Spatial and Temporal Development of Common Rust in Susceptible and Partially Resistant Sweet Corn Hybrids

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ABSTRACT

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The spatial and temporal development of common maize rust (*Puccinia sorghi*) was studied in isolated field plots of sweet corn hybrids Florida Staysweet (susceptible) and Sugar Loaf (partially resistant) at Urbana, IL, in 1984 and 1985. A single plant at the eight-leaf stage was inoculated in each plot to serve as an infection focus. Selected plants were evaluated for incidence and severity two times per week from the first observation of uredinia at the foci until fresh market harvest. Incidence was measured as the proportion of diseased leaves per plant. Severity was measured as the percentage of the total plant leaf area infected. Three-dimensional response surfaces of rust incidence or severity in time and by distance were plotted. Average epidemic rates and gradients also were calculated. The Gompertz model (gompit transformation) gave the best statistical fit of the regression of incidence and severity on time and $\log_{10}$ (distance), respectively. Average epidemic rates (k) obtained from the regression of gompit(incidence) and gompit(severity) on time provided a good method of comparing the partial resistance of the hybrids and was consistent over years. The regression coefficient of gompit(incidence) and gompit(severity) on $\log_{10}$ (distance) (i.e., the gradient, b) was not a consistent method of comparing partial resistance. The use of infection rates in conjunction with response surfaces appeared to offer the best method of comparing partial resistance of cultivars based on disease progress and spread. In both years, some leaves of Sugar Loaf were rust free at all distances from the focus, and rust severity was below levels that would be expected to result in substantial yield loss. All leaves of Florida Staysweet were infected by 33 and 36 days after inoculation in 1984 and 1985, respectively.

Common maize rust, caused by *Puccinia sorghi* Schwein., is an economically important disease of sweet corn (*Zea mays* L.) in the midwestern United States. Common rust is most severe during cool, wet seasons and may reduce yields up to 50% in the most susceptible sweet corn hybrids (7). Most commercial sweet corn hybrids do not possess race-specific resistance to common rust. The level of generalized or partial resistance varies considerably among hybrids (6,8,19). The effect of partial resistance on the development and spread of common rust has not been reported. The characterization of disease progress and spread in partially resistant and susceptible sweet corn hybrids can be helpful in hybrid selection and determination of necessity of fungicide application.

The primary analytical method of polycyclic disease progress has been the logistic model described by Vanderplank (22). Other equations have estimated the rate of epidemic development better than the logistic for asymmetrical disease progress curves (1,15) and for disease progress curves with asymptotes of less than 1 (17). Disease gradients often have been analyzed using Gregory's log transformation (5). Gregory's model has been modified to allow for finite y-intercepts (11,16) and gradient curves with variable shapes (12).

Previous investigations have used disease gradients in an attempt to differentiate resistance levels of pure cultivars and/or mixtures of cultivars (2,4,10,11,13,14). MacKenzie (14) was unable to differentiate between susceptible and slow-rusting wheat cultivars using gradients and suggested that infection rates also be calculated. Berger and Luke (2) and Luke and Berger (13) also regarded the use of disease gradients alone as an unreliable method of discerning cultivar resistance. They proposed the use of isopathic rates (spread per unit of time) in conjunction with infection rates, r and k, calculated from the logistic and Gompertz models, respectively. Jeger (9) and Jeger et al (10) developed two-dimensional models to calculate the rate of isopathic movement of *Septoria nodorum* Berk. Differential equations from models describing disease progress (22) and spread (5,11) were combined in pairs based on the characters of the pathosystem. Danos et al (3) used response surfaces obtained from gompit-transformed disease incidence to measure the spread of citrus canker.

The objective of this study was to compare spatial and temporal development of common rust in two sweet corn hybrids differing in partial resistance.

MATERIALS AND METHODS

The experiment was planted on 2 June 1984 and 9 May 1985 at the Pomology Research Farm, Urbana, IL, in a field that was isolated from corn by at least 1 km in all directions. The experimental design was a split-plot of a randomized complete block with a two by two factorial treatment design. Main plots were irrigation treatments. Irrigated plots were watered by overhead sprinklers for 10–15 min two to three evenings per week to provide for or lengthen dew periods. Nonirrigated plots were not watered. Subplots were hybrids. Florida Staysweet is susceptible to common rust. Sugar Loaf is partially resistant to common rust and exhibits a reduced number of uredinia per leaf at all growth stages compared to Florida Staysweet (8,19). Each subplot was 134 m^2, with 16 rows that were 0.76 m wide and 11 m long. Subplots were separated by at least 8 m of dent corn in an effort to reduce interplot interference. All subplots were thinned 3 wk after emergence to a population of 54,000 plants per hectare. There were two replicates of the main plot treatments.

A single plant at the eight-leaf stage in the southwest (windward) corner in each subplot was inoculated to serve as an infection focus. Each inoculated plant was injected at the base of the whorl with 5 ml of a suspension of 16 mg of urediniospores of *P. sorghi*, 100 ml of water and 0.5 ml of Tween 80 (ICN Nutritional Biochemicals, Cleveland, OH). An additional 5 ml of the suspension was poured into the whorl. The urediniospores represented a mixture of isolates of *P. sorghi* collected at several locations in Illinois. Inoculations were made on 4 July 1984 and 15 June 1985. All inoculations were done at dusk to prevent rapid evaporation and aid in urediniospore germination.

Within each subplot, diagonal lines were marked from the focus at 0, 22.5, 45, 67.5, and 90°. Arcs were measured at 0.8, 2.3, 4.6, 6.9, and 9.2 m from the focus (Fig. 1). At the points at which diagonals and arcs intersected, a single plant was tagged for evaluation throughout the season. Thus, there were 22 single plant subsamples per subplot, five at each distance from the focus, except for 0.8 m for which there were two. At maturity there was an average of about 12 leaves per plant, so that approximately 264 leaves per subplot were evaluated. Therefore, in the eight subplots, a total of more than 2,000 leaves on 176 plants were evaluated at each observation date. Tagged plants were evaluated for incidence and severity two times per week from the first observation of uredinia at the foci until fresh market harvest. Incidence was measured as the proportion of infected leaves per plant (21). Severity was measured as the percentage of the total leaf area infected using Peterson's scale (20).

Urediniospores were collected two times per week in each subplot at a point 4.6 m from the infection focus using Rotorod Samplers with U-shaped brass rods (Model 82, Ted Brown Associates, Los Altos Hills, CA). The forward-facing surface of each rod was covered with double-stick tape to provide a collection surface. Samplers were operated for 30 min between 1000 and 1200 hours at the top of the plant canopy. After collection, the tape was removed from the rods and applied to microscope slides for examination at 100×.

Meteorological data obtained from the Illinois State Water Survey, Champaign, IL, were collected at a weather station about 3 km from the location of the experiment. Hygrothermographs (Serdex, Bacharach Instrument Co., Santa Clara, CA) were operated in the plots.

Data were analyzed by analysis of covariance with hybrids and irrigation treatments as qualitative independent variables and distance from the focus and days after inoculation as quantitative independent variables. Rust incidence and severity were plotted as response surfaces over time and distance by hybrid and year to illustrate epidemic development. Data were fit to least-squares linear regression models. Polynomial terms were included in the model based on *F*-statistics ($P < 0.01$) and sums of squares.

Disease progress and spread also were analyzed by ordinary least-squares regression in two dimensions (by time and distance, respectively) to estimate epidemic rates and gradients. The data were transformed by several growth functions in an effort to provide a common dependent variable in both dimensions. The advantage of using a dependent variable common to both progress and spread is to give a complete account of an epidemic (9). Rust incidence and severity were regressed on time without transformation and after logarithmic ($X = \ln(x)$) (22), logistic ($X = \ln(x/1 - x)$) (22) and Gompertz ($X = -\ln(-\ln(x))$) (1) transformations. Rust incidence and severity were regressed on distance without transformation. Also, incidence and severity were transformed by the natural logarithm and regressed on distance (11) and ln(distance) (5) and by the Gompertz expression and regressed on distance and $\log_{10}$ (distance) (3). Epidemic rates and gradients (slopes) for the two hybrids were analyzed for homogeneity. Infection foci were not included in the regression of incidence and severity on distance. Fifteen days (two latent periods) were subtracted from the number of days after inoculation, so that the first observation of uredinia on plants beyond the focus was assigned time 0. *F*-statistics were examined to compare the significance ($P < 0.05$) of models and polynomial terms. Coefficients of determination (r^2) estimated the proportion of variation in disease explained by each model. Residuals were analyzed for homogeneity.

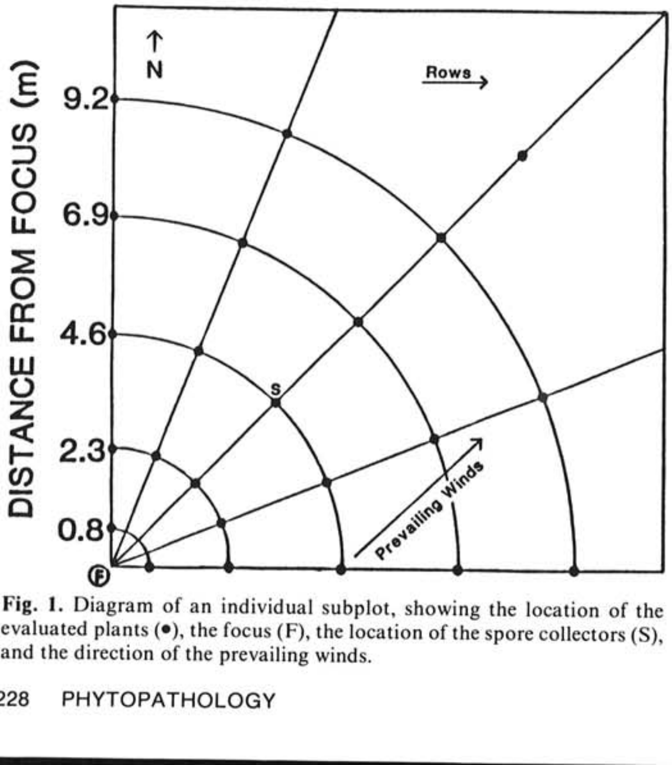

Fig. 1. Diagram of an individual subplot, showing the location of the evaluated plants (●), the focus (F), the location of the spore collectors (S), and the direction of the prevailing winds.

RESULTS

In both years, irrigation did not significantly ($P < 0.05$) affect rust incidence or severity on either hybrid. Thus, main effects of irrigation treatments were combined to compare hybrid effects. There was a significant interaction between hybrids and time and distance for both incidence and severity in each year.

Seasonal comparison. The 1985 growing season was more conducive to rust development and spread than 1984. From inoculation to harvest maturity in 1984, daily mean temperatures averaged 0.4 C below the seasonal mean and total precipitation was 3.8 mm above the seasonal mean. In 1985, daily mean temperatures averaged 1.3 C below the seasonal mean and total precipitation was 32.5 mm above the seasonal mean. Rust incidence on the susceptible hybrid Florida Staysweet was 100% at all distances at 36 days after inoculation in 1984 and 33 days after inoculation in 1985 (Fig. 2A and B). Rust incidence on the partially resistant hybrid Sugar Loaf was 29 and 83% at 9.2 m and 94 and 97% at 0.8 m from the infection focus at harvest maturity in 1984 and 1985, respectively (Fig. 3A and B). Rust severity ranged from 5 to 40% and 24 to 49% on Florida Staysweet at harvest maturity in 1984 and 1985, respectively (Fig. 4A and B), and from 1 to 4% and 3 to 5% on Sugar Loaf, respectively (Fig. 5A and B).

Hybrid comparison using response surfaces. The response surfaces of untransformed rust incidence on Florida Staysweet by distance and time were similar in both years (Table 1, Fig. 2A and B). At all distances beyond the focus, incidence increased very rapidly from 15 to 36 days after inoculation. Incidence was 100% at all distances by 36 days. The Florida Staysweet incidence gradients exhibited hollow curves at the earliest evaluations and flattened with time.

Rust incidence on Sugar Loaf was greater in 1985 than 1984 (Fig. 3A and B). The effect of the focus (i.e., the primary gradient) was always evident in the Sugar Loaf incidence gradients, although the curves began to flatten with time in 1985 as incidence approached 100% at the distance furthest from the focus (Fig. 3B).

There was little increase in severity away from the foci for either hybrid in 1984. Rust severity at the foci in both hybrids was not as great in 1985 as in 1984; however, spread from the focus was more evident in 1985. Severity gradients flattened with time (Figs. 4B and 5B). Rust severity at the foci in Sugar Loaf decreased over time after initially high values resulting from inoculation (Fig. 5A and B).

Transformation. The Gompertz transformation (gompit) gave the best statistical fit of incidence and severity on time and $\log_{10}$ (distance). Rust incidence by distance for a given time and severity in time for a given distance were explained equally well without transformation. However, untransformed incidence in time and severity by distance could not be fit by least-squares linear models.

Thus, the transformations were used to provide a common dependent variable in both dimensions. Coefficients of determination for the logistic model were approximately equal to those for the Gompertz model; however, analysis of residuals indicated a better fit with the Gompertz model.

Comparison of disease progress using the Gompertz model. The average epidemic rate, k, was always greater for Florida Staysweet than Sugar Loaf for both gompit(incidence) and gompit(severity) except for severity at the greatest distance from the focus in 1984 (Table 2, Figs. 2C and D and 5C and D). When gompit(incidence) was regressed on time at a particular distance, k ranged from 0.35 to 0.41 for Florida Staysweet (Fig. 2C and D). Distance from the focus did not affect k for Florida Staysweet. When gompit(incidence) was regressed on time, k ranged from 0.05 to 0.18 for Sugar Loaf (Fig. 3C and D). In both years, k values for Sugar Loaf were greatest near the focus.

When gompit(severity) was regressed on time, k ranged from 0.02 to 0.06 for Florida Staysweet (Fig. 4C and D), and from 0.0090 to 0.019 for Sugar Loaf (Fig. 5C and D). In 1984, k values for both hybrids were highest near the focus. In 1985, k values were not affected by distance from the focus.

For both Florida Staysweet and Sugar Loaf, k values for both gompit(incidence) and gompit(severity) were comparable for the different environments of the 2 yr. Gompit-transformed disease progress provided a good approximation of actual disease progress.

Comparison of disease gradients using the Gompertz model. The relationship of rust incidence and severity to distance was not always linearized by the gompit and $\log_{10}$ transformations. In several cases, the regression of gompit(incidence) and gompit(severity) on $\log_{10}$ (distance) was described best by a quadratic model (Table 3). The quadratic response did not allow direct comparison of all gradients by b values (slopes) but did not preclude comparisons based on the examination of gradients in time. The gradients of gompit(incidence) by $\log_{10}$ (distance) were steeper for Florida Staysweet than for Sugar Loaf early in both seasons (Figs. 2E and F and 3E and F). The gradients for Florida Staysweet flattened rapidly beyond 30 days after inoculation because of secondary spread. Slopes were not significantly different from 0 by 36 days after inoculation (Figs. 2E and F). The gradients for Sugar Loaf became steeper in time. In both years, the gradients up to 36 days after inoculation in Sugar Loaf were linear. At 48 days, the gradients were curvilinear because of large increases in incidence near the foci (Fig. 3E and F).

In a limited number of cases, the gradients of gompit(incidence) by $\log_{10}$ (distance) did not correspond well with gradients of untransformed incidence by distance. For example, gompit (incidence) by $\log_{10}$ (distance) for Sugar Loaf in 1985 at 48 days after inoculation was described by a quadratic function that was a steeper gradient than at earlier rating dates (Fig. 3F). The gradient of untransformed incidence by distance at 48 days after inoculation was considerably flatter and was a much flatter gradient than those observed earlier in the season (Fig. 3B). The discrepancy between the transformed and untransformed gradients was due to the rapid increase in gompit transformed values of X as incidence approached 100%.

The gradients of gompit(severity) by $\log_{10}$ (distance) were always steeper for Florida Staysweet than for Sugar Loaf. The gradients for Florida Staysweet in 1984 became steeper in time (Fig. 4E). The increase in severity in time at 0.8 m from the focus was larger than

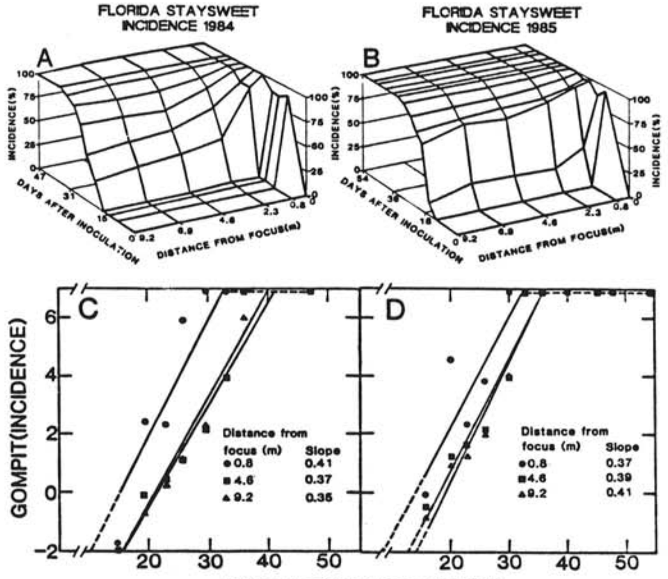

Fig. 2. Development and spread of common rust (*Puccinia sorghi*) on Florida Staysweet sweet corn in 1984 and 1985. Incidence of rust in time and by distance, **A,** 1984 and **B,** 1985. Gompit transformed rust incidence in time, **C,** 1984 and **D,** 1985. Gompit transformed rust incidence by $\log_{10}$ (distance), **E,** 1984 and **F,** 1985.

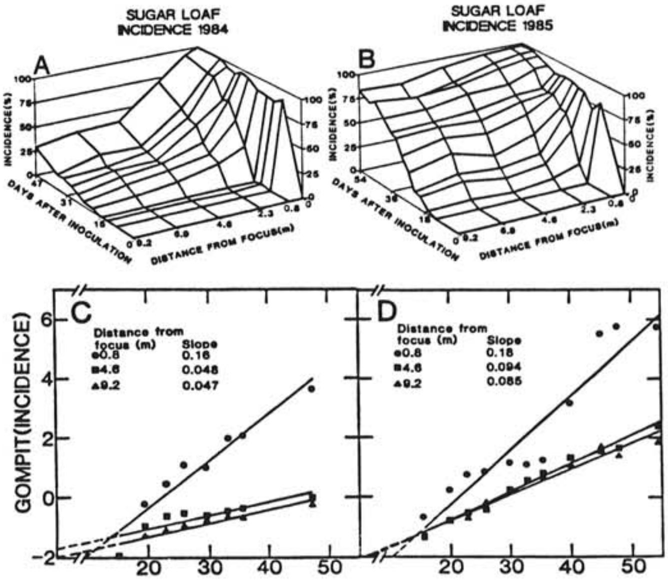

Fig. 3. Development and spread of common rust (*Puccinia sorghi*) on Sugar Loaf sweet corn in 1984 and 1985. Incidence of rust in time and by distance, **A,** 1984 and **B,** 1985. Gompit transformed rust incidence in time, **C,** 1984 and **2,** 1985. Gompit transformed rust incidence by $\log_{10}$ (distance), **E,** 1984 and **F,** 1985.

at further distances, resulting in a quadratic relationship of gompit(severity) on $\log_{10}$ (distance) late in the season (Fig. 4A and E). The gradients for Sugar Loaf in 1984 became slightly steeper in time (Fig. 5E). Severity did not increase appreciably beyond 0.8 m from the focus. For both Florida Staysweet and Sugar Loaf in 1985, there was little change in the gradients in time. Rust severity increased in time at all distances on Florida Staysweet (Fig. 4F). There was very little increase in severity over time at any distance on Sugar Loaf (Fig. 5F).

Spore collection. The number of urediniospores collected per 3,600 L of air in Florida Staysweet was much greater than the number collected in Sugar Loaf (Fig. 6). The differences in the number of spores collected between the two hybrids generally became greater in time. An effect of temperature or precipitation on the number of spores collected was not discernible.

DISCUSSION

The partial resistance of Sugar Loaf limited common rust progress and spread. In both years, some leaves of Sugar Loaf were

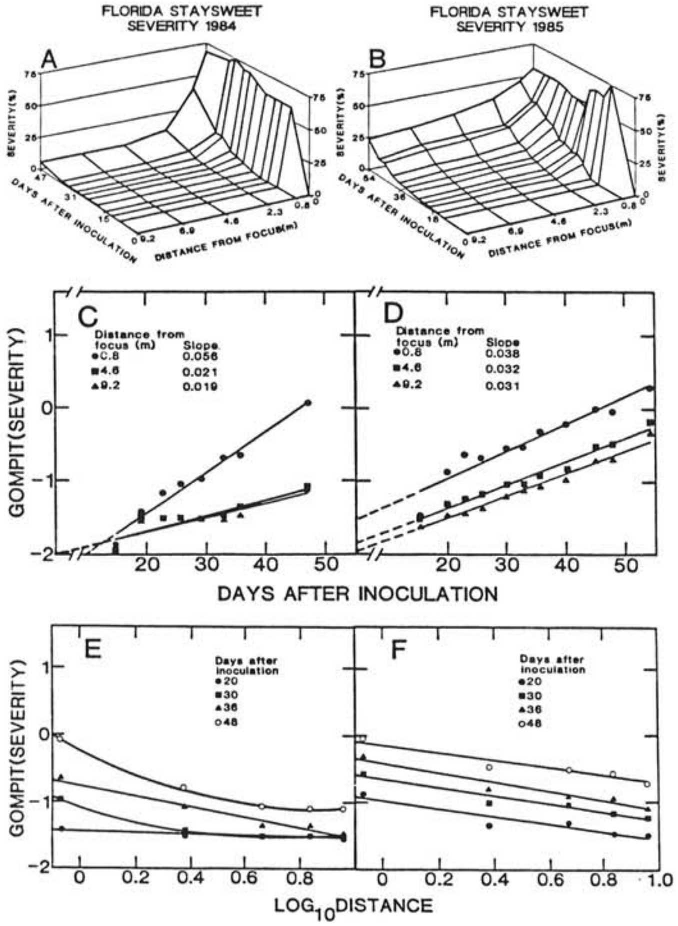

Fig. 4. Development and spread of common rust (*Puccinia sorghi*) on Florida Staysweet sweet corn in 1984 and 1985. Severity of rust in time and by distance, **A,** 1984 and **B,** 1985. Gompit transformed rust severity in time, **C,** 1984 and **D,** 1985. Gompit transformed rust severity by $\log_{10}$ (distance), **E,** 1984 and **F,** 1985.

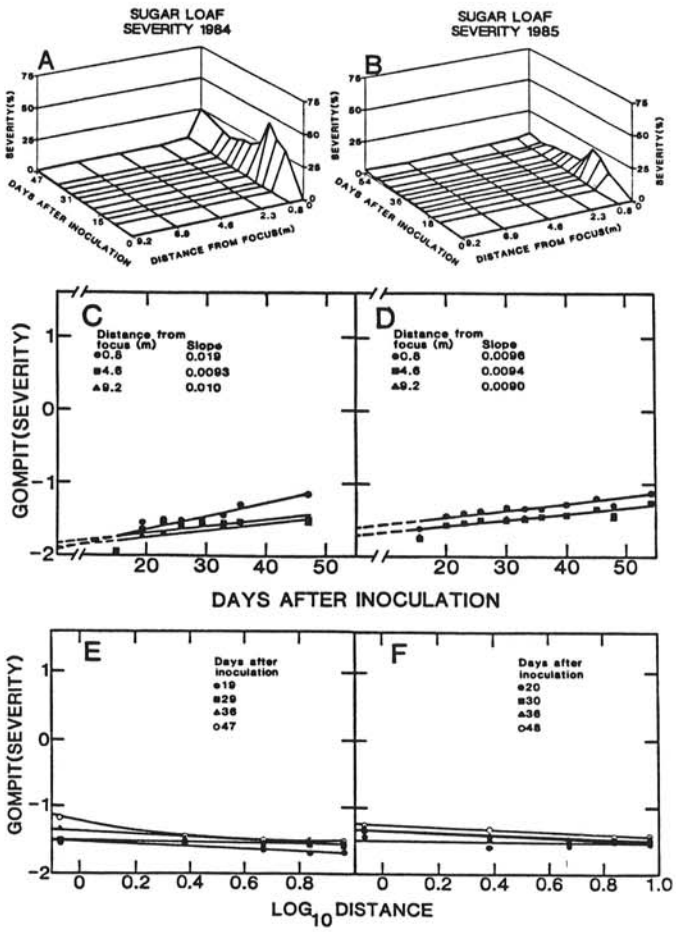

Fig. 5. Development and spread of common rust (*Puccinia sorghi*) on Sugar Loaf sweet corn in 1984 and 1985. Severity of rust in time and by distance, **A,** 1984 and **B,** 1985. Gompit transformed rust severity in time, **C,** 1984 and **D,** 1985. Gompit transformed rust severity by $\log_{10}$ (distance), **E,** 1984 and **F,** 1985.

TABLE 1. Multiple regression models describing common rust progress and spread on sweet corn hybrids Florida Staysweet and Sugar Loaf at Urbana, IL, in 1984 and 1985

Hybrid[a]	Year	Dependent variable[b]	Model[c]	R^2[d]
FSS	1984	INC	$Y = 89.9 - 29.7D + 3.1D^2 - 0.016D^3 + 15.8T - 0.27T^2 + 0.016DT^2 - 0.0059TD^3$	0.89
FSS	1985	INC	$Y = 142.4 - 32.1D + 2.0D^2 - 0.051D^3 + 58.7T - 2.1T^2 + 0.024T^3 + 1.2DT - 0.015DT^2 - 0.0028TD^3$	0.89
SL	1984	INC	$Y = 65.8 - 46.8D + 12.3D^2 - 0.75D^3 + 6.2T - 0.079T^2 + 0.012DT^2 - 0.22TD^2 + 0.015TD^3$	0.88
SL	1985	INC	$Y = 52.8 - 29.6D + 3.2D^2 - 0.088D^3 + 4.2T - 0.043T^2 + 0.32DT - 0.0026TD^3$	0.89
FSS	1984	SEV	$Y = 51.1 - 43.4D + 9.0D^2 - 0.54D^3 + 0.011T + 0.0059T^2$	0.79
FSS	1985	SEV	$Y = 43.4 - 29.2D + 5.8D^2 - 0.35D^3 + 0.14T - 0.0076T^2 + 0.00026T^3$	0.82
SL	1984	SEV	$Y = 19.9 - 15.2D + 3.2D^2 - 0.20D^3 - 0.74T + 0.011T^2$	0.59
SL	1985	SEV	$Y = 11.3 - 6.2D + 1.2D^2 - 0.072D^3 - 0.27T + 0.0025T^2 + 0.00031DT^2$	0.51

[a] FSS = Florida Staysweet, SL = Sugar Loaf.

[b] INC = Incidence, measured as the proportion of diseased leaves per plant; SEV = severity, measured as the percentage of the total loaf area infected.

[c] Model and polynomial terms significant at $P < 0.01$; D = distance from the focus in meters, T = time ($X - 15$), days after inoculation minus two latent periods.

[d] Coefficient of multiple determination.

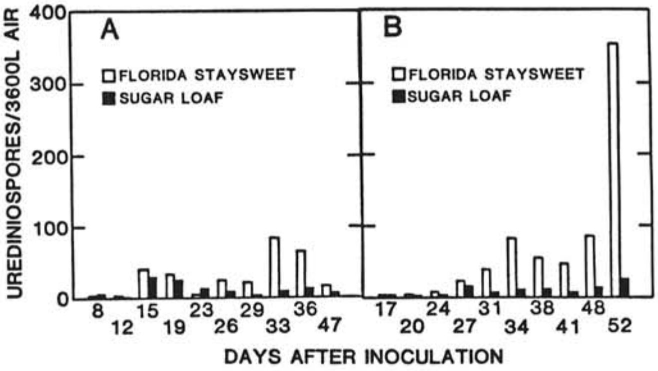

Fig. 6. Number of urediniospores per 3,600 L of air in Florida Staysweet and Sugar Loaf subplots in **A,** 1984 and **B,** 1985.

rust free at all distances from the focus, and rust severity was below levels that would be expected to result in substantial yield loss (7,18). Severity decreased in time at the Sugar Loaf foci as sporulation ceased in uredinia that had resulted from inoculation, and very little autoinfection occurred. On the Florida Staysweet focus plants, the level of autoinfection was sufficient to result in a relatively constant severity over a number of infection cycles.

Differences in progress and spread caused by partial resistance are important with respect to yield loss. For fresh market sweet corn hybrids (e.g., Florida Staysweet and Sugar Loaf), Pataky (18) determined the best estimate of yield reduction due to rust to be approximately 6.5% for each 10% of rust severity measured 1 wk before harvest. In 1985, rust severity on Florida Staysweet 1 wk before harvest at 0.8 m from the focus was 35% and at 9.2 m from the focus was 13%, which would be expected to result in yield reductions of approximately 23 and 9%, respectively. In 1985, rust

TABLE 2. Least squares linear regression equations describing common rust progress on sweet corn hybrids Florida Staysweet and Sugar Loaf at Urbana, IL, in 1984 and 1985[a]

Hybrid[b]	Year	Distance from focus (m)	Incidence[c]	r^{2}[d]	Severity[e]	r^2
FSS	1984	0.8	$Y = -0.17 + 0.41(X - 15)$*[f]	0.84	$Y = -1.72 + 0.056(X - 15)$*[f]	0.98
		4.6	$Y = -2.24 + 0.37(X - 15)$*	0.92	$Y = -1.77 + 0.021(X - 15)$*	0.81
		9.2	$Y = -2.20 + 0.35(X - 15)$*	0.96	$Y = -1.76 + 0.019(X - 15)$*	0.76
FSS	1985	0.8	$Y = 0.49 + 0.37(X - 15)$*	0.77	$Y = -1.17 + 0.038(X - 15)$*	0.91
		4.6	$Y = -1.14 + 0.39(X - 15)$*	0.91	$Y = -1.54 + 0.032\ (X - 15)$*	0.98
		9.2	$Y = -1.61 + 0.41(X - 15)$*	0.92	$Y = -1.69 + 0.031(X - 15)$*	0.98
SL	1984	0.8	$Y = -1.10 + 0.16(X - 15)$	0.93	$Y = -1.75 + 0.019(X - 15)$	0.80
		4.6	$Y = -1.30 + 0.048(X - 15)$	0.71	$Y = -1.73 + 0.0093(X - 15)$	0.48
		9.2	$Y = -1.57 + 0.047(X - 15)$	0.87	$Y = -1.79 + 0.010(X - 15)$	0.66
SL	1985	0.8	$Y = -1.19 + 0.18(Y - 15)$	0.89	$Y = -1.53 + 0.0096(X - 15)$	0.82
		4.6	$Y = -1.23 + 0.094(X - 15)$	0.99	$Y = -1.66 + 0.0094(X - 15)$	0.84
		9.2	$Y = -1.18 + 0.085(X - 15)$	0.96	$Y = -1.66 + 0.0090(X - 15)$	0.85

[a] Gompit-transformed incidence and severity regressed on time. Time $= X - 15$, days after inoculation minus two latent periods.

[b] FSS = Florida Staysweet, SL = Sugar Loaf.

[c] Measured as the proportion of diseased leaves per plant. Model and polynomial terms significant at $P < 0.05$.

[d] Coefficient of simple determination.

[e] Measured as the percentage of the total leaf area infected. Model and polynomial terms significant at $P < 0.05$.

[f] * = Slope significantly different from Sugar Loaf in the same year at the same distance from the focus.

TABLE 3. Least squares linear regression equations describing common rust spread on sweet corn hybrids Florida Staysweet and Sugar Loaf at Urbana, IL, in 1984 and 1985[a]

Hybrid[b]	Year	Days after inoculation	Incidence[c]	r^{2}[d]	Severity[e]	r^2
FSS	1984	19	$Y = 1.75 - 5.18X + 3.26X^2$	0.98	$Y = -1.45 - 0.094X$	0.79
		29	$Y = 5.55 - 10.25X + 7.19X^2$	0.99	$Y = -1.11 - 1.07X + 0.70X^2$	0.99
		36	NS		$Y = -0.79 - 0.73X$*[f]	0.96
		47	NS		$Y = -0.18 - 2.15X + 1.26X^2$	0.99
FSS	1985	20	$Y = 3.72 - 3.18X$	0.86	$Y = -1.00 - 0.54X$	0.87
		30	$Y = 6.13 - 6.07X + 3.87X^2$	0.99	$Y = -0.69 - 0.58X$*	0.94
		36	NS		$Y = -0.46 - 0.65X$*	0.95
		48	NS		$Y = -0.16 - 0.54X$*	0.92
SL	1984	19	$Y = -0.22 - 1.03X$	0.99	$Y = -1.54 - 0.16X$	0.87
		29	$Y = 0.80 - 1.69X$	0.96	$Y = -1.51 - 0.065X$	0.81
		36	$Y = 1.66 - 2.56X$	0.96	$Y = -1.37 - 0.22X$	0.89
		47	$Y = 2.92 - 5.90X + 2.72X^2$	0.99	$Y = -1.25 - 0.61X + 0.34X^2$	0.99
SL	1985	20	NS		NS	
		30	$Y = 0.99 - 0.88X$	0.92	$Y = -1.37 - 0.16X$	0.82
		36	$Y = 1.20 - 0.55X$	0.96	$Y = -1.38 - 0.12X$	0.87
		48	$Y = 4.83 - 7.32X + 3.75X^2$	0.99	$Y = -1.30 - 0.16X$	0.92

[a] Gompit-transformed incidence and severity regressed on $\log_{10}$ distance from focus.

[b] FSS = Florida Staysweet, SL = Sugar Loaf.

[c] Measured as the proportion of diseased leaves per plant. Model and polynomial terms significant at $P < 0.05$. NS = Not significant.

[d] Coefficient of simple determination.

[e] Measured as the percentage of the total plant leaf area infected. Model and polynomial terms significant at $P < 0.05$. NS = Not significant.

[f] Slope significantly different from Sugar Loaf in the same year at the same number of days after inoculation.

severity on Sugar Loaf 1 wk before harvest at 0.8 m from the focus was 3% and at 9.2 m was 1%, which would be expected to result in yield reductions of approximately 2% or less.

The use of three-dimensional response surfaces of disease proportion by distance and time appeared to be an effective method of comparing the partial resistance of sweet corn hybrids to common rust. The disease severity, rates of progress, and gradients could easily be examined when untransformed disease proportion was used as the dependent variable. Characteristics of particular hybrids or experiments also could be discerned, such as the decrease in rust severity in time at the foci in Sugar Loaf. Gregory (5) and Jeger et al (10) also considered the untransformed plot to give the best measure of a gradient. The disadvantage of using untransformed data as a response surface is that the epidemic rate (k) and gradient (b) are not linear, thus the regression coefficients cannot be used to compare epidemics. One must therefore decide between using actual data that allow the derivation of an empirical model in time and space or transformations that provide a method of direct mathematical comparison of epidemic rates and gradients in two dimensions but may not allow for desired statistical and biological interpretations. Jeger (9), Jeger et al (10), Berger and Luke (2), and Danos et al (3) have proposed the use of three-dimensional models of disease development in time and space, and have used transformations to fit biological models that allow calculation of epidemic rates and disease gradients. The problem encountered in previous studies and in the present study is finding a transformed dependent variable that fits both disease progress and spread and, thus, gives a complete account of an epidemic (2,9,10).

In the present study, the Gompertz model of disease provided the best-fitting dependent variable common to both independent variables, time and $\log_{10}$ (distance). The logistic model often overestimated disease early and late in disease progress (data not presented), as was observed by Berger (1). The Gompertz model may be more appropriate for common rust of sweet corn than the logistic model because of adult plant resistance. The logistic model assumes that all infection sites are equally susceptible; however, for common rust of sweet corn, infection sites become less susceptible as plants mature. Headrick and Pataky (8) demonstrated that sweet corn hybrid resistance to rust increases with plant age. Thus, rust progress is likely to be less rapid late in the epidemic when plants are at reproductive growth stages. Possibly, the Gompertz model is more appropriate for diseases in which infection sites become less susceptible with age.

In general, k values obtained from the linear regression of gompit(incidence) and gompit(severity) on time provided a good method of comparing the partial resistance of the hybrids to common rust and were consistent for hybrids over years. The results from the present study and previous investigations indicate that epidemic rates and partial resistance levels are negatively correlated (2,13,14,22).

In the present study, k values were always less for Sugar Loaf than for Florida Staysweet. High k values at distances near the foci and lower k values at distances further from the foci for Sugar Loaf indicated that the increase in rust incidence on the partially resistant hybrid was primarily due to alloinfection. In Florida Staysweet, k values were about equal at all distances. This suggests that after initial alloinfection associated with the primary gradient, the increase in incidence on the susceptible hybrid was primarily caused by autoinfection. Although the same relationship between the hybrids and alloinfection and autoinfection was assumed for rust severity, k values for rust severity were higher near the foci for Florida Staysweet in 1984. This did not necessarily imply that autoinfection was not important in the increase in severity on Florida Staysweet in 1984. Rather, the level of autoinfection was higher near the focus than at greater distances because of a higher initial spore concentration. In 1985, k values for Florida Staysweet were not affected by distance from the focus, due to a more rapid spread of rust under more favorable environmental conditions.

There were large differences between epidemic rates based on incidence and those based on severity for both hybrids. The differences between epidemic rates for incidence and severity are a function of the assessments themselves. A single new infection can increase the percentage of infected leaves on a plant (incidence), but many new infections are necessary to increase the percentage of leaf area infected (severity).

The gradient (b), the linear regression coefficient of gompit(incidence) or gompit(severity) regressed on $\log_{10}$ (distance), was not a good method of comparing partial resistance of the hybrids to common rust. The b values were not consistent for the hybrids in time. For example, b values were more negative (the gradient was steeper) for Florida Staysweet than Sugar Loaf for gompit(incidence) regressed on $\log_{10}$ (distance) early in the season, but steeper for Sugar Loaf late in the season. The b values also were inconsistent over years. Although the Gompertz model provided a common dependent variable regressed on time and distance, the results support the findings of MacKenzie (14), Berger and Luke (2), Luke and Berger (13), and Danos et al (3), who could not differentiate cultivar resistance based on disease gradients. The use of infection rates in conjunction with response surfaces and/or isopathic rates (2,13) appears to offer the best method of comparing partial resistance of cultivars based on disease progress and spread.

The problems encountered in using gradients to compare partial resistance illustrate the difficulty of determining a common dependent variable to describe both disease progress and spread. In this study, the Gompertz model adequately described disease progress and allowed for comparison of epidemic rates between hybrids but did not as accurately describe disease spread. The nonlinearity of the Gompertz model produced cases where the gradients were not comparable to those observed using untransformed data, thus resulting in different conclusions. Several of the gradients were not linearized by the gompit transformation. Gradients could be compared in such cases by observing hybrid responses in time; however, transformation offers little advantage over actual data in these instances.

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