Alteration of Physiological Processes in Wheat Flag Leaves Caused by Stem Rust and Leaf Rust

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ABSTRACT

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The severity of rust on flag leaves of winter wheat (*Triticum aestivum* 'Tyler') infected by *Puccinia recondita* f. sp. *tritici*, the causal agent of leaf rust, and/or *P. graminis* f. sp. *tritici*, the causal agent of stem rust, was associated with decreased apparent photosynthetic rates per unit of leaf area (PRA), photosynthetic rates per unit of chlorophyll (PRC), chlorophyll content (CC), ratio of chlorophyll a/chlorophyll b (A/B), and transpiration rate (TR). Severity was also associated with increased internal CO_2 concentration (C_i) and stomatal resistance (R_s). These response variables were measured on attached leaves of field-grown plants during the grain-filling period. Variability due to time of observation was removed by expressing each observation as relative to the value predicted for a rust-free leaf at the same time. The relative response variables were linearly related to the base 10 logarithm of rust severity plus one. Leaves with 9% stem rust in 1986 were predicted by regression analysis to exhibit a 66% reduction in PRA, a 42% reduction in PRC, a 54% reduction in CC, an 8% reduction in A/B, a 20% reduction in TR, a 10% increase in C_i, and an 88% increase in R_s as compared with rust-free leaves. Leaves with 9% stem and/or leaf rust in 1987 were predicted to exhibit a 60% reduction in PRA, a 35% reduction in PRC, a 54% reduction in CC, a 12% reduction in A/B, an 18% reduction in TR, a 23% increase in C_i, and a 68% increase in R_s. These two diseases affected their host similarly. Loss of photosynthetic tissue on an area basis could not account for the reduced photosynthetic rate since the percent reduction greatly exceeded the percent leaf area covered by uredinia. This reduced rate was partially due to decreased chlorophyll content.

Additional keywords: photosynthesis, physiology.

Mechanistic or explanatory mathematical models that simulate yield reduction caused by disease are derived from knowledge of the biological basis for yield reduction, and, thus, theoretically have greater utility and predictive ability than empirical or regression-based models (8,34). This type of modeling requires quantitative information on the effect of disease on physiological processes.

Plants infected with viruses, fungi, or bacteria usually exhibit a reduced photosynthetic rate (12). Abnormalities in form and function of chloroplasts are a common feature of diseased tissues. There is typically a decline in photosynthetic phosphorylation (2,4,23,32), Hill reaction activity (24,39,51), and carbon dioxide assimilation. These changes may be partially (1,4,23,31) or completely (4,49) accounted for by a reduction in chlorophyll content. A few researchers have demonstrated that the diseased state also is associated with decreased mesophyll conductance due to reduced concentration and activity of ribulose-1,5-bisphosphate carboxylase (14,15,29). Others have detected an increase in leaf carbohydrate concentration (5,9,21,45). Excessive carbohydrate accumulation in leaves may inhibit photosynthesis (52).

Water loss through transpiration has been reported to increase (7,9,13,16,17,42,44,46), decrease (29,50), decrease before sporulation then increase (10,50), initially increase then decrease (3), or not change (40) in plants infected by foliar fungal pathogens. Acceleration of water loss from infected tissue has been attributed most frequently to epidermal rupture by pathogens (7,13,40,42) and secondarily to enhanced permeability of the tissues as a result of infection (50), inhibition of stomatal closure (43), or direct water loss through the fungus (16,17). Decreased transpiration is induced by pathogens that cause stomatal closure, hypertrophy of chlorenchyma or spongy mesophyll cells, thereby obliterating intercellular spaces, an intoxicating action upon host cells, reduction of air spaces by hyphae, and/or obstruction of conducting tissue and stomates (7,13,40).

Previous researchers have demonstrated qualitatively through experiments under controlled environmental conditions that stem rust (*Puccinia graminis* (Pers.) f. sp. *tritici* Eriks. & E. Henn.) and leaf rust (*P. recondita* Rob. ex Desm. f. sp. *tritici*) independently increase the transpiration rate of wheat plants and that stem rust reduces the photosynthetic rate of wheat leaves (4,31). Our primary objective was to obtain quantitative information on the relationships between rates of physiological processes, such as photosynthesis and transpiration, and rust severity of wheat flag leaves under field conditions during the grain-filling period. Preliminary reports of this work have been published (25,26).

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 Co., PA (40° 42′ 53″ N, 77° 56′ 25″ W). Soft red winter wheat (*Triticum aestivum* L. em. Tell. 'Tyler') was established and managed using agronomic practices recommended for Pennsylvania (41). There were two 0.4-ha fields during 1985–1986 and during 1986–1987. The preceding crop in each field was oats. Planting dates were 19 September 1985 and 9 and 18 September 1986, rate of planting was 168 kg/ha, and depth of seed placement was about 4 cm. Wheat was fertilized at planting with 10-10-10 (N-P-K) at a rate of 178.6 kg/ha and in April at growth stage (GS) 5 on the Feekes

scale (18) with 133.9 kg/ha of ammonium nitrate in 1986 and 160.7 kg/ha in 1987. The herbicide MCPA (Weedar, Union Carbide Agricultural Products Co., Danbury, CT) was applied at GS 4 to 5 at a rate of 0.58 L a.i./ha in both years. These fields were divided into eight 6.1-m-wide strips oriented parallel to the prevailing wind direction and separated by 1.5-m-wide alleyways. Powdery mildew (*Erysiphe graminis* D.C.:Fr. f. sp. *tritici* E. Marchal) and leaf rust (*Puccinia recondita* f. sp. *tritici*) were controlled, prior to inoculating with *P. graminis* f. sp. *tritici*, with 282 g of product per hectare (g p/ha) of triadimefon (Bayleton 50WP, Mobay Corp., Pittsburgh, PA) and 2,259 g p/ha mancozeb (Dithane M-45 80WP, Rohm and Haas Co., Philadelphia, PA) applied on 30 April 1986 and 26 April 1987. Fungicides were applied with a tractor-mounted, nitrogen-powered boom sprayer calibrated to deliver 280 L/ha of material at 0.12 MPa. A second application of triadimefon on 14 May 1987 was required to control leaf rust. 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.

Method of inoculation. Plants established in 28 rows near the upwind end of each field were inoculated with urediniospores of Race 56 of *P. g. tritici* (Cereals Rust Laboratory, St. Paul, MN). Urediniospores from greenhouse-grown plants were diluted 1:10 (w/w) with pharmaceutical-grade talc and applied to these spreader rows 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 night afterwards. The inoculation dates were 17 and 25 May 1986 and 16, 17, and 24 May 1987. The inoculated rows also served as foci for leaf rust in 1987 due to natural infection by *P. r. tritici*. The two peripheral strips of each field were sprayed biweekly in 1986 and weekly in 1987 with mancozeb at a rate of 2.2 kg p/ha to maintain rust-free plants. These strips functioned as controls.

Gas exchange measurements. A portable photosynthesis monitoring system (Model LI-6000, LI-COR, Inc., Lincoln, NE) was used to measure apparent photosynthetic rate per unit of leaf area (mg $CO_2/m^2/sec$) (PRA), transpiration rate (mg $H_2O/m^2/sec$) (TR), stomatal resistance (s/cm) (R_s), and internal CO_2 concentration (ppm) (C_i) of flag leaves. PRA is the difference between the gross photosynthetic rate and the respiration rate. The system console and CO_2 analyzer were shaded by an umbrella to minimize machine error caused by differential heating and the leaf chamber was shaded between measurements.

Physiological processes were measured on 7 days from 29 May (day 149) through 18 June (day 169) in 1986 and on 9 days from 29 May (day 149) through 20 June (day 171) in 1987. On the first sampling date in both years, wheat was in the early flowering stage of development (GS 10.5.1) and rust was present only on plants in the inoculated rows. Wheat was in the early soft dough stage of development (GS 11.1–11.2) on the last sampling date. Natural senescence of the leaves was a confounding factor after this date. Measurements were made alternately on healthy and infected leaves between 10:15 am and 1:30 pm EDT while the sky was clear, except on the last sampling date in 1987 when the sky was overcast.

The flag leaves were selected based on rust severity and orientation towards the sun, rather than their position relative to the spreader rows. Most leaves were selected from the two fungicide-treated strips and adjacent nontreated strips in each field. The length of time leaves remained in the chamber was adjusted to obtain a total CO_2 drawdown (reduction in CO_2 concentration) of at least 20 ppm and a relative humidity increase of less than 10% without exceeding the recommended maximum measurement period of 90 sec. The CO_2 and RH criteria necessitated keeping severely infected leaves in the chamber for longer periods than healthy leaves.

The LI-COR photosynthesis monitoring system measures CO_2 concentration, relative humidity, photosynthetically active radiation (PAR), and leaf and air temperatures 10 times during each measurement period. Initial values of the various parameters are determined by linear regression because a leaf may respond to being enclosed in the chamber. The apparent photosynthetic rate of wheat flag leaves usually declined steadily or remained constant during the measurement period. Occasionally the first measurements of this parameter were much lower or higher than the other values because data recording was initiated before the CO_2 concentration had begun to fall steadily or data recording was initiated when the CO_2 concentration within the chamber was above the ambient level. In these cases, the abnormal values were excluded in fitting regression lines to determine initial values.

The portion of each leaf that had been in the chamber was removed from the plant at the end of the morning after all measurements were made and its area was determined with a leaf area meter (Model LI-3000, LI-COR, Inc.). These leaf area measurements were used to recalculate values of the physiological variables for each leaf with the microprocessor of the photosynthesis monitoring system. A standard leaf area had been used to obtain preliminary values in the field.

The photosynthetic rates of rust-free leaves that had been sprayed with mancozeb the previous day were compared with the rates of rust-free leaves that had not been sprayed to verify that the fungicide treatment did not influence photosynthesis.

PRA, TR, R_s, and C_i of flag leaf sheaths and peduncles (top internodes) also were measured. Culms were carefully bent at their base such that these tissues were perpendicular to the direct solar beam during the measurement. The apparent photosynthetic rate of healthy heads was approximately zero, which indicates their photosynthetic and respiration rates are almost equal; therefore, heads were not further examined in this study.

Chlorophyll was extracted from the intact leaf pieces by soaking these pieces in 80% acetone for at least 3 days. The amount of total chlorophyll, chlorophyll a, and chlorophyll b extracted from these leaf pieces was determined from optical density readings at 645, 652, and 663 nm (47). Chlorophyll content per unit of leaf area (mg chlorophyll/dm^2) (CC), the ratio of chlorophyll a content to chlorophyll b content (A/B), and photosynthetic rate per unit "essential" chlorophyll (mg CO_2/mg chlorophyll/hr) (PRC) were calculated for each leaf. PRC was determined by adjusting chlorophyll concentrations to a maximum value of 3.2 mg/dm^2.

Disease severity measurements. Rust severity of the chlorophyll-cleared leaf pieces was assessed with a computer-controlled video image analysis system, which consists of a microcomputer, a black-and-white video camera, a television monitor, and a video image storage unit (20,38). This system digitizes the video image, groups the picture elements into three user-determined intensity categories corresponding to background, leaf, and uredinium, determines the area of each uredinium, and calculates the severity. Each leaf was examined in five 2.2-cm segments. The endpoint intensity levels demarcating the three categories were carefully selected for each leaf section to ensure the video images of the uredinia accurately represented the actual uredinia in size and shape.

Data analysis. Linear and polynomial regression were used to determine the relation of rust severity and time of day that physiological processes were measured to PRA, CC, TR, R_s, and C_i for flag leaves. Model selection was based on adjusted R^2 values, general F test results, significance levels of linear and quadratic regression coefficients, and graphic plots of data, predicted values, and residuals. The model assumption of normality was checked with normal probability plots and the homoscedasticity (constant variance) assumption was checked by examining plots of residuals versus time and residuals versus predicted values. The computer software packages SAS (36) and MINITAB (30) were used to perform the analyses.

To combine data from all sampling dates, variability in physiological processes associated with the time and the day of observation was removed from the analysis of the relationships between these processes and rust severity. Ordinary least squares regression was used to select the model of each physiological process on time that best fit the data from control leaves for

a particular day. The regression coefficients were used to calculate relative values for each physiological response variable. Observed values for all leaves were divided by the predicted value for a control leaf at the same time to obtain a relative value. The assumption that infected and healthy leaves exhibit a similar trend with time is acceptable because for each day and each physiological process, the regression equation of the response variable on both time and base 10 logarithm of rust severity plus 1 (hereafter referred to as log severity) and the regression equation of the relative response variable on log severity have similar adjusted R^2 values; thus, these pairs of equations explain a similar amount of variability. RPRA, RPRC, RTR, RR_s, and RC_i are the relative response variables for PRA, PRC, TR, R_s, and C_i, respectively. Relative values were not calculated for CC and A/B because these variables were expected to be constant during a sampling day.

Logarithmic transformation of (rust severity plus 1) was used to stabilize variance and linearize the relationship between each physiological process and the independent variable severity. The constant was added to severity to allow for the inclusion of data from rust-free leaves because log of 0 is undefined.

For each physiological process, regression equations were fit to the data from each sampling date. This set of equations formed the full or most general model. The full models for 1986 and 1987 consisted of seven and nine regression equations, respectively. Reduced models consisting of fewer parameters were also fit to the data. The general linear F test was used to determine if the reduced models were statistically different from the full model and to identify the most parsimonious model, which is the reduced model with the fewest parameters that does not differ significantly from the full model. For each physiological process, a reduced model consisting of one intercept and one slope also was fit to all the data from each year and all the data from both years to determine the average response, which is important for mechanistic modeling. This type of reduced model is referred to as a coincident regression model because the regression lines are all the same.

The relationships between CC and PRA or RPRA were analyzed for data of each sampling date by fitting piecewise linear regression models consisting of two pieces. Values of CC selected for the location of the slope change in these models included 3 mg chlorophyll/dm^2 leaf surface, which is the level required for saturation of the CO_2 assimilating capacity of most higher plant leaves (22).

RESULTS

Only stem rust was present during 1986, whereas both leaf rust and stem rust occurred in 1987. During 1987, leaves with uredinia only of leaf rust were sampled on day 167, 168, and 171, whereas several leaves selected on the other days were infected by both fungi. Leaves of plants in and near the inoculated rows were infected by both fungi. *P. r. tritici* predominated on leaves throughout the rest of each field. *P. g. tritici* infected culms throughout these fields. Rust severity of the most severely infected leaf examined on the successive days of monitoring ranged from about 10 to 25% in 1986 and from 3 to 30% in 1987.

Selected control leaves were rust-free in 1986 and nearly rust-free (usually $\leq 0.1\%$) in 1987. Very few leaves without rust uredinia could be found after the second sampling date in 1987, because mancozeb was less effective against leaf rust. These low levels of rust did not appear to have a detectable impact on host physiology based on examination of graphs of nontransformed data.

PRA, PRC, TR, R_s, and C_i of rust-free leaves usually varied during each day as well as between days. For example, on 29 May 1986 (day 149) the PRA of rust-free (control) leaves increased linearly during the morning and the average rate was 1.06 mg $CO_2/m^2/sec$. On 3 June 1986 (day 154) the rates were not time dependent and the average rate was 0.57 mg $CO_2/m^2/sec$. On 4 June 1986 (day 155) the average rate was 0.56 mg $CO_2/m^2/sec$ and there was a quadratic trend with time. This variation is not abnormal but rather reflects daily variation in temperature, soil moisture, and other environmental conditions. Variability of PRA, PRC, TR, R_s, and C_i associated with the time and day of observation was removed from the analysis of the relationships between each of these physiological processes and rust severity by expressing measurements as relative to the predicted value for a control leaf at the same time.

Regression analysis was used to examine the relationships between rust severity and CC, A/B, and the relative response variables RPRA, RPRC, RTR, RR_s, and RC_i (Tables 1 and 2). Each coincident regression model was significantly different from the corresponding full model; however, the variation among sampling dates appeared to be due to chance rather than a biological factor such as leaf age. Most of the intercept estimates for equations with RPRA, RPRC, RTR, RC_i, and RR_s as the independent variable were not statistically different from 1.0 ($\alpha = 0.05$). The only exceptions were with RC_i for day 168 in 1987, and with RPRA and RC_i for the coincident model (days 149–171) in 1987. Therefore the slope estimates can be interpreted directly as predicted proportion reductions in these physiological parameters relative to rust-free leaves for leaves with log severity equal to 1. The predicted proportion reductions in PRA, PRC, TR, R_s, and C_i were the same as the corresponding predicted values for RPRA, RPRC, RTR, RR_s, and RC_i because expressing these physiological parameters as relative values did not affect the relationships between these variables and rust severity.

The relationship between each physiological process and log severity evidently did not differ for stem rust and leaf rust, since similar regression parameter estimates were obtained for most sampling dates, although wheat was not infected by *P. r. tritici* in 1986 and leaves measured on days 167, 168, and 171 in 1987 were not infected by *P. g. tritici*. These relationships did not exhibit a temporal trend during the grain-filling period, thus the effect of disease on physiological processes of the host apparently did not vary with age of leaf or pustule. Furthermore, the effect of disease did not vary with the amount of photosynthetically active radiation (PAR). Average PAR values during measurements on the first eight sampling days in 1987 ranged from 1,241 to 2,176 $\mu E/sec/m^2$ and usually exceeded 1,500 $\mu E/sec/m^2$; whereas on day 171 the average PAR values ranged from 227 to 809 $\mu E/sec/m^2$.

Leaf rust and stem rust of flag leaves were associated with a reduction in PRA and RPRA (Tables 1 and 2 and Fig. 1A). Leaves with negative RPRA values were respiring faster than they were photosynthesizing. The RPRA of a flag leaf with a value of 1 for log severity, which is equivalent to 9% rust, was predicted to be reduced by 54.8–80.5% relative to rust-free leaves on the seven sampling dates in 1986 (Table 1) and by 33.3–84.0% on the nine sampling dates in 1987 (Table 2). The relationship between each response variable and disease severity was logarithmic. The two extremes for 1987 may represent atypical values. On the first sampling date the highest severity of the selected leaves was only 3.2% because the epidemics were just beginning. Only 14 leaves could be measured on day 165 before clouds developed and only six of these leaves had greater than 1% rust severity. The estimated intercepts of all lines for each year were not different ($\alpha = 0.05$). There were differences among the estimated slopes, consequently the coincident regression model was different from the concurrent regression model, which consists of equal intercepts and arbitrary slopes, for data collected in 1986 ($F = 5.68$; $P = 0.0001$) and 1987 ($F = 6.34$; $P = 0.0001$). However, these differences probably reflected chance or unexplainable variation. From the combined data, the RPRA of leaves with 9% stem rust in 1986 and leaves with 9% stem and leaf rust in 1987 were predicted to be 65.6% and 60.1%, respectively, as compared with rust-free leaves (Tables 1 and 2). An average reduction in RPRA of 61.3% was predicted for both years. The standard error was 0.0164; therefore, the 95% confidence interval was $\pm$ 0.0368 or $\pm$ 3.68%. Predicted reductions in RPRA and PRA would be the same because expressing PRA as a relative value does not affect its relationship with rust severity. The adjusted R^2 values for the full model, which consisted of 16 regression equations fit to the data from each sampling date,

and the reduced model that was comprised of one intercept and one slope (coincident regression model) were 79.93 and 75.34%, respectively. These models were different ($F = 4.69$; $P = 0.0001$).

The concentration of chlorophyll a and b was associated negatively with the severity of rust (Fig. 1B and Tables 1 and 2). The CC of leaves with 9% rust was predicted to be reduced by an average of 54.4% (range = 45.4–64.8% for the individual regression lines) in 1986 and 54.2% (range = 22.5–77.9%) in 1987. Estimated slopes for the regression lines fit independently to the data for each sampling date within each year were not different

TABLE 1. Regression parameter estimates and their standard errors (SE) for the linear relationships of relative photosynthetic rate per unit of leaf area (RPRA), relative photosynthetic rate per unit of chlorophyll (RPRC), chlorophyll a/chlorophyll b ratio (A/B), chlorophyll content (CC) (mg/dm^2), relative transpiration rate (RTR), relative stomatal resistance (RR_s), and relative internal CO_2 concentration (RC_i) to $\log_{10}$ (stem rust severity + 1) for wheat flag leaves in 1986

Dependent variable[a]	Day of the year	Intercept		Slope		R^2 (%)	df
		Estimate	SE	Estimate	SE		
RPRA	149	1.0079	0.0381	−0.5476	0.0542	83.63	20
	154	0.9284	0.0492	−0.6658	0.0846	74.66	21
	155	1.0195	0.0366	−0.7167	0.0660	81.37	27
	160	1.0008	0.0262	−0.6119	0.0398	85.19	41
	161	0.9998	0.0212	−0.6373	0.0370	90.82	30
	167	1.0050	0.0308	−0.6597	0.0413	93.06	19
	169	1.0064	0.0312	−0.8053	0.0542	88.29	29
	149–169	0.9937	0.0130	−0.6559	0.0206	83.50	200
RPRC	149	1.0094	0.0909	−0.2159[b]	0.1294	12.22	20
	154	0.9067	0.0542	−0.5235	0.0932	60.04	21
	155	1.0102	0.0407	−0.4291	0.0735	55.79	27
	160	1.0136	0.0281	−0.4985	0.0432	76.03	41
	161	1.0004	0.0235	−0.4522	0.0410	80.26	30
	167	1.0033	0.0277	−0.2974	0.0372	77.07	19
	169	1.0428	0.0461	−0.5302	0.0800	60.21	29
	149–169	0.9974	0.0178	−0.4237	0.0283	52.72	200
A/B	149	3.5801	0.1093	−0.3798	0.1555	22.97	20
	154	3.5873	0.0666	−0.2769	0.1171	20.27	21
	155	3.4924	0.0540	−0.3481	0.0976	32.04	27
	160	3.1254	0.0337	−0.1856	0.0512	24.27	41
	161	3.1487	0.0389	−0.0554[b]	0.0678	2.18	30
	167	3.0035	0.0486	−0.2735	0.0654	47.94	19
	169	2.9497	0.0529	−0.2907	0.0854	27.85	30
	149–169	3.2504	0.0301	−0.2698	0.0478	13.67	200
CC	149	3.7280	0.1841	−1.7605	0.2620	69.31	20
	154	4.3602	0.1786	−2.3395	0.3072	73.41	21
	155	4.2969	0.1862	−2.6237	0.3363	69.28	27
	160	4.6432	0.1205	−2.2750	0.1853	78.21	41
	161	4.1495	0.1415	−1.8846	0.2465	66.08	30
	167	3.9962	0.1481	−2.4359	0.1990	88.74	19
	169	3.6222	0.1520	−2.3488	0.2453	75.35	30
	149–169	4.1702	0.0678	−2.2685	0.1076	68.87	200
RTR	149	0.9989	0.0259	−0.0662[b]	0.0368	13.88	20
	154	1.0032	0.0139	−0.1438	0.0239	63.31	21
	155	1.0072	0.0141	−0.2254	0.0255	74.36	27
	160	0.9906	0.0164	−0.2016	0.0252	60.29	41
	161	0.9796	0.0206	−0.2619	0.0358	64.06	30
	167	0.9960	0.0180	−0.2821	0.0242	87.75	19
	169	0.9877	0.0205	−0.1964	0.0330	54.09	30
	149–169	0.9941	0.0082	−0.1966	0.0130	54.13	200
RR_s	149	1.0141	0.0975	0.4997	0.1387	39.36	20
	154	1.0053	0.0390	0.3494	0.0670	56.42	21
	155	0.9778	0.0292	0.6882	0.0529	86.68	27
	160	1.0391	0.0676	0.9660	0.1040	67.28	41
	161	1.0503	0.0658	0.9058	0.1146	67.54	30
	167	1.0169	0.1175	1.4462	0.1579	81.54	19
	169	1.0439	0.0656	0.9463	0.1058	72.71	30
	149–169	1.0136	0.0328	0.8849	0.0520	59.10	200
RC_i	149	0.9965	0.0145	0.0834	0.0206	44.97	20
	154	1.0194	0.0210	0.1093	0.0360	30.46	21
	155	0.9984	0.0102	0.0903	0.0184	47.22	27
	160	0.9944	0.0078	0.0368	0.0120	18.43	41
	161	0.9788	0.0144	0.1133	0.0250	40.63	30
	167	0.9961	0.0090	0.0335	0.0121	28.66	19
	169	0.9693	0.0224	0.3000	0.0362	69.58	30
	149–169	0.9958	0.0073	0.1010	0.0115	27.63	200

[a] Values predicted by the regression model are relative to the predicted value for a leaf unaffected by rust at the same time. Logarithmic transformation of (rust severity + 1) was used.

[b] Based on the t statistic, parameter estimate is not different from 0 ($P = 0.05$).

($\alpha = 0.05$) for 1986, whereas they were different for 1987 ($F = 6.50$; $P = 0.0001$). There were differences among the intercepts for both years; therefore, models consisting of parallel regression lines were fit to the data. The common slopes for these two reduced models were −2.2339 and −1.4527 for 1986 and 1987, respectively, and the adjusted R^2 values were 75.80 and 70.01%, respectively. The coincident regression model was different from the parallel regression model for 1986 ($F = 10.80$; $P = 0.0001$) and 1987 ($F = 23.17$; $P = 0.0001$). The adjusted R^2 values for these coincident regression models were 68.72 and 51.41%, respectively. The CC of leaves with 9% rust was predicted to be reduced by 55.3% based on the combined data from both years (adj. $R^2 = 53.11\%$).

The concentrations per gram of tissue of both chlorophyll a and chlorophyll b were reduced in diseased tissue, but chlorophyll a was lost preferentially. Consequently, rust severity was inversely related to A/B (Fig. 1C and Tables 1 and 2). The A/B of leaves with 9% rust was predicted to be reduced by an average of 8.3% (range = 1.8–10.6%) in 1986 and 12.0% (range = 0.0–22.3%) in 1987. Differences existed among estimated intercepts for both years and estimated slopes for 1987 ($F = 5.23$; $P = 0.0001$), but not among slopes for 1986 ($F = 1.56$; $P = 0.1621$). The adjusted

TABLE 2. Regression parameter estimates and their standard errors (SE) for the linear relationships of relative photosynthetic rate per unit of leaf area (RPRA), relative photosynthetic rate per unit of chlorophyll (RPRC), chlorophyll a/chlorophyll b ratio (A/B), chlorophyll content (CC) (mg/dm^2), relative transpiration rate (RTR), relative stomatal resistance (RR_s), and relative internal CO_2 concentration (RC_i) to $\log_{10}$ (rust severity + 1) for wheat flag leaves in 1987

Dependent variable[a]	Day of the year	Intercept		Slope		R^2 (%)	df
		Estimate	SE	Estimate	SE		
RPRA	149	0.9979	0.0204	−0.3330	0.0688	52.76	21
	150	0.9849	0.0205	−0.5845	0.0462	91.44	15
	156	1.0154	0.0293	−0.5168	0.0619	67.85	33
	161	1.0394	0.0314	−0.6547	0.0566	77.43	39
	162	1.0658	0.0328	−0.6862	0.0501	81.37	43
	165	1.0340	0.0381	−0.8399	0.0654	93.22	12
	167	1.0790	0.0408	−0.5537	0.0723	57.12	44
	168	1.0843	0.0527	−0.5149	0.0841	49.02	39
	171	1.0569	0.0483	−0.6322	0.0687	75.84	27
	149–171	1.0503	0.0132	−0.6011	0.0231	70.01	289
RPRC	149	0.9956	0.0182	−0.3083	0.0695	50.87	20
	150	0.9634	0.0286	−0.3012	0.0644	59.34	15
	156	0.9865	0.0322	−0.1699	0.0671	16.67	32
	161	1.0043	0.0368	−0.1889	0.0658	17.82	38
	162	1.0033	0.0349	−0.3218	0.0535	46.26	43
	165	0.9751	0.0700	−0.2222[b]	0.1201	22.18	12
	167	1.0409	0.0396	−0.2389	0.0709	20.91	44
	168	1.0178	0.0706	−0.3120	0.1127	16.42	39
	171	0.9615	0.0814	−0.4690	0.1146	39.18	27
	149–171	1.0107	0.0156	−0.3030	0.0273	30.15	286
A/B	149	3.6051	0.0486	−0.1699[b]	0.1858	4.21	20
	150	3.4369	0.0711	−0.4621	0.1600	35.75	15
	156	3.3797	0.0426	−0.1446[b]	0.0889	7.64	32
	161	3.4809	0.0431	−0.3255	0.0770	31.96	38
	162	4.0879	0.0846	−0.5962	0.1291	33.14	43
	165	3.5248	0.0816	−0.3473	0.1401	33.86	12
	167	3.2661	0.0398	−0.2379	0.1705	20.55	44
	168	4.0644	0.0906	−0.8485	0.1446	46.90	39
	171	3.5618	0.1325	−0.7959	0.1885	39.76	27
	149–171	3.6116	0.0323	−0.4337	0.0564	17.11	286
CC	149	3.6549	0.0640	−1.2016	0.2261	58.55	20
	150	3.5473	0.0886	−1.5530	0.1993	80.19	15
	156	3.6342	0.0914	−1.7987	0.1904	73.61	32
	161	3.0478	0.0978	−1.7571	0.1747	72.69	38
	162	2.6161	0.0864	−1.3996	0.1319	72.37	43
	165	3.3804	0.1281	−2.6321	0.2199	92.27	12
	167	3.4954	0.1337	−1.6713	0.2371	53.03	44
	168	2.1760	0.1599	−0.4887[b]	0.2552	8.59	39
	171	1.9972	0.2604	−0.6060[b]	0.3706	9.01	27
	149–171	3.1589	0.0563	−1.7135	0.0982	51.58	286
RTR	149	1.0072	0.0176	−0.0031[b]	0.0593	0.00	21
	150	1.0351	0.0234	−0.0599[b]	0.0526	7.96	15
	156	1.0212	0.0210	−0.1726	0.0445	31.33	33
	161	1.0093	0.0218	−0.1665	0.0393	31.50	39
	162	1.0057	0.0275	−0.2239	0.0420	39.80	43
	165	1.0124	0.0278	−0.2958	0.0477	76.24	12
	167	0.9961	0.0283	−0.1219	0.0502	11.81	44
	168	1.0037	0.0283	−0.0691[b]	0.0446	5.94	39
	171	0.9810	0.0435	−0.2377	0.0610	36.90	27
	149–171	1.0148	0.0097	−0.1803	0.0169	28.31	289

Continued on next page

TABLE 2. (*continued from preceding page*)

Dependent variable[a]	Day of the year	Intercept		Slope		R^2 (%)	df
		Estimate	SE	Estimate	SE		
RR_s	149	0.9802	0.0504	0.0018[b]	0.1701	0.00	21
	150	0.9565	0.0399	0.2823	0.0897	39.97	15
	156	0.9585	0.0445	0.2750	0.0942	20.54	33
	161	0.9848	0.0474	0.4929	0.0855	46.03	39
	162	0.9596	0.0587	0.5314	0.0896	44.97	43
	165	0.9370	0.1120	1.5786	0.1924	84.87	12
	167	0.9986	0.1066	0.7528	0.1890	26.50	44
	168	0.9408	0.0547	0.3127	0.0862	25.71	39
	171	0.7245	0.2151	1.6358	0.3016	53.08	27
	149–171	0.9388	0.0338	0.6928	0.0591	32.29	289
RC_i	149	1.0027	0.0163	0.1117[b]	0.0550	16.42	21
	150	1.0170	0.0167	0.2020	0.0376	65.85	15
	156	0.9918	0.0148	0.2388	0.0313	63.77	33
	161	0.9818	0.0178	0.3108	0.0322	70.55	39
	162	0.9158	0.0343	0.4634	0.0523	64.62	43
	165	0.9866	0.0169	0.1206	0.0290	59.02	12
	167	0.9750	0.0199	0.0592[b]	0.0353	6.01	44
	168	0.9360	0.0304	0.2487	0.0485	40.26	39
	171	0.9737	0.0197	0.0324[b]	0.0280	4.72	27
	149–171	0.9643	0.0107	0.2262	0.0189	33.36	289

[a] Values predicted by the regression model are relative to the predicted value for a leaf unaffected by rust at the same time. Logarithmic transformation of (rust severity + 1) was used.
[b] Based on the t statistic, parameter estimate is not different from 0 ($P = 0.05$).

R^2 values for the full and coincident regression models were 59.06 and 13.24% for 1986 and 55.87 and 16.82% for 1987. The predicted reduction in A/B for leaves with 9% rust based on all data was 10.2%.

CC and PRA or RPRA were linearly related only for control and infected leaves with a CC that was equal to or less than 3.2 mg chlorophyll/dm^2 (Fig. 2). Most leaves infected by *P. r. tritici* and/or *P. g. tritici* had a CC below 3.2 mg/dm^2. Piecewise linear regression models consisting of two pieces were used to analyze these relationships (Fig. 2). Slope change at 3.2 provided the best fit to the data. The slope for the relation between CC and RPRA from 0 to 3.2 mg/dm^2 was significant for all dates in both years (Table 3). The null hypothesis that the second slope equals zero could be rejected ($\alpha = 0.05$) for three of the seven dates in 1986 based on a t test; however, the slope estimate for the regression line between 0 and 3.2 mg/dm^2 for these three dates was much larger than the slope estimate for the line beginning at 3.2 mg/dm^2 (0.3453 versus 0.1798, 0.3841 versus 0.1258, and 0.3408 versus 0.0883) (Table 3). The second slope was not different from 0 for six of seven sampling dates in 1987 (Table 3). CC did not exceed 3.2 mg/dm^2 for any leaves on 2 days.

RPRC was regressed on log severity to determine whether the reduction in RPRA for infected leaves could be accounted for by the reduction in CC. The estimated intercepts of all lines for each year were not different ($\alpha = 0.05$). The coincident and concurrent regression models were different for data collected in 1986 ($F = 7.86$; $P = 0.0001$) and 1987 ($F = 5.42$; $P = 0.0001$), which indicates the slopes are different. The full and coincident regression models fit to the combined data were different ($F = 4.70$; $P = 0.0001$). Log severity accounted for less variability in RPRC than in RPRA, based on R^2 values (Tables 1 and 2); therefore, reduction in the latter dependent variable is partially due to decreased CC. For each increase of 1 in log severity, the RPRA was predicted to decrease by 61.3% (SE = 0.016; adj. $R^2 = 75.34\%$), whereas the RPRC was predicted to decrease by only 34.5% (SE = 0.021; adj. $R^2 = 35.69\%$) based on all the data collected in 1986 and 1987. There are additional effects of stem and leaf rust on the light reactions of photosynthesis, since the regression lines for the relationship between RPRC and log severity were statistically significant for all sampling dates except the first (day 149) in 1986 and the sixth (day 165) in 1987.

Stem rust and leaf rust also significantly reduced RTR, increased RR_s, and increased RC_i of the flag leaves on most sampling dates (Fig. 1D–F and Tables 1 and 2). Significant relationships may not have been detected on the first sampling date in 1987 because rust does not affect these variables within a few days of infection or because there was an insufficient range in severity among leaves at that time. The highest severity observed was only 3.2%. Leaves with 9% rust were predicted to exhibit a 19.1% reduction in RTR (SE = 0.0110; adj. $R^2 = 38.35\%$), a 79.6% increase in RR_s (SE = 0.0416; adj. $R^2 = 42.97\%$), and a 16.5% increase in RC_i (SE = 0.0118; adj. $R^2 = 28.04\%$) in 1986 and 1987. The full and coincident regression models fit to all the data were different for RTR ($F = 4.49$; $P = 0.0001$), RR_s ($F = 10.86$; $P = 0.0001$), and RC_i ($F = 14.04$; $P = 0.0001$). The adjusted R^2 values for the full models were 49.32, 64.60, and 60.20%, respectively.

The effects of stem rust and leaf rust on the physiological processes of the peduncle and the flag leaf sheath were similar to the effects of these diseases on the physiological processes of flag leaves. Flag leaf sheaths with 9% stem rust in 1986 were predicted to exhibit a reduction in RPRA of 74.0% (SE = 0.109), a reduction in RTR of 24.6% (SE = 0.0527), an increase in RR_s of 65.9% (SE = 0.1293), and an increase in RC_i of 18.2% (SE = 0.0448) compared with rust-free leaf sheaths based on 13 measurements made on day 172. The adjusted R^2 values for these regression equations were 78.98, 67.55, 63.43, and 56.32%, respectively. Peduncles with 9% stem rust were predicted to exhibit a reduction in RPRA of 52.9% (SE = 0.0689), a reduction in RTR of 19.0% (SE = 0.0353), an increase in RR_s of 25.9% (SE = 0.0530), and an increase in RC_i of 14.3% (SE = 0.0260) based on 24 measurements made on day 172. The adjusted R^2 values for these regression equations were 71.61, 54.85, 49.85, and 55.89%, respectively. Flag leaf sheaths with 9% stem and leaf rust were predicted to exhibit a reduction in PRA of 64.9%, a reduction in PRC of 67.4%, and an increase in C_i of 18.1% based on measurements made on day 176 in 1987. Estimated slopes for CC, A/B, TR, and R_s regressed on log severity were not different from 0 ($\alpha = 0.05$) because of the large variation among samples. Likewise none of the regression equations for these response variables were significant for peduncles. Furthermore, variation among successive observations within each measurement was much greater for flag leaf sheaths and peduncles than for flag leaf blades. This variation may have been due to a poor seal when the chamber was closed on these stem structures. However, graphs of the data for flag leaf sheaths and peduncles exhibited trends of similar direction to the trends for leaf blades.

DISCUSSION

PRA was reduced in wheat flag leaves infected by *P. g. tritici* and *P. r. tritici* in 1986 and 1987. Relative photosynthetic rate was linearly related to the $\log_{10}$ of rust severity plus 1. The percent reduction greatly exceeded the percent leaf area covered by pustules, therefore loss of photosynthetic tissue on an area basis could not account for the reduced photosynthetic rate. Leaves with 9% stem rust in 1986 and 9% stem rust and leaf rust in 1987 were predicted to photosynthesize at 38.7% of the rate of noninfected leaves. Leaves with 41.7% rust were predicted to have a PRA equal to 0. Leaf rust and/or stem rust in these experimental field plots reduced the rate and duration of grain growth and decreased grain dry weight at maturity by up to 50% (27). The relation between photosynthetic rate and severity for barley leaves infected with *Erysiphe graminis* D.C. f. sp. *hordei* Marchal, the

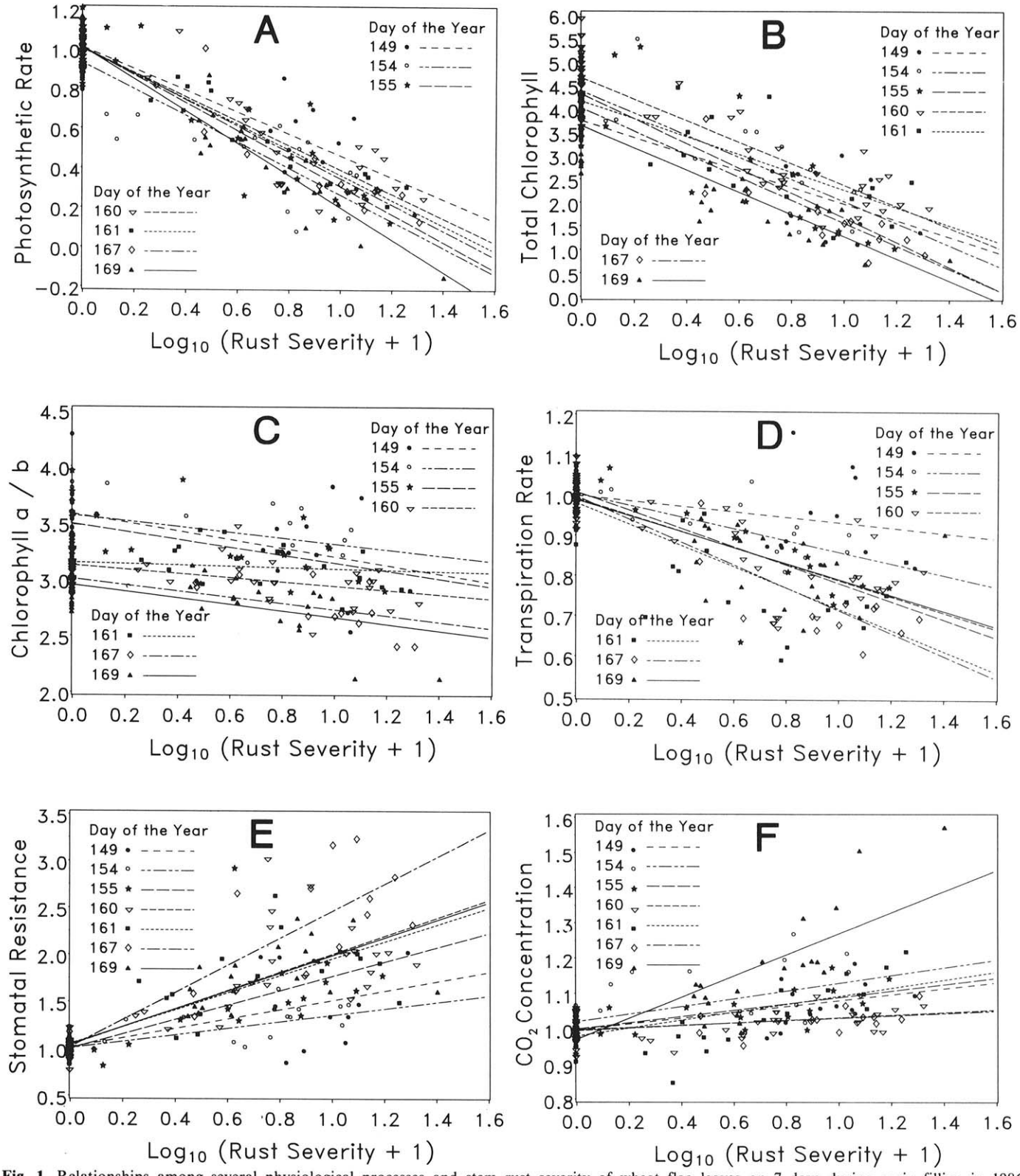

Fig. 1. Relationships among several physiological processes and stem rust severity of wheat flag leaves on 7 days during grain filling in 1986. Lines represent the fitted regression equations for each day. Dependent variables are **A,** relative apparent photosynthetic rate; **B,** total chlorophyll content (mg/dm^2); **C,** chlorophyll a/chlorophyll b; **D,** relative transpiration rate; **E,** relative stomatal resistance; and **F,** relative internal CO_2 concentration.

TABLE 3. Piecewise regression parameter estimates for the relationship between relative photosynthetic rate per unit of leaf area and total chlorophyll with slope change at 3.2 mg of chlorophyll/dm^2

Year	Day of the year	Slope 1[a]		Slope 2[b]		R^2 (%)	df
		Estimate	SE	Estimate	SE		
1986	149	0.2744	0.0636	0.1100[c]	0.1151	63.72	19
	154	0.3267	0.0752	0.1464[c]	0.0721	71.56	20
	155	0.3562	0.0519	0.0647[c]	0.0534	79.02	26
	160	0.3453	0.0481	0.1798	0.0309	85.62	40
	161	0.3841	0.0626	0.1258	0.0566	77.77	29
	167	0.3408	0.0220	0.0883	0.0403	97.21	18
	169	0.3866	0.0340	0.1095[c]	0.0562	89.34	29
1987	149	0.7515	0.2337	0.1121[c]	0.0726	54.29	19
	150	0.3319	0.0760	0.2188[c]	0.1464	72.40	14
	156	0.2937	0.0456	0.1019[c]	0.0810	64.96	31
	161	0.3536	0.0344	0.0315[c]	0.1434	77.92	37
	162	0.4108	0.0337	...[d]	...	77.94	43
	165	0.3445	0.0399	−0.0541[c]	0.2153	90.93	11
	167	0.3135	0.0378	−0.0700[c]	0.0787	66.67	43
	168	0.1591	0.0659	...[d]	...	13.00	39
	171[e]	0.2205	0.0710	−0.9168[c]	0.8608	27.50	26

[a] Slope estimate for the regression line between 0 and 3.2 mg/dm^2.
[b] Slope estimate for the regression line beginning at 3.2 mg/dm^2.
[c] Based on the t statistic, parameter estimate is not different from 0 ($P = 0.05$).
[d] Chlorophyll content did not exceed 3.2 mg/dm^2 for any leaf.
[e] Chlorophyll content exceeded 3.2 mg/dm^2 for only one leaf.

causal agent of powdery mildew, also appeared to be logarithmic (19). In contrast to wheat leaves infected by *P. g. tritici*, barley leaves with 50–100% powdery mildew severity continued to photosynthesize. The maximum reduction reported was 71%. Reduction of photosynthesis induced by apple (*Malus domestica* Borkh.) scab (*Venturia inaequalis* (Cke.) Wint.) was apparently partially compensated for by increased CO_2 assimilation of the remaining healthy tissue since the average percentage of leaf area diseased exceeds the percentage of reduction in CO_2 assimilation based on whole leaf measurements (40).

The PRA of wheat leaves infected by *P. g. tritici* and/or *P. r. tritici* may have been reduced due to chlorosis around the pustules and a general yellowing of the leaf blade. CC is not considered a limiting factor to photosynthesis in healthy leaves because most higher plant leaves contain more than about 3 mg chlorophyll/dm^2 leaf surface, which is the level required for saturation of the assimilating capacity in higher plants (22). In contrast, most infected leaves had concentrations below this critical level. The CC of leaves with 9% rust in both years was predicted by regression analysis to be reduced by 55.3% compared with rust-free leaves. PRA and RPRA of infected and rust-free leaves were related to CC only when CC was less than 3.2 mg chlorophyll/dm^2. This reduced CC could not completely explain the reduced PRA, since the relation between RPRC and log severity was statistically significant. An average reduction in PRC of 34.5% was predicted for leaves with 9% rust. Therefore, rust infection must have additional effects on the light reactions of photosynthesis. Similar results have been obtained previously for wheat stem rust (4,31), wheat powdery mildew (1), and sugar beet (*Beta vulgaris* L.) powdery mildew (*Erysiphe polygoni* D.C.) (23). The A/B was reduced in leaves infected by *P. g. tritici* and/or *P. r. tritici*, which implies that chlorophyll breakdown was occurring. A common feature of leaf senescence is a slight decrease in A/B due to more rapid destruction of chlorophyll a than of chlorophyll b (11,48).

There are several potential explanations for the reduction in PRC associated with stem rust and leaf rust. A suppression of ATP formation in noncyclic photophosphorylation has been demonstrated for faba bean (*Vicia faba* L.) rust (*Uromyces viciaefaba* (Pers.) Shroet) (32) and sugar beet powdery mildew (23). Another possible explanation is end product inhibition of photosynthesis by starch and other carbohydrates accumulating around rust pustules. Carbon compounds previously have been shown to accumulate in wheat leaves infected by *Puccinia* species (5,37,45). Stem and leaf rust were associated with an increase in R_s. However,

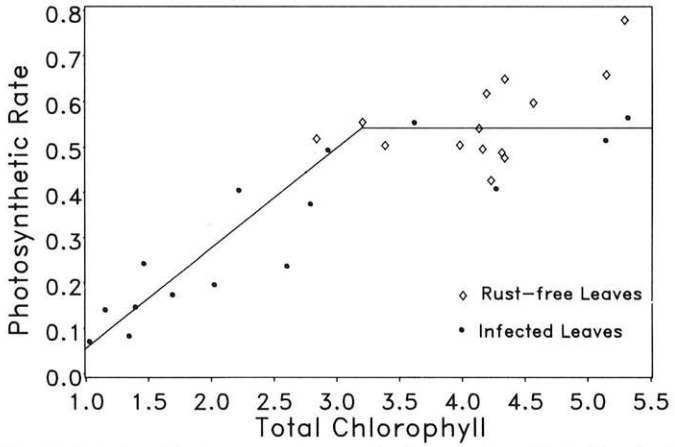

Fig. 2. Relationship between photosynthetic rate (mg CO_2/m^2/sec) of wheat flag leaves and chlorophyll content (mg/dm^2) on 4 June 1986 (day 155). The curve was fit to the data using piecewise linear regression with slope change at 3.2 mg/dm^2.

a decrease in stomatal conductance to CO_2 and water vapor is not a feasible explanation for the reduced PRC because stem and leaf rust also were associated with an increase, rather than a decrease, in C_i. Therefore CO_2 apparently was not a limiting factor. This increase is due to a decrease in photosynthesis and/or an increase in host as well as fungal respiration. Leaves with 9% rust were predicted to exhibit an increase in R_s of 79.6% and an increase in C_i of 16.5%. Apparent photosynthetic rate is equal to gross photosynthetic rate minus respiration rate; therefore, an increase in respiration may account for a small fraction of the observed reduction in apparent photosynthetic rate. Several studies involving other pathosystems have shown that there is only a small increase in dark respiration and photorespiration associated with infection (5,15,19,29,31).

The decreased TR in flag leaves infected by *P. g. tritici* and/or *P. r. tritici* contrasted with increased TRs previously reported in wheat leaves affected by leaf rust and stem rust (17,44,46), as well as in several other hosts with rust diseases (6,7,10,13,42,50). Accelerated water loss from infected tissue has been attributed most frequently to epidermal rupture by pathogens (7,13,40,42). The discrepancy in observations may have resulted from the procedures or tissues used to measure the TR, or the conditions under which the measurements were made. Measurements in

previous studies were made on tissues ranging from portions of leaves to whole plants, which in most instances were grown in containers under controlled conditions. The gravimetric or lysimeter method, which involves weighing plants that are growing in sealed, waterproof containers at regular intervals, has been used frequently to determine TR (7,10,17,35,44,46,50). This method does not facilitate measuring transpiration over periods of less than about 24 hr, and it does not account for possible weight gain due to photosynthesis or weight loss due to respiration (10). Results obtained with this method for diseased plants may be misleading. For example, bean plants with two primary leaves infected by *U. phaseoli* transpired at a faster rate than healthy leaves during day and night periods based on results obtained gravimetrically; however, measurements made on primary or trifoliate leaves enclosed in a chamber with a hygrometer revealed that diseased leaves transpired at a slower rate than healthy leaves during the day and at a faster rate during the night (6,7). The TR of apple leaves with cedar rust (*Gymnosporangium juniperi-virginianae* Schw.) was shown to be lower than the TR of healthy leaves during the day by enclosing nondetached branches in glass cylinders with calcium chloride to absorb transpired water for 2 hr (33). These results confirm the findings for wheat rust obtained during our study.

An increase in TR caused by stem rust or leaf rust may not have been observed during this study because measurements were made during sunny mornings on field-grown plants with adequate soil moisture. Under these conditions, stomates of healthy plants are expected to be fully open because of high light intensity, low wind speed, high leaf water content, large water vapor pressure deficit, as well as their endogenous rhythm (28). The difference in water vapor pressure between leaf and atmosphere increases as the sun warms the air. Consequently, stomatal transpiration is expected to be maximal. It can equal about 90% of the evaporation rate from an open water surface of similar size and shape for a leaf with an entire margin, such as wheat, although the total pore area of open stomata amounts to only 1–2% of the leaf area. Stomata form very efficient paths for vapor diffusion because their small size and spatial distribution in the epidermis allows relatively fast diffusion into the atmosphere. The ratio of perimeter to area decreases geometrically with increasing pore size; therefore, a few large openings such as uredinia are relatively less efficient than the many small stomatal pores they replace. Efficiency would be inversely related to rust severity, which was shown during the current study to be inversely related to TR. Furthermore, R_s and cuticular resistance as well as C_i were positively related to severity. This suggests that the reduced PRA associated with stem and leaf rust may cause an increase in C_i, which in turn causes a closure of stomata, a consequent increase in leaf resistance, and thus a decrease in transpiration. On the other hand, infected leaves are expected to transpire at a faster rate than comparative healthy leaves under conditions such as darkness and water stress that cause stomates of healthy leaves to close, because of the inability of infected leaves to prevent water vapor diffusion through breaks in the cuticle from sporulation. This hypothesis is supported by results from experiments with bean rust (6,7). Diseased leaves with a relative water content greater than 85% transpired at a slower rate during the day and at a faster rate during the night than comparable healthy leaves. When the relative water content decreased below 85%, the diffusive resistance of healthy leaves increased markedly due to stomatal closure, whereas diseased leaves exhibited a negligible increase in resistance although their stomates also closed. As a result, the diseased leaves transpired at a faster rate than healthy leaves when water stressed.

This study is an important contribution because disease severity was measured quantitatively, in contrast with many previous studies; consequently, regression analysis could be used to describe the relations between severity and physiological response variables.

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