Ecology and Epidemiology

Reduction in the Rate and Duration of Grain Growth in Wheat Due to Stem Rust and Leaf Rust

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A portion of the first author's Ph.D. dissertation submitted to The Pennsylvania State University.

Contribution 1777, Department of Plant Pathology, The Pennsylvania Agricultural Experiment Station.

This research was supported in part by the U.S. Department of Agriculture Grant 83-CRSR-2-2330 and the Pennsylvania Agriculture Experiment Station.

Accepted for publication 5 February 1991 (submitted for electronic processing).

ABSTRACT

McGrath, M. T., and Pennypacker, S. P. 1991. Reduction in the rate and duration of grain growth in wheat due to stem rust and leaf rust. Phytopathology 81:778-787.

Leaf and/or stem rust epidemics differing in date of disease onset after anthesis and area under the disease progress curve (AUDPC) were established at various distances from rows of inoculated winter wheat in two fields during each of the 1986 and 1987 growing seasons. Rate and duration of grain growth were reduced by rust. Piecewise linear regression proved to be useful for describing the nonlinear growth curves. Square root-transformed grain dry weight increased linearly at a similar rate (0.19–0.21 $mg^{1/2}$/day) at each of four field sites for at least the first 12 days from anthesis (DFA). Rust had a greater impact on grain growth in 1986, when stem rust occurred alone, than in 1987, when both leaf and stem rust were present. In 1986, growth rates were inversely related to disease severity in two fields and ranged from 0.04 to 0.20 and 0.06 to 0.21 $mg^{1/2}$/day between 15 and 22 DFA and 16 and 23 DFA, respectively, when wheat was in growth stage (GS) 11.1–11.2. Only the most severely infected wheat plants exhibited reduced growth (0.13–0.14 mg $^{1/2}$/day) during this period in 1987. Growth rates ranged from 0.00 to 0.16 $mg^{1/2}$/day between 23 and 27 DFA in 1987 when wheat was in GS 11.2–11.3. Grain growth had ceased by 23 DFA for plants with an AUDPC for rust on peduncles greater than about 640 percent-days in both years. Grain growth of plants with low disease severity ceased by 33–36 DFA in 1986 and by 27 DFA in 1987. The rate of grain growth over 5- to 7-day intervals was related to the concurrent average percent green leaf area of flag leaves throughout the grain-filling period. Grain number per head was not affected by rust infection. The amount of dry matter lost from culms during the grain-filling period was not related to disease severity; however, culm dry weight of the most severely rust-infected wheat in each field decreased more rapidly than the culm weight of the other epidemics.

Additional keywords: Puccinia graminis f. sp. *tritici, P. recondita* f. sp. *tritici, Triticum aestivum.*

Predicting the yield reduction in wheat caused by rust diseases has attracted the interest of many scientists. Wheat (primarily *Triticum aestivum* L. em. Tell.) is one of the most important food crops in the world, and the most destructive disease on wheat has been stem rust (synonyms black rust, black stem rust), which is caused by *Puccinia graminis* (Pers.) f. sp. *tritici* Eriks. & E. Henn. (17). Several empirical models have been proposed to describe the relationship between stem rust or leaf rust and yield reduction in wheat (6,7,13,28). Empirical models theoretically have limited predictive ability compared with mechanistic models because they lack the explanatory ability to handle the dynamic nature and complexity of the interacting environment, host, and pathogen (11,29). Mechanistic modeling of yield reduction due to disease involves coupling explanatory models of crop growth with models of pathogen population dynamics and disease progress, or incorporating the effects of a pathogen into a plant growth model (29).

Grain weight is the yield component affected by foliar fungal diseases such as stem rust that develop primarily during the grain-filling period. Reduced yield potential presumably is the result of these diseases reducing both the photosynthetic rate (12) and the leaf area remaining green during the grain-filling period (26). These changes adversely affect grain growth because, under most circumstances, carbon dioxide fixation after anthesis supplies 90–95% of the carbohydrate in grain (10). Green area duration in the period from heading to maturity is closely correlated to grain yield (35). Previous studies of foliar diseases have tended to focus on quantifying the relation between disease severity and grain weight at harvest. Mechanistic modeling of yield reduction requires information on the impact of disease on yield development. Low grain weight at crop maturity reflects a reduction in the rate of grain growth and/or the duration of the grain-filling period. Leaf rust was shown to reduce the rate of grain growth in a field study involving one disease intensity (23). The objectives of this study were to determine the effects of stem rust and leaf rust on rate and duration of grain growth, percent green area of flag leaves, and culm weight for several epidemics differing in disease intensity. Preliminary reports of this work have been published (19,20).

MATERIALS AND METHODS

Field design and agronomic practices. Field experiments were conducted on Hagerstown silt loam (fine, mixed, mesic Typic Hapludalf) soils at The Pennsylvania State University's Agricultural Research Center at Rock Springs, Centre County, PA (40° 42′ 53″ N, 77° 56′ 25″ W). Soft red winter wheat (*Triticum aestivum* L. em. Tell. 'Tyler'), a locally adapted cultivar susceptible to stem rust, was established and managed by using recommended agronomic practices (39). Two 0.4-hectare fields, previously planted to oats, were established during 1985–86 (fields 1 and 2) and during 1986–87 (fields 3 and 4). Seeds were planted (168 kg/ha) to a depth of about 4 cm on 19 September 1985 and 9 and 18 September 1986. The seed was fertilized (178.6 kg/ha) at the time of planting with 10-10-10 (N-P-K) and the plants were fertilized in April at growth stage (GS) 5 on the Feekes scale (15) with 133.9 kg of ammonium nitrate per hectare in 1986 and 160.7 kg/ha in 1987. The herbicide MCPA (Weedar, Union Carbide Agricultural Products Co., Ambler, PA) was applied at GS 4–5 at a rate of 0.58 L a.i./ha in both years.

A grain drill adjusted to plant 14 rows at a spacing of 17.8 cm was used to establish each field. The 14-row areas were separated by 0.5 m. Rows in fields 1–3 were oriented perpendicular to the prevailing wind direction. These fields were divided into eight strips oriented perpendicular to the rows and separated by 1.5 m wide alleyways. The center six strips in fields 1 and 2 were 6.1 m wide and the two peripheral strips were 3 m wide, whereas in field 3 all eight strips were 6.1 m wide. Rows in field 4 were oriented parallel to the prevailing wind and strips were 5.3 m wide. The alleyways were planted to winter barley (*Hordeum vulgare* L. 'Pennrad') in the fall. In the spring, the barley was treated with the herbicide glyphosate (Roundup, Monsanto Agricultural Co., St. Louis, MO) and then mowed periodically.

Powdery mildew (*Erysiphe graminis* f. sp. *tritici*) and leaf rust (*Puccinia recondita* f. sp. *tritici*) were controlled, before inoculating with *P. g. tritici*, by spraying 0.141 kg a.i./ha of triadimefon (Bayleton 50WP, Mobay Corporation, Kansas City, MO) and 1.807 kg a.i./ha mancozeb (Dithane M-45 80WP, Rohm and Haas Co., Philadelphia, PA) on 30 April 1986 and 26 April 1987. Triadimefon was applied a second time on 14 May 1987. Triadimefon applied at flowering has been shown to be ineffective against stem rust late in the season (16). The rows of wheat to be inoculated with *P. g. tritici* did not receive the second fungicide treatment because inoculation was scheduled to occur at that time. The two peripheral strips of each field were sprayed biweekly in 1986 and weekly in 1987 with mancozeb at a rate of 1.807 kg a.i./ha to maintain rust-free plants. These strips functioned as controls, and as a check for potential nonuniformity in soil conditions within the field, which would be a confounding factor. Fungicides were applied with a tractor-mounted, nitrogen-powered boom sprayer calibrated to deliver 280 L/ha of material at 0.12 MPa.

Method of inoculation. Plants in two 2.4-m-wide sections near the upwind end of each field were inoculated with urediniospores of race 56 of *P. g. tritici* (Cereals Rust Laboratory, St. Paul, MN) on 17 and 25 May 1986 and 16, 17, and 24 May 1987. These two line sources of inoculum (spreader rows) were separated by a 2.4-m width of uninoculated wheat. Urediniospores from greenhouse-grown plants were diluted 1:10 (w/w) with pharmaceutical-grade talc and applied at a rate of 247 g of spores per hectare with a hand-held duster. Inoculation was performed after dew had formed during a clear evening when the air was calm and the temperature was not expected to drop below 10 C. Plants were in the early boot growth stage (GS 10). Inoculations were repeated both years because the temperature was below 10 C during at least one of five nights afterwards. The inoculated rows also served as foci for leaf rust in 1987 due to natural infection by *P. r. tritici.*

Measurements of grain growth and disease severity. Disease severity, grain growth rate, and duration of grain fill were measured for plants in plots that were 14 rows (2.4 m) by 6.1 m in fields 1–3 and 2.4 m by 28 rows (5.3 m) in field 4. These plots were located various distances upwind and downwind from the inoculated plants. Plants located between the two spreader rows (epidemic 1) of each field were assessed at 5- to 7-day intervals. Other plots were located 8.5, 14.0, 22.5, and 42.5 or 48.0 m downwind (epidemics 2–5) from the plot between the two line sources of inoculum. Plots in three fields were located 8.5 m upwind (epidemic 6). Plots were not established upwind of the inoculum source in field 2 because soil conditions in this section of the field were less favorable for plant growth. Replicates or blocks were the four central strips of a field. Control plots were labeled epidemics 7 and 8.

Seven times during grain filling, at 5- to 7-day intervals, five to seven main culms per plot were randomly identified and cut at ground level. Culms and heads were separated while in the field, then stored in a cooler. Culm length was measured and leaf blades were removed. Only the lowest leaf sheath was removed from the culm. Heads and culms were dried at 50 C in a convection drying oven for at least 7 days and weighed to the nearest milligram immediately after they were removed from the oven. Grains were removed from the heads either by hand or with a single head thresher. Grains from each head were counted and weighed.

Percent green area was visually assessed on the flag leaf and on the penultimate leaf (the leaf below the flag leaf). A distinction was not made between chlorosis due to natural senescence, stem rust, and other pathogens. *Leptosphaeria nodorum* (anamorph: *Septoria nodorum*) and *E. g. tritici* were observed occasionally on penultimate leaves and rarely on flag leaves.

Stem and leaf rust uredinia were counted on all culms and on the living flag and penultimate leaves sampled from each plot, when severity was low. Counting was discontinued when the intensity exceeded about 250 uredinia per leaf or 1,500 per culm. Spores were examined periodically with a microscope to ensure that stem and leaf rust uredinia were being accurately distinguished (43). Stem rust severity assessments were made on the peduncle and on the flag leaf sheath with a modified Cobb scale (25). The "relative" severity (0–100%) scale was used. The cut culms from each sample area were examined as a group.

Area under the disease progress curve (AUDPC) for rust severity on peduncles was calculated by using the procedure of Shaner and Finney (31). Severity values for the early assessment dates were estimated by extrapolating from data on both uredinia per culm and rust severity obtained for several culms. The grain-filling period was approximately 35 days in both years, therefore AUDPC was calculated over the same number of days for each field.

Measurement of grain yield components. At physical maturity, 1-m row lengths of wheat were cut at ground level from the center rows of each plot that had been sampled for the grain growth study in fields 1–3. Field 4 was not harvested. Samples were dried at room temperature for at least 10 wk. Then they were weighed, culms and heads were counted, and seeds were removed with a small, hand-operated head thresher. Dry weight was determined for three groups of 50 seeds and the remaining seeds for each sample. Thousand kernel weight (TKW), seeds/head, and harvest index (HI) were calculated. HI is the weight of the harvested portion of a crop divided by the total weight of the crop that is aboveground. Number of seeds per square meter, heads per square meter, and culms per square meter were calculated for an average row width of 17.8 cm.

Data analysis. Culm weight, seed number, seed weight at the start of grain filling, and final yield were assessed with analysis of variance. A randomized complete block design with subsampling was used in these analyses. Variability among plots due to field position was assessed at the start of the grain-filling period before rust had developed. The fungicide-treated plots also were compared at the end of grain filling. The modified Ryan-Einot-Gabriel-Welsch multiple range test (8) was used for making multiple comparisons among means when a significant ($P < 0.05$) *F* test was obtained in the analysis of variance. A repeated measures model (24) was used to examine the effect of rust on grain number and culm dry weight for the entire grain-filling period.

Linear and polynomial regression were used to describe the relation between grain growth rate or seed weight and several measures of disease level, including rust severity and green leaf area for each field. Growth rates during each of four consecutive time periods in each field were determined with piecewise linear regression. These periods encompassed the time interval between successive harvests. Grain dry weights from each harvest date as well as average weights for pairs of successive dates also were used as dependent variables in this analysis. Independent variables selected for analysis were measurements of green leaf area of flag leaves and stem rust severity of peduncles made at the start and end of each of the consecutive time periods, measurements made on preceding and subsequent harvest dates, and average values for each time interval. Number of uredinia per flag leaf was not selected as an independent variable for this analysis because uredinia could not be counted accurately throughout the grain-filling period due to leaf senescence and high uredinium density. The analysis involved examining plots of these dependent and independent variables for data from each time period as well as for data from all time periods combined, then fitting regression lines when trends were observed. Plots of data, predicted values, and residuals; normality tests; significance levels of linear and quadratic regression coefficients; F tests; and coefficients of determination (adjusted R^2 values) were examined to determine the appropriateness of each model.

Piecewise linear regression was used to model the nonlinear grain growth curves (24). Models consisting of three or four pieces were fit to the grain growth data for each field. Indicator variables were used to construct these pieces. The resulting model is given by

$$Y_i = (\alpha_0 + \alpha_1 X_i)I_1 + (\beta_0 + \beta_1 X_i)I_2 + (\gamma_0 + \gamma_1 X_i)I_3 + e_i \quad (1)$$

where Y_i is grain dry weight; α_0, β_0, and γ_0 are the three Y intercepts; α_1, β_1, and γ_1 are the slopes of the three regression lines; and I_1, I_2, and I_3 are the indicator variables. The variance of seed weight increased with the mean. This nonconstant variance was most successfully stabilized with a square root transformation. The individual linear regression lines join at specific values of X_i, which is time from anthesis. Indicator variables also were used to fit the full or most general model, which consisted of separate equations for each replicate of each epidemic. Candidate dates for the two times the rate of grain growth changed during the season were selected through examination of plots of the raw data. The best-fitting dates were chosen based on the residual sum of squares of the candidate models. Reduced models with one or more common parameters for each epidemic or group of epidemics were developed from the full model. General linear F tests were used to compare models and identify the most parsimonious model, i.e., the most reduced model with the fewest parameters that is not statistically different from the full model.

The computer software packages SAS (30) and MINITAB (22) were used to perform the analyses.

RESULTS

Disease development in 1986. Inoculated plants became infected with *P. g. tritici* on 17 May 1986 because uredinia were observed in the spreader rows 10 days after this inoculation date, which is a typical incubation period for this pathogen. Anthesis occurred 11 and 12 days after wheat was inoculated in fields 2 and 1, respectively. The date that uredinia were first observed, or the date of disease onset, of epidemics 1–6 in fields 1 and 2 ranged from anthesis to 12 days from anthesis (DFA). Leaf rust was not detected in 1986.

Stem rust progressed very rapidly in fields 1 (Fig. 1) and 2. Green leaf area decreased rapidly between 16 and 26 DFA in field 1 (Fig. 2A) and field 2. Wheat was in GS 11.1 and 11.2, respectively, on these 2 days. Disease progress curves are similar for epidemics 3 and 6 in field 1 (Fig. 1), which were located 14.0 m downwind and 8.5 m upwind, respectively, from epidemic 1. Otherwise the order of epidemics with respect to uredinium counts and AUDPC values corresponds to the physical order of these epidemics in both field 1 and field 2. AUDPC values for percent severity on peduncles were 1,283.8, 1,021.8, 881.9, 632.6, 258.3, and 104.2 percent-days for epidemics 1, 2, 3, 4, 5, and 7 (fungicide treated), respectively, in field 2. Epidemics at the same location with respect to the spreader rows in each field had similar AUDPC values.

Disease development in 1987. Both leaf and stem rust occurred on wheat in 1987. Leaf blades were infected primarily by *P. r. tritici*, whereas culms and leaf sheaths were infected primarily

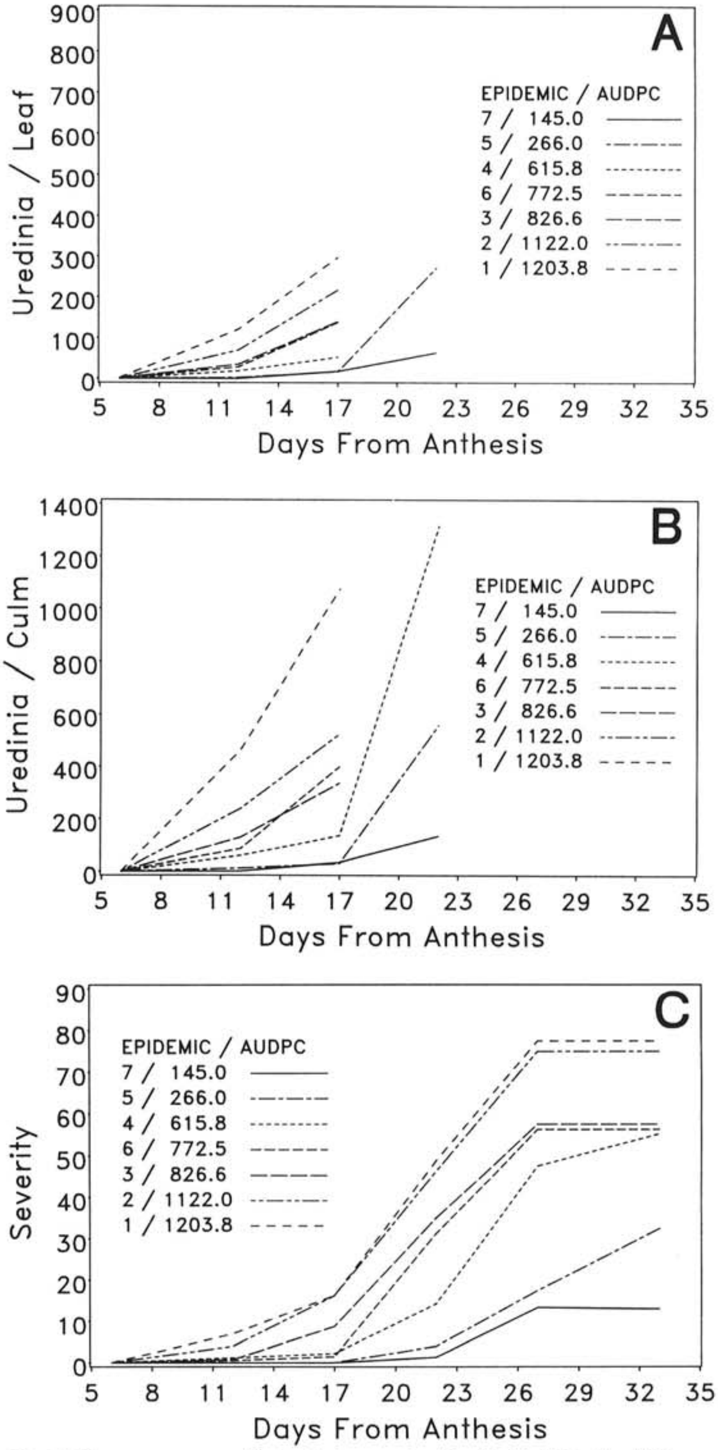

Fig. 1. Disease progress of wheat stem rust epidemics in field 1 in 1986. Dependent variables are: **A,** uredinia per leaf; **B,** uredinia per culm; and **C,** rust severity (%) on peduncles. Treatments are denoted by their epidemic number and area under disease progress curve value for rust severity on peduncles.

by *P. g. tritici*. Leaf rust uredinia were observed in mid-May on wheat in the spreader rows. Stem rust uredinia appeared on these plants on 26 May 1987, which was 10 days after the first artificial inoculation and 3 days before anthesis. Leaf rust was observed 1 and 2 DFA throughout fields 3 and 4, respectively. Stem rust was observed 6 DFA on wheat from epidemics 1 and 2 in field 3 and 7 DFA on wheat from epidemics 1, 2, 3, and 5 in Field 4. The number of leaf rust uredinia per flag leaf increased rapidly over time, particularly for epidemic 1 (Fig. 3A). Green leaf area began decreasing rapidly between 16 and 21 DFA in field 3 (Fig. 2B) and field 4. AUDPC values for percent severity on peduncles were 760.1, 596.2, 410.9, 178.8, 52.1, 359.8, and 20.0 percent-days for epidemics 1–7, respectively, in field 4. The shape of the disease progress curves for stem rust severity on peduncles beginning 16 and 18 DFA are quite similar for fields 3 and 4, although the onset of this phase differed by 2 days. The steepness of these curves is inversely related to distance from the source of inoculum (Fig. 3C).

Grain growth of wheat infected by stem and leaf rust fungi. Fungicide treatment reduced the rate of disease progress rather than excluding disease occurrence. The prevailing wind direction during June was from the south-southwest in 1986 (36) and the south-west in 1987 (37). As a result, rust was more severe and had an impact on grain growth in the fungicide-treated strip along the east side of each field. Therefore, only data from control plots in the strip along the west side of each field were used to calculate average values for epidemic 7.

Variation in grain weight throughout each field was associated with rust severity rather than field position. Although grain dry weight varied significantly among plots on the second sampling date (6–8 DFA), the variation was relatively small and could not account for variability at the end of the season based on results from using initial grain weight as a covariate in analysis of variation for final grain weight.

Grain dry weight increased linearly at a similar rate throughout each field before the influence of leaf rust and/or stem rust (Fig. 4). After the establishment of rust, the growth rate was inversely related to disease severity. The duration of grain growth was also reduced by rust. Similar trends occurred for fields 2 and 4. These three observations were incorporated into the regression analysis by fitting piecewise linear regression models consisting

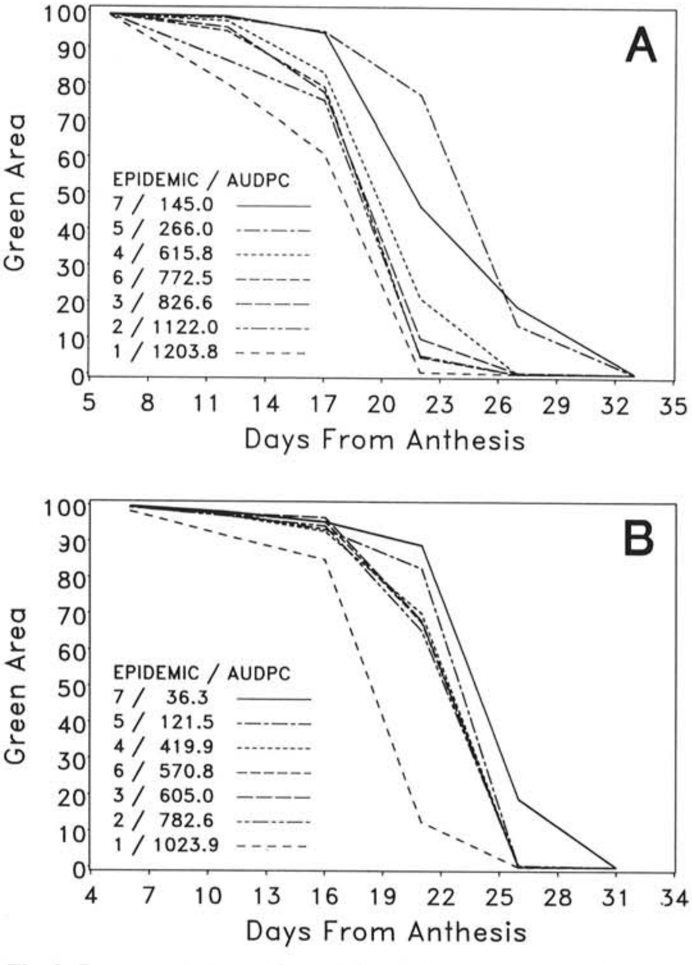

Fig. 2. Percent green area of wheat flag leaves. **A,** Field 1 in 1986. **B,** Field 3 in 1987. The seven rust epidemics are denoted by their area under disease progress curve values for rust severity on peduncles.

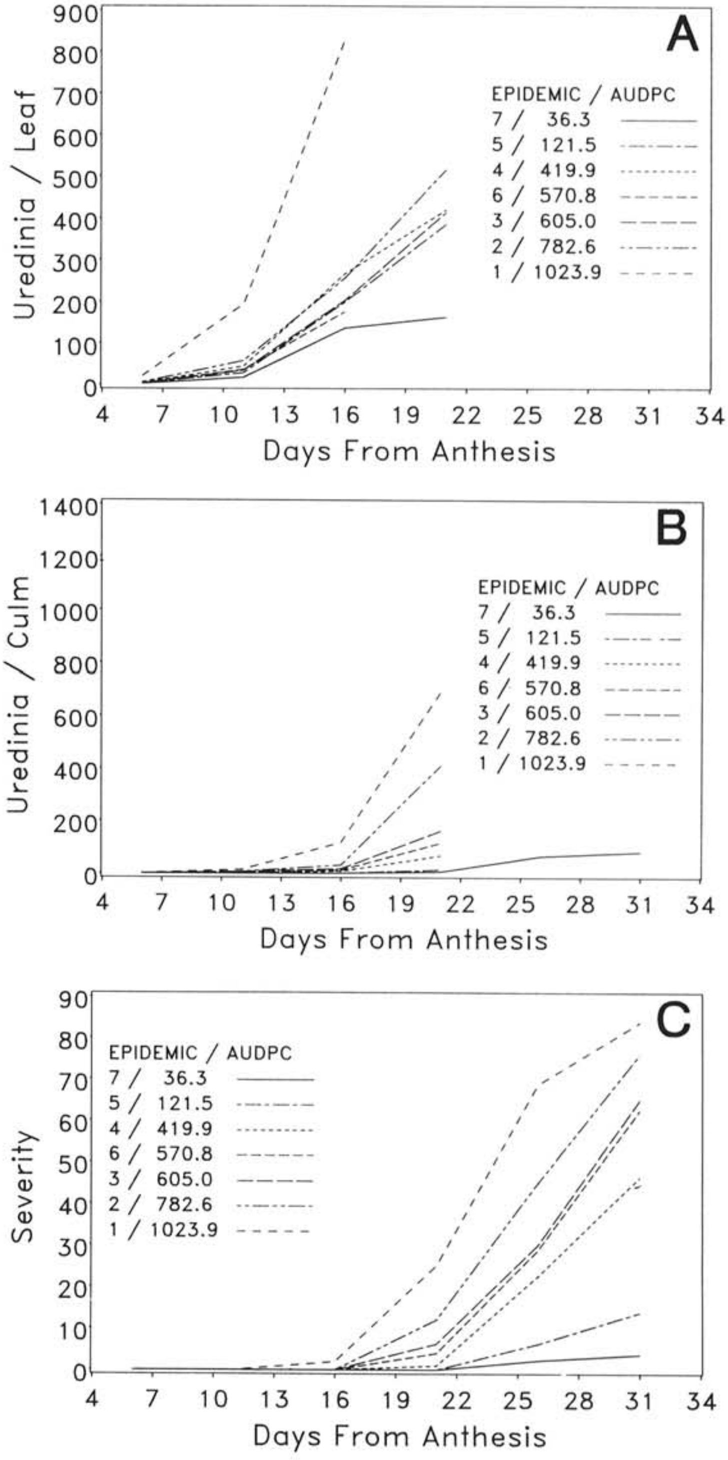

Fig. 3. Disease progress of wheat stem rust and leaf rust epidemics in field 3 in 1987. Dependent variables are: **A,** uredinia per leaf; **B,** uredinia per culm; and **C,** rust severity (%) on peduncles. Treatments are denoted by their epidemic number and area under disease progress curve value for rust severity on peduncles.

of three or four pieces to the grain growth data for each field.

Analysis of grain growth in 1986. For fields 1 and 2, the piecewise linear regression models with slope changes on 13 June and 20 June 1986, which were 15 or 16 and 22 or 23 DFA, respectively, had smaller residual sums of squares than models with slope changes on other dates. The model of interest consisted of a common intercept, a common slope for the first piece of the model (α_1), separate slopes for each epidemic between 15 or 16 DFA and 22 or 23 DFA (β_1), and separate slopes between 22 or 23 DFA and maturity (γ_1) for each epidemic (Table 1 and Fig. 5A). The third slopes were greater than zero only for epidemics 4, 5, and 7, based on 95% confidence intervals. The model of scientific interest (Table 1) is not the best-fitting model based on general linear F tests. The most parsimonious model differs from the model of scientific interest by separate intercepts and second slopes for each replicate. Although these models are statistically different ($\alpha = 0.05$), they are not practically different. The adjusted R^2 values are 99.77 and 95.80% for these two models fit to the data from field 1 in 1986 and 99.85 and 96.59% for the same models fit to the data from field 2 in 1986. The statistical lack of fit is manifested as a small increase in the standard errors and, therefore, the confidence intervals of the selected models. Although the models are statistically different, the penalty is small, which reflects the high power or sensitivity of the test.

Rate of grain growth was affected by stem rust beginning 15 or 16 DFA, when plants were at GS 11.1, according to the piecewise regression model. Growth rates ranged from 0.04 to 0.20 (Table 1) and from 0.06 to 0.21 $\text{mg}^{1/2}$/day between 15 and 22 DFA and 16 and 23 DFA for wheat in fields 1 and 2, respectively. The average number of uredinia counted on culm tissue from field 2 16 DFA ranged from 10 uredinia per culm for plants from epidemic 7 to 431 uredinia on culms from epidemic 1. Average percent green leaf area was 97.2 and 77.5% for plants from epidemics 7 and 1, respectively. The average number of

TABLE 1. Piecewise regression model of grain dry weight ($\text{mg}^{½}$) on time (days from anthesis) with slope changes 15 and 22 days from anthesis for field 1 during the 1986 growing season

Variable[a]	Parameter estimate	Standard error	95% Confidence interval[b]
Intercept	0.7188	0.0308	0.6310–0.8066
α_1	0.2073	0.0029	0.1990–0.2156
β_{11}	0.0415	0.0044	0.0290–0.0540
β_{12}	0.0620	0.0044	0.0494–0.0745
β_{13}	0.0964	0.0044	0.0838–0.1089
β_{14}	0.1310	0.0060	0.1139–0.1481
β_{15}	0.1557	0.0060	0.1386–0.1728
β_{16}	0.1223	0.0044	0.1098–0.1348
β_{17}	0.2046	0.0059	0.1878–0.2214
γ_{14}	0.0115	0.0054	−0.0039–0.0269
γ_{15}	0.0474	0.0054	0.0320–0.0628
γ_{17}	0.0540	0.0052	0.0392–0.0688

[a] α_1, β_{1i}, and γ_{1i} refer to the slopes of the first, second, and third parts, respectively, of the piecewise regression model. The second subscript denotes the epidemic, with seven referring to the fungicide-treated plants.

[b] Joint confidence region for the 12 parameters was computed with the Bonferroni t statistic.

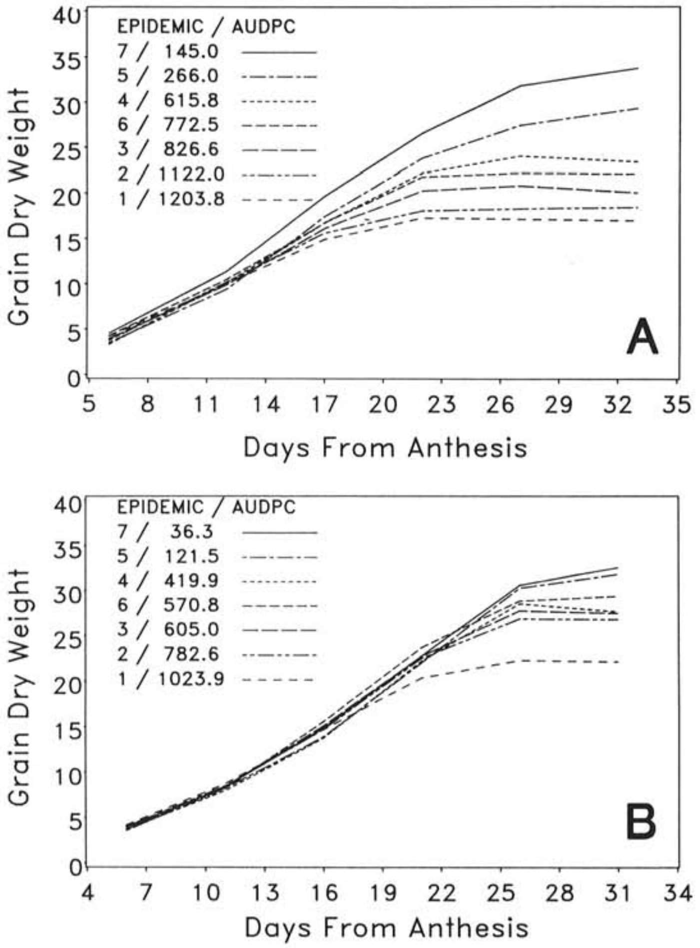

Fig. 4. Grain growth (mg/grain) curves for: **A,** The seven wheat stem rust epidemics in field 1 in 1986; and **B,** the seven wheat stem and leaf rust epidemics in field 3 in 1987. The epidemics are denoted by their area under disease progress curve values for rust severity on peduncles.

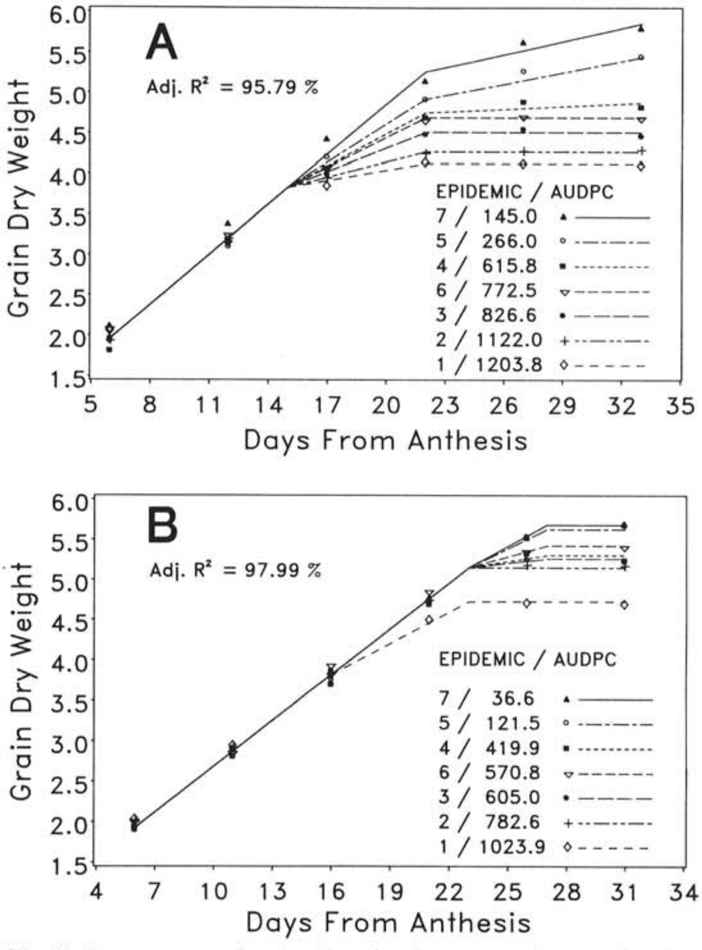

Fig. 5. Curves representing the piecewise linear regression equation fit to the wheat grain growth data ($\text{mg}^{1/2}$/grain) from: **A,** field 1 in 1986; and, **B,** field 3 in 1987. Data points are averages for the seven rust epidemics denoted by their area under disease progress curve values for rust severity on peduncles.

uredinia per flag leaf ranged from 5 to 154. The average number of uredinia per culm 12 DFA ranged from 1 to 463 for culms from epidemics 7 and 1, respectively, in field 1 (Fig. 1B). Five days later the average count ranged from 34 to 1,076 for culms from the same areas in field 1, while the average number of uredia per flag leaf ranged from 17 to 297 (Fig. 1A). Average percent green leaf area for these plants was 93.9 and 60.7%, respectively (Fig. 2A).

Stem rust also influenced the duration of grain growth. According to the piecewise regression model, grain dry weight stopped increasing 23 DFA for epidemics 1, 2, 3, and 6 in fields 1 (Fig. 5A) and 2 in 1986. At that time, wheat was in GS 11.2. The average percent green leaf area 22 DFA was less than 10% for flag leaves from these four epidemics in field 1 (Fig. 2B). Average stem rust severity of peduncles for these epidemics was between 31 and 49% (Fig. 1C). Average stem rust severity of peduncles for epidemics 1–3 in field 2 ranged from 10 to 45% 21 DFA and from 64 to 71% 26 DFA. The average grain weight 23 DFA for the six epidemics in field 1 was reduced from 10.3 to 35.1% as compared with the weight of grain for epidemic 7. Percent reduction for the five epidemics in field 2 26 DFA ranged from 3.0 to 36.8%. Grain of severely infected wheat (epidemics 1, 2, 3, and 6) matured relatively quickly as compared to grain from fungicide-treated wheat (epidemic 7). Rate of grain growth from 23 DFA until maturity (GS 11.4) for epidemics 4, 5, and 7 was lower than the rate during the previous two phases of grain growth (Figs. 4A and 5A). Percent reduction in observed average grain weight at GS 11.4 ranged from 13.2 to 49.8% and 8.5 to 43.9% for the epidemics in fields 1 and 2, respectively. Final grain weight was determined more by rate of grain growth between 16 and 23 DFA than duration of grain growth, based on a comparison of the reduction in grain weight at GS 11.2 with the reduction at GS 11.4. Different final grain weights were associated with plants harvested from each of the seven epidemics (Table 2).

TABLE 2. Average grain dry weight of wheat at physical maturity for the seven stem rust epidemics established in two fields in 1986 and the seven stem and leaf rust epidemics established in two fields in 1987

	Average grain dry weight (mg)[a]			
	1986		1987	
Epidemic[b]	Field 1	Field 2	Field 3	Field 4
1	16.92 f	20.17 f	22.12 d	24.30 e
2	18.43 e	23.47 e	26.78 c	28.30 d
3	20.02 d	27.20 d	27.46 c	29.65 cd
4	23.40 c	30.00 c	27.63 c	30.74 bc
5	29.30 b	32.90 b	31.79 a	33.75 a
6	22.08 c	···	29.39 b	31.99 b
7	33.73 a	35.95 a	32.56 a	34.52 a

[a] Means within a column followed by the same letter are not different according to the modified Ryan-Einot-Gabriel-Welsch multiple range test ($\alpha = 0.05$).

[b] Epidemic 7 was the fungicide-treated area along the western side of each field. Epidemic 1 was located between the artificially inoculated spreader rows. Epidemics 2–6 were located 8.5, 14.0, 22.5, and 42.5 or 48.0 m downwind, and 8.5 m upwind from epidemic 1.

TABLE 3. Piecewise regression model of grain dry weight ($mg^{1/2}$) on time (days from anthesis) with slope changes 16, 23, and 27 days from anthesis for field 3 during the 1987 growing season

Variable[a]	Parameter estimate	Standard error	95% Confidence interval[b]
Intercept	0.8448	0.0206	0.7878–0.9017
α_1	0.1860	0.0017	0.1812–0.1909
β_{11}	0.1289	0.0035	0.1191–0.1387
β_1	0.1893	0.0029	0.1814–0.1973
γ_{13}	0.0283	0.0080	0.0062–0.0503
γ_{14}	0.0395	0.0079	0.0176–0.0614
γ_{15}	0.1204	0.0080	0.0984–0.1425
γ_{16}	0.0694	0.0080	0.0474–0.0915
γ_{17}	0.1346	0.0069	0.1154–0.1537

[a] α_1, β_{1i}, and γ_{1i} refer to the slopes of the first, second, and third parts, respectively, of the piecewise regression model. The second subscript denotes the epidemic, with seven referring to the fungicide-treated plants. β_1 was fit to epidemics 2 through 7.

[b] Joint confidence region for the 12 parameters was computed with the Bonferroni t statistic.

Analysis of grain growth in 1987. A model with four pieces was selected for fields 3 (Fig. 5B) and 4 because the grain growth rate of the most severely infected wheat (epidemic 1) was reduced earlier in the season than the other epidemics (Fig. 4B). The fourth slopes, which cover the period from 27 to 31 DFA, did not differ from 0 ($\alpha = 0.05$) for any epidemics in field 3; therefore, the final model selected consisted of only three pieces (Table 3) because parameters with estimates of zero are not included in a model. Grain dry weight increased linearly at a rate of 0.19 $mg^{1/2}$/day throughout field 3 during the first 16 DFA (Table 3 and Fig. 5B). The growth rate of the most severely infected plants was reduced by 30% to 0.13 $mg^{1/2}$/day between 16 and 23 DFA (GS 11.1–11.2), whereas the rate was unchanged throughout the rest of the field (Table 3). The average number of uredinia counted on culm tissue from field 3 16 DFA was 120, 33, and 2 on culms from epidemics 1, 2, and 7, respectively (Fig. 3B). The average numbers of uredinia per flag leaf for these epidemics were 829, 256, and 136, respectively (Fig. 3A). From 23 to 27 DFA, growth rates ranged from 0.00 to 0.14 $mg^{1/2}$/day and were inversely related to disease level. Wheat was in GS 11.2–11.3 during this period. Slopes for epidemics 1 and 2 were not significantly greater than 0; therefore, grain growth had ceased by 23 DFA for plants with an AUDPC greater than about 610 percent-days. Average percent green area for flag leaves from these epidemics was 12.6 and 65.3% 21 DFA and 0 and 0.5% 26 DFA, respectively (Fig. 2B). Average stem rust severity of peduncles was 25 and 12% 21 DFA and 69 and 45% 26 DFA, respectively (Fig. 3C). Grain growth had ceased by 27 DFA throughout field 3 because the growth rates between 27 and 31 DFA were not significantly different from zero.

Grain dry weight increased linearly at a rate of 0.20 $mg^{1/2}$/day throughout field 4 during the first 16 DFA. From 16 to 23 DFA, growth rates were 0.14 $mg^{1/2}$/day for epidemic 1 and 0.18 $mg^{1/2}$/day for epidemics 2–7. Plants were in GS 11.1–11.2. The average number of uredinia per culm from field 4 18 DFA was 267, 81, and 3 for epidemics 1, 2, and 7, respectively. Grain growth had ceased by 23 DFA for epidemic 1, which had an AUDPC value of 760.1 percent-days. Wheat from epidemic 1 23 DFA had an average green leaf area of 1.0% and an average rust severity on peduncles of 25%. From 23 to 27 DFA, growth rates ranged from 0.00 to 0.16 $mg^{1/2}$/day and were inversely related to disease level. After 27 DFA, grain dry weight continued to increase at a rate significantly greater than 0.00 (0.03 $mg^{1/2}$/day; SE = 0.013) only for epidemic 6.

Grain number per head. Average numbers of grains per head (± SE) at GS 11.4 were 36.11 (0.22), 35.38 (0.18), 36.84 (0.22), and 43.09 (0.31) for fields 1, 2, 3, and 4, respectively. Grain number did not vary significantly ($\alpha = 0.05$) among epidemics on either the second or last sampling dates for fields 1 and 2 in 1986. There were small but significant differences among epidemics in field 3 on both the second and last sampling dates and in field 4 on the last sampling date. However, these differences appear to be chance variability rather than variability due to rust level or field position. Grain number was not related to disease level over the entire grain-filling period based on results from a repeated measures model. Statistical differences, which corresponded to fewer than two grains per head, were apparently due to field variability that did not occur systematically within these fields.

Dry weight of culms. Culm dry weight increased during the first 11 DFA, then slowly decreased until GS 11.4 (Fig. 6). Culm dry weight (± SE) on the third sampling date, which was 12, 16, 11, and 12 DFA, averaged 1.414 g (0.0103), 1.465 g (0.0095), 1.447 g (0.0096), and 1.637 g (0.0136) for fields 1, 2, 3, and 4, respectively. Reductions in dry weight between the third and last sampling dates, expressed as a percentage of the average weight on the third sampling date, were 18.93, 23.22, 20.69, and 22.79%, respectively. The loss in weight over this time period was significant for each epidemic based on Student's *t* tests comparing the two dry weights. Epidemic 1 wheat lost the most weight in both fields in 1986. However, this amount was not significantly different from the weight loss exhibited by epidemic 7. The reduced culm dry weight for epidemic 1 wheat in field 3 in 1987 was not significantly different from the weight loss of the other epidemics. The effect of rust on culm dry weight for the entire grain-filling period was tested with a repeated measures model. There was a significant overall effect on culm weight attributable to the different epidemics in each field. However, the average culm dry weight for epidemic 1 wheat was less than the culm weight for wheat from all other epidemics only in field 3 ($\alpha = 0.05$), and it was different from the culm weight for epidemic 7 wheat only in fields 1 and 3.

Culm dry weight of epidemic 1 wheat in each field began to decrease earlier in the grain-filling period than culm dry weight from other epidemics. These plants did not have the lowest culm weight between anthesis and 6–11 DFA, which suggests that this rapid loss in dry matter from culms is due to rust. Furthermore, the rate of decline in culm weight was inversely related to disease level in each field. Length of the culm could not account for differences in culm weight among epidemics.

Yield components of wheat. Stem rust in 1986 and stem and leaf rust in 1987 were associated with a reduction in TKW and HI based on samples from plants within 1-m sections of rows harvested at GS 11.4 (Table 4). TKW for wheat from epidemic 1 in fields 1, 2, and 3 was reduced by 48.9, 47.5, and 36.9%, respectively, relative to TKW for wheat from epidemic 7. HI was reduced by 30.5, 28.8, and 19.2%, respectively. Weight of nonharvested material per culm from epidemic 1 wheat in fields 1, 2, and 3 was reduced by 12.8, 13.9, and 4.9%, respectively, as compared with wheat from epidemic 7. The number of grains per head, grains per square meter, heads per square meter, and culms per square meter were not affected by these diseases (Table 4) because they developed after these yield components were set. Although variability occurred in grains per head, grains per square meter, and heads per square meter among epidemics in field 3,

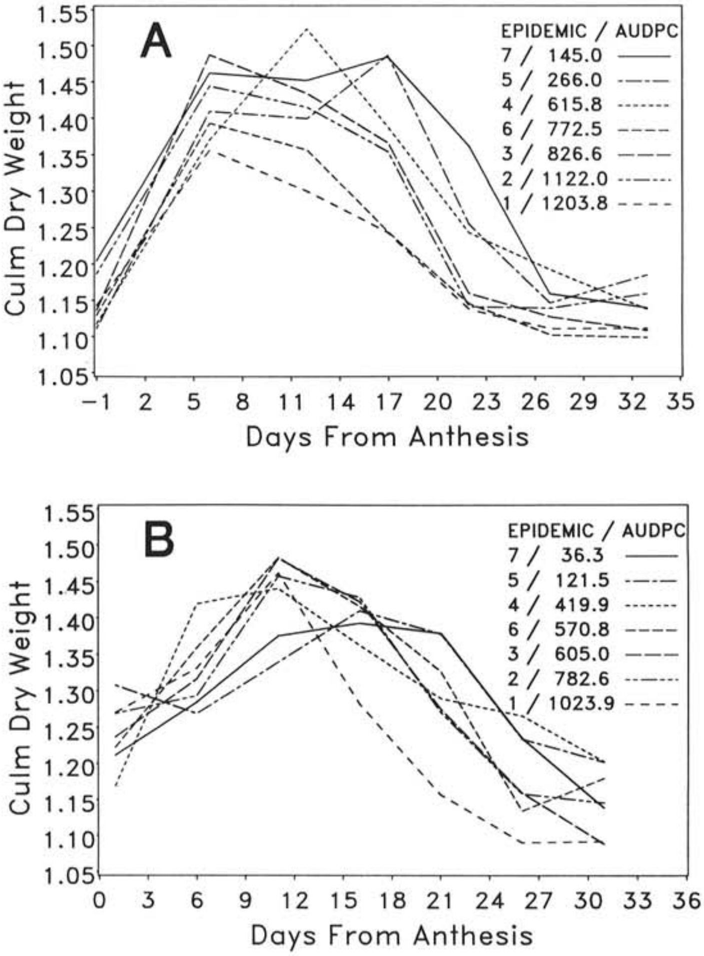

Fig. 6. Culm dry weight (g/culm) for: **A,** the seven wheat stem rust epidemics in field 1 in 1986; and, **B,** the seven wheat stem and leaf rust epidemics in field 3 in 1987. The epidemics are denoted by their area under disease progress curve values for rust severity on peduncles.

TABLE 4. Yield components[a] of wheat infected by stem and leaf rust fungi determined from samples harvested at physical maturity

Field	Epidemic	Thousand kernel weight (g)	Grains/head	Grains (m^2)	Heads (m^2)	Culms (m^2)	Harvest index
1	1	15.62 f	21.02 a	11,778 a	563.7 a	660.3 a	0.223 f
	2	17.13 e	21.72 a	12,721 a	584.6 a	686.4 a	0.243 e
	3	19.85 d	21.87 a	12,632 a	580.8 a	724.7 a	0.268 d
	4	21.93 c	21.02 a	12,064 a	586.7 a	715.9 a	0.272 cd
	5	25.65 b	22.00 a	12,644 a	578.6 a	694.9 a	0.304 b
	6	20.63 d	21.01 a	12,222 a	579.4 a	660.9 a	0.280 c
	7	30.59 a	21.10 a	12,374 a	582.4 a	706.5 a	0.321 a
	Mean	21.04	21.42	12,357	579.5	693.2	0.269
2	1	17.42 f	20.05 a	11,240 a	561.4 a	628.9 a	0.237 d
	2	22.17 e	21.74 a	12,450 a	576.4 a	695.9 a	0.282 c
	3	25.39 d	21.52 a	12,196 a	569.8 a	669.7 a	0.303 b
	4	27.47 c	21.45 a	12,203 a	562.2 a	716.3 a	0.316 b
	5	30.64 b	20.94 a	11,594 a	553.4 a	692.8 a	0.335 a
	6	...	...	...	...	...	...
	7	33.16 a	19.96 a	11,278 a	565.2 a	673.6	0.333 a
	Mean	25.34	20.97	11,836	564.5	679.1	0.298
3	1	18.69 d	21.01 a	16,743 a	789.3 b	950.5	0.244 d
	2	22.79 c	19.96 a–c	15,553 ab	777.0	964.5 ab	0.272 c
	3	24.77 b	19.67 a–c	15,661 ab	798.1 b	970.2 ab	0.286 b
	4	25.67 b	19.42 bc	16,718 a	861.7 a	1,026.0 a	0.297 ab
	5	24.82 b	20.74 ab	15,182 ab	735.2 b	935.4 b	0.289 ab
	6	24.67 b	20.35 a–c	15,594 ab	767.6 b	955.4 ab	0.290 ab
	7	29.64 a	18.98 c	14,430 b	761.7 b	921.4 b	0.302 a
	Mean	24.96	19.92	15,602	783.7	958.2	0.285

[a] Means within a column for a field followed by the same letter are not different according to the modified Ryan-Einot-Gabriel-Welsch multiple range test ($\alpha = 0.05$).

it was not associated with disease severity and the range of values for these variables was small.

Green leaf area. The best overall predictor of grain growth during each time period was the average percent green leaf area of flag leaves during the same period (Fig. 7). The relation between these variables was fairly consistent over time. The data for the four time periods in each field in 1986 could be combined and described by one regression equation (Fig. 7A). The slopes and intercepts of the regression equations for fields 1 and 2 were not significantly different based on a general linear F test. In 1987, grain growth rate was approximately equal to 0.19 $mg^{1/2}$/day for wheat with flag leaves that were at least 75% green. The linear relation between percent green leaf area, for values less than 75%, and grain growth rate was described by parallel regression equations for fields 3 and 4. The relation between these variables either varied between years or the influence of stem rust on grain growth was greater in 1986 than the influence of leaf and stem rust in 1987. Stem rust may have had a greater influence in 1986 because culms were more severely infected in 1986 than in 1987 and consequently had less green photosynthetically active tissue. Linear or quadratic trends were evident in plots of grain growth rate versus stem rust severity on peduncles for individual time periods; however, the relation varied over time.

DISCUSSION

Grain dry weight was similar throughout each field for at least the first 12 DFA; then both the rate and duration of grain growth were reduced by leaf and/or stem rust (Figs. 4 and 5). Grain number per head was not affected. Rust may not have affected grain growth during the first 12 DFA because the disease level was too low to have a detectable impact or because grain growth during this period is not affected by stress. The first explanation is feasible because only the most severely infected plants exhibited a reduced growth rate over the next few days. A disease threshold probably occurs because grain requirements are exceeded by assimilate supply from the uppermost parts of most plants that are healthy or moderately stressed (41). This assimilate supply includes current photosynthate as well as carbohydrates stored temporarily in the culms. Head photosynthesis during the first week after anthesis may produce enough carbohydrate for head and grain respiration and up to 75% of the grain growth (10). The second explanation was suggested for the reason that leaf rust or water stress affected grain growth rate only after this initial phase in previous studies (23). Increase in grain weight during the first 2 wk after anthesis is primarily due to growth of the maternal outer pericarp and grain coat and division of endosperm cells (10,41). Starch accumulation begins 1–2 wk after anthesis (10). A temporary water deficit during the first 7 days after anthesis affected concurrent photosynthesis, grain set, and final grain weight, but not grain growth rate (41). Reduced yield occurred through accelerated senescence and shortened grain growth duration. Grain number, but not growth rate, also was reduced by high temperature and/or low light intensity during the first 10 DFA (3,34,40). Grain number and weight were reduced in winter wheat exposed to elevated levels of O_3 from 17 days before flowering until 8–10 days before harvest (14). In contrast, exposure to O_3 initiated at head emergence reduced the rate and duration of dry weight increase of heads beginning at anthesis (1). Although this stress was imposed before anthesis, final grain size but not grain number was affected. Thus, wheat generally responds to stress during the early stages of grain development (from before anthesis to at most 10 DFA) by aborting grains, which allows the remaining grains to receive sufficient assimilates to maintain their growth rate. Grain number per head was not affected by leaf and/or stem rust in 1986 or 1987 because the seven epidemics developed after the period when grain set is sensitive to stress.

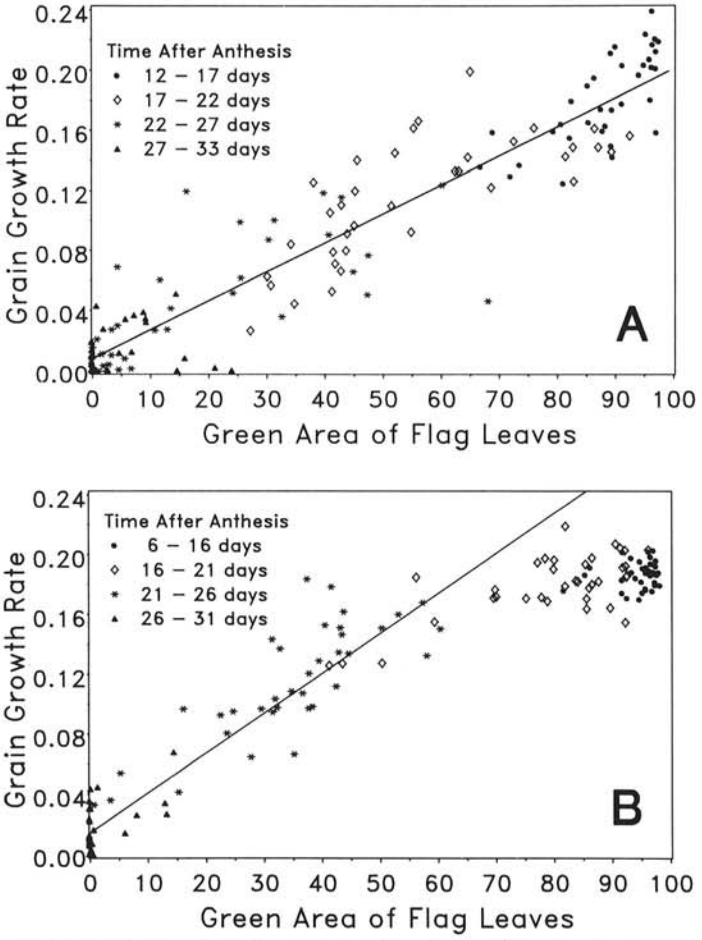

Fig. 7. Relationship between grain growth rate ($mg^{1/2}$/day) and average percent green flag leaf area of wheat infected by: **A,** *Puccinia graminis* f. sp. *tritici* from field 1 in 1986 ($Y = 0.0076 + 0.0020X$); and **B,** wheat infected by *P. g. tritici* and *P. recondita* f. sp. *tritici* from field 3 in 1987 ($Y = 0.0144 + 0.0027X$). Data points are the averages for the seven rust epidemics.

Stem and leaf rust reduced both the rate and duration of grain growth. After starch storage begins, the weight of healthy wheat grains increases almost linearly for 2–4 wk, then asymptotically approaches its mature value (10). Rust did not affect grain growth by merely reducing the length of the linear growth phase because the growth rate of infected wheat was inversely related to disease severity when wheat was in GS 11.1–11.3 (Figs. 2 and 4).

Rust had a greater impact on wheat grain growth in 1986, when stem rust occurred alone, than in 1987, when both leaf and stem rust were present. The grain growth curves for epidemic 7 in fields 1 and 3 are similar (Fig. 4). In contrast, the curve for epidemic 1 in 1987 parallels the curve for epidemic 6 in 1986. These epidemics had average AUDPC values of 1,024 and 772 percent-days, respectively. However, the curves of stem rust progress on peduncles for these two epidemics were similar during the first half of the grain-filling period (Figs. 1C and 3C). Most of the growth curves for the 1987 data fall between the 1986 curves for epidemics 5 and 7.

Although rust had a greater impact on grain growth in 1986, uredinia were more numerous on flag leaves in 1987 during grain growth (Figs. 1A and 3A). However, stem rust uredinia tend to be larger than leaf rust uredinia. Leaf rust was observed throughout fields 3 and 4 in 1987 by 7 DFA, whereas stem rust was observed only on leaves of epidemics 1 and 6 wheat at the same time in 1986. In contrast, although plants were initially inoculated at the same time each year, stem rust epidemics on culms began earlier, the rate of increase was faster, and final severities were greater in 1986 than in 1987 (Figs. 1C and 3C). These differences may reflect the greater quantity of stem rust inoculum present in 1986 due to the occurrence of stem rust on leaves as well as culms. As a result, average stem rust severity on peduncles equal distances from the spreader rows was greater during grain growth in 1986 than in 1987. Consequently, AUDPC values were larger for epidemics in 1986, although epidemic lengths were the same. This is not sufficient to account for differences between epidemics in the 2 yr, however, because epidemics with similar AUDPC values do not have similar grain growth curves.

The observed reduction in rate and duration of grain growth may be due to the fact that these diseases reduce the photosynthetic rate of their host before leaf senescence, as was demonstrated during a concurrent study involving these same fields (21), and accelerate leaf senescence. Grain growth was more closely associated with percent green leaf area of flag leaves than with stem rust severity of peduncles throughout the grain-filling period. Initial reductions in these variables occurred at the same time. Percent green leaf area, as well as grain growth rate, began to decline earlier for most leaves infected by *P. g. tritici* in 1986 than for leaves infected primarily by *P. r. tritici* in 1987 (Figs. 2 and 4). Most leaves infected by *P. g. tritici* in 1986 tended to have a lower percent green leaf area than most leaves infected by *P. r. tritici* in 1987 at any time, although the uredinial density was greater on the leaves infected by *P. r. tritici.* This occurred because stem rust uredinia usually are larger than leaf rust uredinia, and they are surrounded by chlorotic tissue. Leaves infected by *P. g. tritici* appeared to senesce more quickly. The fungicide-treated wheat (epidemic 7) from both years exhibited fairly similar reductions in green leaf area and had similar grain growth curves. Wheat from epidemic 1 in field 3 in 1987 and epidemic 6 in field 1 in 1986 had similar grain growth curves and green leaf area curves. Cessation of grain growth for most epidemics coincided with complete senescence of the leaf, although culms and heads were still partially green.

The majority of the carbon for grain filling is assimilated after anthesis. The amount of dry matter accumulated by grains in nonstressed wheat is believed to be less than assimilate supply during the first third of the grain-filling period (32,38). Some of this carbon is temporarily stored as nonstructural carbohydrate in the vegetative parts of the plant, particularly the upper two internodes (4,9,27,42). This stored carbohydrate is used later in the grain-filling period, thereby compensating for the fact that flag leaves reach maximum photosynthate production at anthesis (18) or about 2–4 wk after their emergence (5). Carbon translocated from culms was estimated to have contributed 2.7–12.2% (27), 5–10% (42), and 23% (4) to final grain yield in container-grown wheat (27,42) and field-grown wheat (4). The amount of dry matter mobilized to the grain was estimated to be 39% of the dry weight from the culms (4). Utilization of stored carbohydrates is increased when plants are under stress, including intermittent drought initiated at anthesis, high temperature, and darkness or shading (2,3,27,34). The reduction in water-soluble carbohydrate content of culms at elevated temperatures was caused by higher respiration rates as well as greater mobilization to grains (34). During the first 2 wk after anthesis, wheat receiving a normal water supply accumulated carbohydrates while plants subjected to water stress or high temperature utilized stored sugars (2,3,34).

We hypothesized that wheat stem rust and leaf rust could accelerate the movement of assimilates out of culms and/or increase the amount moved in response to carbohydrate demand exerted by the grain that was not being met due to reduced photosynthesis. Culm dry weight was reduced by 0.19–0.44 g during the grain-filling period, which is within the range of 0.14–0.52 g reported during previous studies (4,34,42). The amount of dry matter lost was not related to disease level, suggesting that rust did not increase the amount of assimilate translocated from culms to grains, in contrast with previous results obtained with stressed wheat. However, culm dry weight of severely infected wheat decreased more rapidly during the grain-filling period. Movement of assimilates from culms to grains may have been accelerated in infected plants, or the weight loss may have been the result of increased respiration in response to infection. Weight of nonharvested material, which consists of culms, leaves, and chaff, per culm for 1-m row lengths collected at GS 11.4 was inversely related to rust severity in 1986. One possible explanation is redistribution of nonstructural carbohydrates; however, loss of leaf tissue and reduced growth of secondary culms are also feasible explanations. The reduction in HI associated with rust was not as great as the reduction in TKW because of the reduction in nonharvested material. Discrepancies in results among current and previous experiments may be due partially to cultivar differences in the quantity of grain dry matter that normally originates from carbohydrates stored in the stem (38).

Piecewise linear regression proved to be useful for describing the nonlinear grain growth curves. This procedure forces the individual linear regression lines to join at specific values of X, thereby maintaining continuity in the curve. The individual lines are fit simultaneously with ordinary least squares regression and have a common estimate of variance, $\hat{\sigma}^2$ (24). The resulting equation is a more biologically realistic description of grain growth than either a linear or polynomial regression equation because of the way the reduced growth rate associated with natural senescence or disease and the end of grain filling are handled. Cubic polynomial regression, which has been used by other researchers to describe grain growth curves (33), produces false peaks and consequently overestimates final yield.

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