-leaf stage in 1985 (Table 2).

Significant differences in rust severity occurred among plant growth stages, hybrids, and the plant growth stage × hybrid interaction in each of the four trials. For all hybrids in all trials, adult plants were more resistant to rust than were seedlings (Table 2, Figs. 1 and 2). Averaged over hybrids, rust severity ranged from 1.4 to 4.6% on plants inoculated at the late silk stage and from 8.5 to 20.7% on plants inoculated at the five- to six-leaf stage (Table 2).

TABLE 2. Mean rust severity at eight plant growth stages

Growth stage at inoculation[a]	Mean rust severity[b]			
	1984		1985	
	Champaign	Urbana	Champaign	Urbana
Late silk	2.3	1.4	4.6	3.7
Midsilk	2.7	2.9	4.7	4.2
Early silk	3.0	4.7	4.4	4.3
Early tassel	3.6	5.0	6.9	4.9
10–12 Leaves	3.8	7.4	9.0	9.7
8–10 Leaves	7.5	5.6	10.5	10.7
7–8 Leaves	11.2	8.0	12.9	13.7
5–6 Leaves	13.9	8.5	20.7	18.5

[a] Growth stages on 10 August 1984 and on 19 July 1985.

[b] Rust severity measured as relative percent leaf area infected (21). Mean of six hybrids.

As plant age increased, there was a decrease in rust severity that lessened during the latter, mostly reproductive stages (Figs. 1 and 2).

The level of partial resistance in each of the six hybrids was apparent at all growth stages. Rankings of hybrid resistance were relatively consistent over growth stages and trials (Figs. 1 and 2) with the exception of Gold Cup. The rankings of the other five hybrids in order from susceptible to partially resistant were Florida Staysweet, Stylepak, Jubilee, Sugar Loaf, and Miracle. In 1984 (Fig. 1), rust severity on Gold Cup at the seedling stages was comparable to that observed on the susceptible hybrids Florida Staysweet and Stylepak. At the adult plant stages, rust severity on Gold Cup was comparable to that observed on the more resistant hybrids.

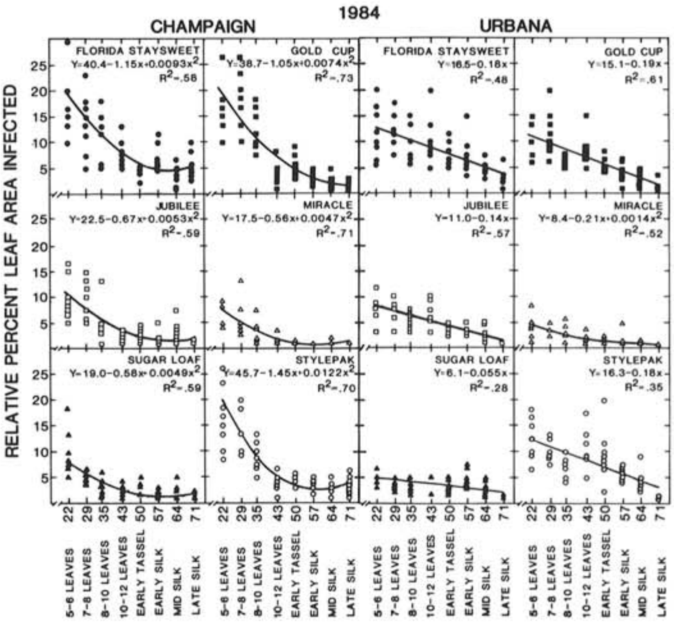

Fig. 1. Regressions of common rust severity on host plant age (at the time of inoculation) for hybrids Florida Staysweet, Gold Cup, Jubilee, Miracle, Sugar Loaf, and Stylepak at Champaign and Urbana, 1984. Multiple observations are hidden.

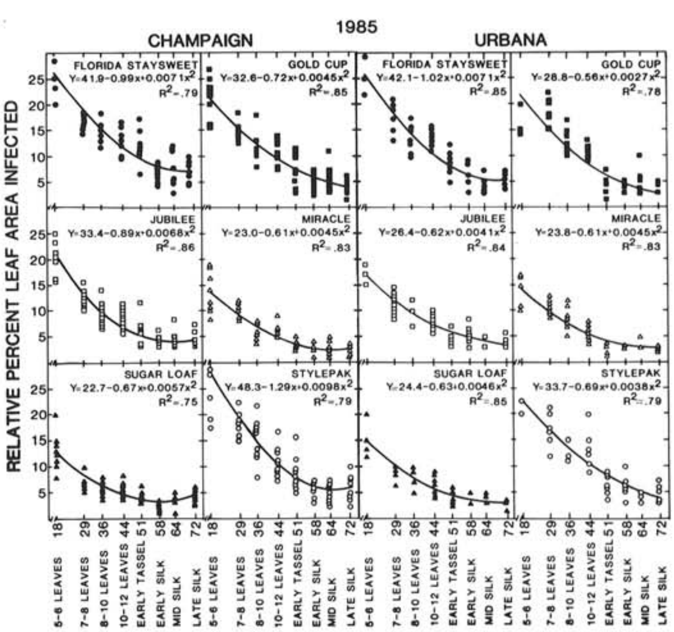

Fig. 2. Regressions of common rust severity on host plant age (at the time of inoculation) for hybrids Florida Staysweet, Gold Cup, Jubilee, Miracle, Sugar Loaf, and Stylepak at Champaign and Urbana, 1985. Multiple observations are hidden.

Regressions of rust severity on plant age by hybrid were usually fit best by a quadratic model (Figs. 1 and 2). In 1984, regressions of rust severity on plant age for Florida Staysweet, Gold Cup, Jubilee, Stylepak, and Sugar Loaf at the Urbana location were fit best by a linear model (Fig. 1). In Figures 1 and 2, hidden data points resulting from multiple observations at given severity values gave the appearance of unequal replication. For the same reason, the significance of the model and the pattern of residuals may appear to be in error; however, all terms presented in Figures 1–3 were significant ($P < 0.05$). Coefficients of determination were higher in 1985 than in 1984 and reflected the greater amount of variation among subsamples in 1984 than in 1985.

Regression of rust severity means for the four trials on plant age were fit best by a quadratic model for five of the six hybrids (Fig. 3). The relationship between severity and plant age for Gold Cup was described best by a linear model. Coefficients of determination for the regressions of trial means ranged from 0.62 to 0.78.

The significant interaction between plant growth stage and hybrid indicated that rust severity among hybrids was affected differently by plant growth stage. From Figures 1 and 2 it is apparent that all hybrids were more resistant to rust at later growth stages; however, the rate at which the hybrids became resistant as plants became older was different. Slopes of lines tangent to the quadratic functions describing rust severity on age described differences in the rate of decrease in rust severity as a function of plant age (Fig. 4). The slope of the first derivative represents the rate of change in the curvature of the quadratic functions or the rate of the rate of change in severity as a function of plant age.

The rate of the rate of change in severity as a function of plant age was 0.0062, 0.0064, and 0.0066 for Sugar Loaf, Miracle, and Jubilee, respectively. The rate of the rate of change for Florida Staysweet and Stylepak was 0.0092 and 0.0088, respectively. Thus, the rate at which plants became resistant with age was slower for partially resistant hybrids than for susceptible hybrids. Rust severity on Gold Cup as a function of plant age was described best by a linear function, and consequently, the derivative was a line with a slope of 0 and intercept of −0.284.

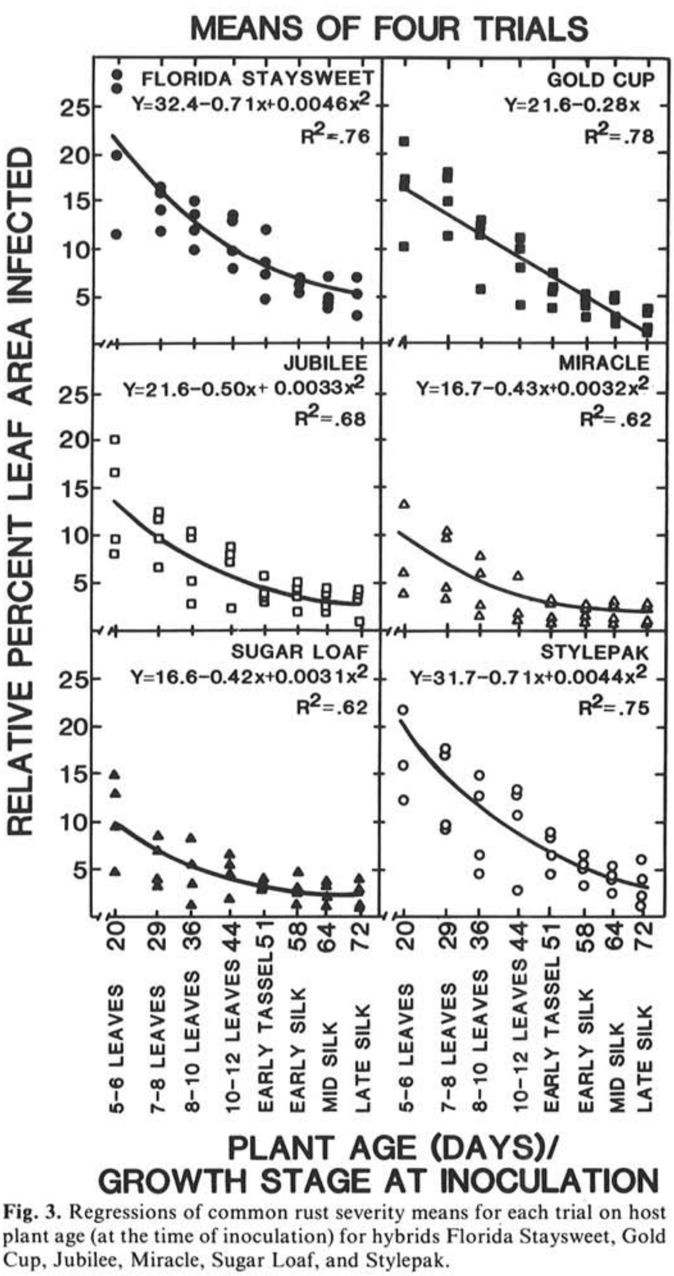

Fig. 3. Regressions of common rust severity means for each trial on host plant age (at the time of inoculation) for hybrids Florida Staysweet, Gold Cup, Jubilee, Miracle, Sugar Loaf, and Stylepak.

DISCUSSION

Adult plant resistant reactions to common rust were observed in the six sweet corn hybrids in this study. All hybrids were most resistant to rust when inoculated at the late silk stage and most susceptible when inoculated as five- to six-leaved seedlings. This reaction is similar to that described in dent corn (11,13). Hooker (11) and Hooker and Russell (13) used the terms mature plant resistance, adult plant resistance, and generalized resistance to describe common rust resistance that was based on number of uredinia per leaf area at growth stages after anthesis. They stated that this type of resistance could not be detected during seedling stages. We have used the term partial resistance in reference to sweet corn hybrids that show reduced numbers of uredinia per leaf area at all growth stages.

Partial resistance and the adult plant resistant reaction observed in this study appear to be independent. The adult plant resistant reaction is apparently a universal property of sweet corn and is a function of plant age, whereas partial resistance is a genotype-specific trait and functions at all growth stages. Partial resistance

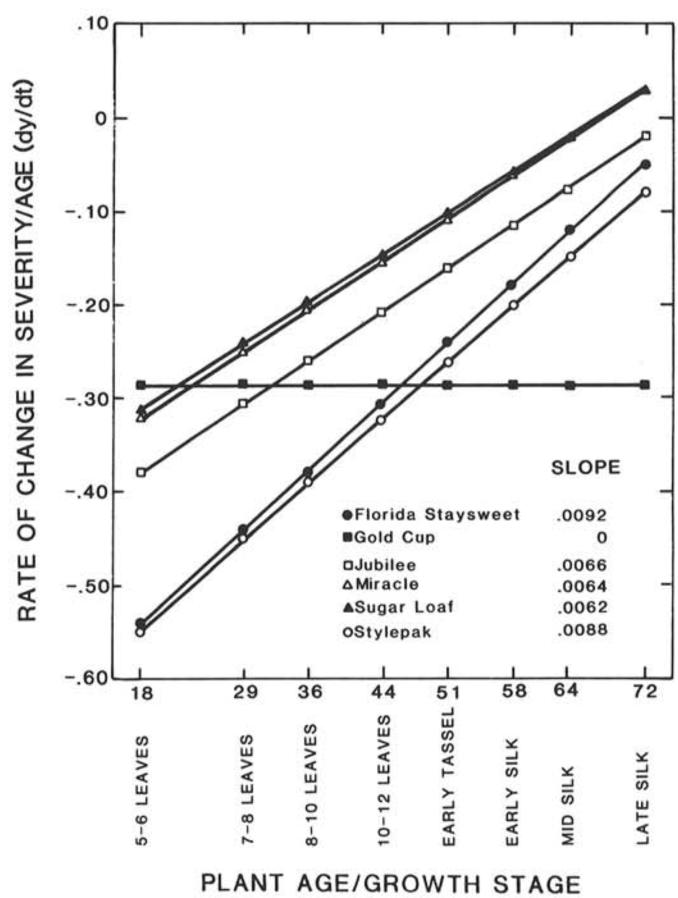

Fig. 4. Rates of change in common rust severity per plant age for hybrids Florida Staysweet, Gold Cup, Jubilee, Miracle, Sugar Loaf, and Stylepak.

and the adult plant resistant reaction were similar in that both reduced the number of uredinia per leaf area. Both should be more durable than race-specific resistance.

In this study, the adult plant resistant reaction was evident for all hybrids at the onset of reproductive growth, whereas partial resistance was detected in Miracle and Sugar Loaf at all growth stages. The effects of partial resistance and the adult plant reaction could be compared among hybrids at different growth stages. For example, mean rust severity for Miracle and Sugar Loaf at the eight- to 10-leaf stage was comparable to that for Jubilee at the early tassel stage, Stylepak at the midsilk stage, and Florida Staysweet at the late silk stage (Fig. 3). Therefore, the partial resistance in Miracle and Sugar Loaf was equivalent to about four or five additional growth stages (28–36 days) for the susceptible hybrids Stylepak and Florida Staysweet. Thus, predictive models developed for common rust must include the growth stage and partial resistance level of the host.

The expression of partial resistance during seedling stages indicates that screening for resistance may be possible in the field before anthesis. Similar results were observed for partial resistance of wheat to *P. striiformis* (1) and from studies quantifying components of resistance to *P. sorghi* in sweet corn seedlings (19). In the present study, the observed disease severity was principally a result of primary infection. Differences in severity ratings among hybrids were largest during seedling stages. In a breeding nursery, several infection cycles would occur before evaluation of adult plants so that differences in partial resistance among hybrids may be most evident on adult plants. However, these differences on adult plants would result from partial resistance, which reduces infection efficiency, uredinium size, and sporulation during each cycle of infection (7,19). Therefore, during the growing season, differences between partially resistant and susceptible hybrids may become greater, even though all hybrids would become more resistant with age because of the adult plant reaction.

The importance of the adult plant resistant reaction in disease management is that the natural defenses of the host are at a level that may make fungicide treatments unnecessary after anthesis. The need for fungicide treatments on partially resistant or susceptible hybrids may differ depending on host growth stage at the time of primary infection. If a susceptible hybrid is planted early in the growing season and reaches reproductive growth before the influx of inoculum, it is not likely that rust would develop to levels that would warrant fungicide treatment even if primary inoculum was heavy. If, however, a susceptible hybrid is planted late in the season and is at the seedling stage when inoculum levels are high, fungicide control will probably be necessary. For a partially resistant hybrid, fungicide treatments after anthesis are likely to be unnecessary, but the need for treatment at the seedling stage would depend on inoculum levels and the level of partial resistance expressed by a given genotype.

The rate at which hybrids with high levels of partial resistance displayed the adult plant resistant reaction was slower than that of hybrids with low levels of partial resistance. Because all hybrids were resistant as adult plants (mean severities of 5% or less, Fig. 3), hybrids that had high levels of partial resistance and had less severe infections as seedlings did not show as rapid a rate of increase in resistance over time as susceptible hybrids.

The mechanisms of the adult plant resistant reaction are not well understood. Morphological characteristics of hosts that have been suggested as physical barriers to fungal ingress include thickening of the epidermis (9), thick-walled sclerenchyma tissue (9), a heavy cuticle layer (3), lack of epicuticular wax (26), epidermal hairs (3,14), and stomatal exclusion (23). Physiological studies have shown the adult plant reaction in wheat to *P. striiformis* results from hypersensitive host cell necrosis for which the causal metabolites are unknown (16). The disruption of host cells may release toxins that inhibit fungal growth in resistant leaves (17). The failure of germ tubes to perceive or interpret stomatal stimuli also may contribute to resistance (26).

The effect of gross morphology of the host on microenvironment also may be a factor in the adult plant resistant reaction. Before tasseling, leaf whorls provide a moist, protected environment conducive to urediniospore germination and infection. After tasseling, whorls are not present and urediniospores are exposed to desiccation and ultraviolet radiation, which could reduce viability.

Partial resistance and the adult plant resistant reaction can be important control measures in the management of common rust on sweet corn. Partial resistance reduces the efficiency of the pathogen throughout the life of the host, thereby retarding epidemic development. The adult plant resistant reaction reduces the efficiency of the pathogen during the reproductive growth stages of the host, thereby usually negating the need for late-season fungicide application even for highly susceptible genotypes. Concurrent studies of rust yield loss, environmental effects on rust infection, and spread of rust in susceptible and partially resistant sweet corn hybrids may provide the basis for a model to forecast rust occurrence and yield loss potential.

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