A Multiple Regression Model to Estimate the Contributions of Leaves and the Effects of Leaf Rust on Yield of Winter Wheat

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ABSTRACT

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The contributions of each wheat leaf to tiller grain yield of cultivar McNair 1003, susceptible to prevalent leaf rust races, and the effect of leaf rust on each leaf were determined by defoliation and inoculation in 1986-87 and 1987-88 winter wheat-growing seasons. The 10 treatments included in the experiment involved removing/retaining flag (F), F-1, F-2, and F-3 leaves in different combinations from both rusted and control tillers. Maximum losses due to leaf rust in tiller grain weight, tiller grain number, and 1,000-grain weight were, respectively, 27.0, 19.0, and 24.0% in 1986-87 and 24.0, 23.0, and 18.0% in 1987-88. Maximum losses in tiller grain weight, tiller grain number, and 1,000-grain weight due to defoliation in rusted treatments were, respectively, 56.7, 46.4, and 29.8% in 1986-87 and 38.8, 27.8, and 19.9% in 1987-88; in control treatments losses were, respectively, 58.8, 41.6, and 38.1% in 1986-87 and 51.1, 35.6, and 31% in 1987-88. Defoliation of F in 1986-87 and F and F-1 in 1987-88 caused significant reduction of all the three yield components measured. Contributions to yield of the different parts of the tiller towards grain weight were estimated by the following regression model: $Y_{ij} = \beta_0 + \beta_1 F_i + \beta_2(F - 1_i) + \beta_3(F - 2_i) + \beta_4(F - 3_i) + \epsilon_{ij}$, in which β_0, β_1, β_2, β_3, and β_4 are the absolute contributions of the nonfoliar parts, F, F-1, F-2, and F-3 leaves, respectively, of the i^{th} tiller in the j^{th} treatment. The partial regression coefficients for the nonfoliar parts, F, F-1, and F-2 of the tiller were, respectively, 0.98 ± 0.08, 0.78 ± 0.13, 0.41 ± 0.19, and 0.23 ± 0.27 in the rusted treatments of 1986-87; 1.21 ± 0.07, 0.79 ± 0.11, 0.42 ± 0.13, and 0.34 ± 0.13 in the control treatments of 1986-87; 0.80 ± 0.05, 0.42 ± 0.09, 0.22 ± 0.09, and 0.14 ± 0.14 in the rusted treatments of 1987-88; and 0.87 ± 0.04, 0.44 ± 0.06, 0.28 ± 0.07, and 0.12 ± 0.07 in the control treatments of 1987-88. Paired *t*-tests for the estimated relative contributions of the leaves between rusted and control treatments each year were not significant, indicating that leaf rust does not alter the relative contribution of leaves of tiller to yield. The regression between the relative healthy area duration for each leaf and tiller grain weight was highly significant ($P = 0.0001$) with an adjusted R^2 of 0.84 and 0.91 for rusted and control treatments, respectively, in 1986-87 and 0.67 and 0.88, respectively, in 1987-88.

Additional keywords: *Puccinia recondita* f. sp. *tritici*, *Triticum aestivum*, yield losses.

Mechanical defoliation experiments have been widely used by agronomists to investigate the sink-source relationships in wheat (*Triticum aestivum* L.) (14,23,24) and to assess the contributions of individual plant parts to components of yield (8,16,23,32). These studies have demonstrated the importance of flag (F) and penultimate (F-1) leaves in increasing grain weight (8,24,32), 1,000-grain weight (8,24), and grains per ear (8,23,24).

Youssef and Salem (32) reported a loss in grain yield of up to 30% after removal of flag leaves. Ibrahim and Elenein (8) showed that, during the grain development period, the percent effective leaf area rather than the total leaf area is a major factor affecting the contributions of different leaves for grain filling. They observed that F-2, F-3, and F-4 leaves make only a minor contribution towards the main stem yield. Other studies have shown that the role for lower leaves increases when flag leaf area is reduced by shading or partial defoliation (15). Although most studies indicate the importance of leaves present during the reproductive phase, some studies report the importance of the foliage in the vegetative phase (4) and the interaction of different leaves for different yield components (12).

In phytopathological research, defoliation in conjunction with disease is a useful means of understanding the functions of the different plant parts and how their functions are affected by the foliar disease. Defoliation experiments were used in the 1930s to mimic the losses due to foliar pathogens of wheat (3). Hendrix et al (7), in a study on the effect of stripe rust (caused by *Puccinia striiformis* Westend.) and mechanical defoliation on yield of spring wheat, demonstrated that stripe rust caused a greater reduction in grain weight, grain size, tillering, number of grains, and average plant height than defoliation. The effect of leaf rust (caused by *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* Eriks.) and the effect of mechanical defoliation were found to be approximately equal with respect to 1,000-grain weight; however, *P. recondita* also exerted a sink effect on the surrounding leaf areas (28). Yang and Zeng (30), by defoliating stripe rust-infected and uninfected plants of the cultivar Yianda 1817, observed that the relative contributions of the individual leaves were the same in both rusted and control plants. Their results indicated that stripe rust affects only the photosynthetic area and that stripe rust on the top three leaves accounts for most of the disease-caused reduction in the grain yield. Losses due to leaf rust have been well documented (1-3,10,21). Seck et al (22) used the concept of average weighted severity in which the rust severity was corrected for leaf position by an empirically determined multiplier to determine the contributions of the top three leaves in wheat toward the final grain weight.

In previous works (8,16,21,23,24,28,30,32), the contribution of each leaf to yield was calculated by subtraction methods using comparisons of yields of treatments lacking specific leaves with the yields of treatments possessing all leaves. This study was undertaken to determine the effect of defoliation and leaf rust on three yield components of soft red winter wheat and to develop a model to estimate the contribution of each leaf towards tiller grain yield.

MATERIALS AND METHODS

Experiments reported here were conducted during the wheat-growing seasons of 1986-87 and 1987-88 at the Ben Hur Research Station of the Louisiana State University located in East Baton Rouge parish.

Plot establishment. The experimental design was a randomized complete block with three replications in 1986-87 and four replications in 1987-88. Plots received 60.8 kg/ha N (ammonium nitrate) before planting. McNair 1003, a soft red winter wheat cultivar susceptible to the prevalent races of leaf rust, was planted with 25-cm row spacings on 24 October 1986 and 21 October 1987. The plots were sprayed for weed control 20 days after emergence with chlorosulfuron at a rate of 0.05 kg/ha. Approximately 25 days after emergence, individual plots 3 m long were delimited, and the most vigorous seedlings in the plots were retained and thinned to give an interplant spacing of 10 cm. The main stem of each plant was tagged, and approximately 75 days after emergence the tillers were trimmed to retain only the main stem. The single-tiller method was adopted from earlier studies (30,32) because tillers would not become physiologically independent from the main stem (19). Trimming was continued as long as necessary to restrict the regeneration of the tillers. All plots in 1986-87 were top-dressed with 18 kg/ha N (urea).

Inoculation and defoliation. Defoliation treatments included in the experiment are listed in Table 1. In treatment 1 (all leaves defoliated), all leaves were clipped beginning at Feekes (13) growth stage 5. Defoliations in the remaining treatments were made as soon as the corresponding leaves unfolded. Leaves in each treatment were clipped at the base using scissors. The dates that each leaf unfolded in different treatments and the final date when the leaves ceased to be functional (senesced) were noted.

The treatments were duplicated in inoculated and experimental check (uninoculated) conditions. Arrangements of rusted and control treatment plots were paired. In inoculated treatments, an aqueous suspension of *P. recondita* urediniospores (approximately 10^6 spores/ml) was sprayed on the plants using an atomizer after 6:00 p.m. when the leaves were mostly wet on 3 March 1987 and 27 February 1988. Inoculations were repeated on 25 March 1987 and 28 March 1988. In control plots, the tillers were sprayed with butrizol, specific for control of leaf rust, at a rate of 0.98 kg/ha with a hand-held sprayer (Model No 21, R. E. Chapin Manufacturing Works, Inc, Batavia, NY) on 15 March 1987 and 27 February 1988 and again 3 wk later in each year.

Data collection and analysis. Severity of leaf rust was scored on 10 randomly selected plants in each treatment beginning 11 March 1987 and 5 March 1988. Severity was scored separately on each leaf using the modified Cobb's scale (17) at 7- to 10-day intervals until leaf senescence.

Twenty tillers in each plot were harvested by hand at maturity and threshed using a single-plant head thresher (Almaco, Nevada, IA). Grain weight per tiller and grain number per tiller were determined on 10 tillers, and because the total number of harvested grains from 10 tillers was not sufficient, 1,000-grain weight was determined after bulking the harvested seed from all 20 tillers. Final weights were expressed at 13% moisture.

Data from each year were analyzed separately, because the overall yields were significantly different in 2 yr, to determine the contributions of different tiller parts to grain yield. Analysis of variance (25) was performed on all of the data, and means for each variable in each treatment were computed. Least significant difference (25) values were calculated at the 5% probability level for comparison of treatment means.

Relative losses due to defoliation were calculated for each component by dividing the yield for each treatment by the yield for no defoliation treatment.

Similarly, relative losses due to leaf rust in each component for each treatment were calculated by dividing the rusted treatment yield by the paired control (but defoliated) treatment yield.

Regression analysis. Areas under the disease progress curves (AUDPC) (27) were calculated for each leaf as follows:

$$\text{AUDPC} = \sum_{i=1}^{n} [(Y_{i+1} + Y_i)/2]\,[X_{i+1} - X_i]$$

in which Y_i = severity on a leaf at the i^{th} observation, X_i = time (days) at the i^{th} observation, and n = total number of observations (= 4−7). The area outside the AUDPC constitutes the healthy part, and if the duration to which it remained healthy is accounted for, the relative healthy area duration can be calculated. The interval between unfolding and complete senescence for each leaf was determined and was considered to be the period that each leaf remained functional. The duration of relative healthy area (RHAD) of each leaf was calculated as follows:

1 − [(AUDPC/100)/number of days the respective leaves were nonsenescent].

Each leaf was considered as a binary variable, and depending on its presence or absence in each treatment, a value of 1 or 0, respectively, was assigned (Table 1). The RHAD of each leaf was multiplied with the value assigned. Regression analysis of the product on tiller grain weight (*Y*) was conducted by the SAS General Linear Models procedure (20) using the following model:

$$Y_{ij} = \beta_0 + \beta_1 \mathrm{F}_i + \beta_2(\mathrm{F} - 1_i) + \beta_3(\mathrm{F} - 2_i) + \beta_4(\mathrm{F} - 3_i) + \epsilon_{ij}$$

in which β_0, β_1, β_2, β_3, and β_4 are the absolute contributions of the nonfoliar parts, F, F-1, F-2, and F-3 leaves of the i^{th} tiller and j^{th} treatment, respectively, towards tiller grain weight and ϵ_{ij} is the residual error. In no-rust treatments, the AUDPC was zero and therefore RHAD was always equal to 1. The matrix used in the regression analysis is identical to that presented in Table 1. Although the predictor variables for healthy treatments seemingly are uniform, the binary weights were either 0 or 1. Regression analysis employed to such categorical predictors also produces the same information as the continuous predictor variables (11). In rusted treatments, the AUDPC was more than 0 but less than or equal to 1, and, correspondingly, the RHAD was between 0 and 1.

The sum of the partial regression coefficients constituting the combined contributions of all parts of the tiller was computed by adding all the parameter estimates. The relative contributions of each leaf and other parts in rusted and control tillers were estimated by dividing the respective partial regression coefficients by the combined contribution. The statistical significance of the estimates between rusted and control tillers each year and between the corresponding estimates within rusted and control tillers in 2 yr was tested by paired *t*-tests (25). To validate the model, data from Yang and Zeng (30) on the cultivar Yianda 1817 were fitted by the model, and absolute and relative contributions of the individual leaves and other tiller parts were estimated.

RESULTS

The year had a significant effect on the three yield components. Leaf rust and defoliation treatments had a significant effect on all the three yield components. Significant interaction between leaf rust × year, defoliation treatments × year, and leaf rust × defoliation treatments were observed only for grain weight. Three-way interactions between leaf rust × defoliation treatment × year were not significant for the three yield components (Table 2).

Effects of defoliation. The grain weight per tiller, grain number per tiller, and 1,000-grain weight in rusted and control tillers for both years are presented in Table 3. In 1986-87, the grain weight per tiller and grain number per tiller were higher in all treatments compared with 1987-88. In treatments lacking the top one and top two leaves (treatments 1 and 2), all three yield components were significantly less than the treatment with all leaves (treatment 6).

The lowest tiller grain weights in both years occurred in rusted and control treatments with no leaves (treatment 1). The highest grain weights per tiller in 1986-87 were in the rusted and control treatments with all leaves (treatment 6 in Table 3); in 1987-88 they were in the rusted and control treatments with the top three leaves (treatment 8 in Table 3). Tiller grain numbers were lowest in rusted and control treatments with no leaves in both years and highest in rusted treatment with all leaves and control treatment with top three leaves in 1986-87 and in rusted treatment with top four leaves (treatment 7) and control treatment with top three leaves in 1987-88. Tiller grain numbers in defoliation treatments (treatments 1-5) were lower than those in leaf retention treatments (treatments 6-10). One-thousand-grain weights of rusted plots were not significantly different from those of control plots for treatments with no leaves and top four leaves defoliated (treatments 1 and 2) in both years; and treatments with all leaves and the top four leaves (treatments 6 and 7) were not significantly different from each other in both years. The 1,000-grain weights among leaf retention treatments 6-10 within rusted and control conditions were significantly different in 1986-87.

Percentage losses caused by defoliation were generally higher in 1986-87 when compared with 1987-88 in both rusted and control treatments. Percentage losses caused by defoliation were similar in rusted and control treatments. In 1986-87, maximum losses in tiller grain weight and tiller grain number were in rusted treatment with no leaves and control treatment lacking the top three leaves (treatment 3 in Table 3). Minimum loss in tiller grain weight was in rusted treatment with top four leaves and control treatment with all leaves. In 1987-88, highest losses in tiller grain weight occurred in the rusted treatment lacking the top four leaves and the control treatment with no leaves. Defoliation of the flag leaf alone resulted in a reduction of up to 15% in 1,000-grain weight.

Effect of leaf rust on yield components. Development of leaf rust on F, F-1, F-2, and F-3 was consistent for all treatments. The disease progress curves for different leaves are given in Figure 1.

Grain weight per tiller for rusted defoliation treatments 1, 2, and 5 and leaf retention treatments (treatments 6-10) were significantly less than the corresponding control treatments in 1986-87 (Table 3). In 1987-88, rusted leaf retention treatments (treatments 6-10) were significantly less than control treatments in tiller grain weight.

Tiller grain numbers in rusted defoliation treatments 2, 4, and 5 and leaf retention treatments 8 and 10 were significantly lower than the corresponding control treatments in 1986-87. In 1987-88, only rusted leaf retention treatments 7, 8, and 10 had lower tiller grain numbers compared to the corresponding control treatments (Table 3).

Calculated losses due to rust were variable between treatments and among plants within treatments. Maximum losses in tiller grain weight were 26.5% in 1986-87 and 23.4% in 1987-88 (Table 4). The maximum loss in tiller grain number was 18.6% in the treatment lacking the top four leaves in 1986-87 and 23% in treatment with the flag leaf alone (treatment 10) in 1987-88. There was a 23.8% 1,000-grain weight loss in treatment 10 in 1986-87 and an 18.1% 1,000-grain weight loss in the treatment lacking the top three leaves in 1987-88 (Table 4).

Contributions of the nonfoliar parts and individual leaves. The estimated partial regression coefficients for the nonfoliar parts, F, F-1, F-2, and F-3 are listed in Table 5. The coefficients for the nonfoliar parts, F, and F-1 were significant in rusted tillers both years. Similarly, coefficients for the nonfoliar parts, F, F-1, and F-2 in 1986-87 and those for the nonfoliar parts, F, and F-1 in 1987-88 were significant in control tillers (Table 5). The partial regression coefficients for rusted and control tillers were not significantly different from each other within each year except for the coefficients for nonfoliar parts in 1986-87. The regression between tiller grain weight and RHAD was highly significant with an adjusted R^2 of 0.84 and 0.67 in rusted treatments and 0.91 and 0.88 for control treatments in 1986-87 and 1987-88, respectively (Table 5).

The absolute contributions of the nonfoliar parts and F, F-1, F-2, and F-3 leaves from the data of Yang and Zeng (30) in control treatments were 0.60, 0.35, 0.33, 0.40, and 0.26, respectively. The regression was significant ($P = 0.0001$) with an adjusted R^2 of 0.95. The relative contributions of nonfoliar parts and F, F-1, F-2, and F-3 leaves were 0.31, 0.18, 0.17, 0.21, and 0.13, respectively.

The maximum relative contribution towards tiller grain weight was from the nonfoliar parts. The nonfoliar parts comprise all parts of the tiller except the leaves that contribute to the yield. Among the leaves in both rusted and control treatments, F contributed the most towards the tiller grain weight, followed by F-1, F-2, and F-3 (Table 5). The relative contributions of the different parts of the rusted tillers were not significantly different from the corresponding parts of the control tillers each year or between years within rusted and control tillers except for rusted nonfoliar parts.

DISCUSSION

Previous work estimated the contributions of individual plant parts by deduction. The regression model proposed in this study appears to be biologically and mathematically reasonable, and the relative contributions estimated by the model are similar to the values reported by others (22). The regression model explained 67-91% of the total variation in tiller grain weight. The intercept constitutes the contribution of the nonfoliar parts because the yield obtained in the absence of leaves is due to the photosynthetic activity of nonfoliar parts (5).

TABLE 1. Treatments included in the experiment and values assigned to estimate the contributions of different parts of the tiller of wheat cultivar McNair 1003

Treatment		Code for foliar and nonfoliar parts[a]					
		Flag (F)	F-1	F-2	F-3	F-4	Nonfoliar parts[b]
1	All leaves defoliated[c]	0	0	0	0	0	1
2	Top four leaves defoliated	0	0	0	0	1	1
3	Top three leaves defoliated	0	0	0	1	1	1
4	Top two leaves defoliated	0	0	1	1	1	1
5	Flag leaf defoliated	0	1	1	1	1	1
6	All leaves retained	1	1	1	1	1	1
7	Top four leaves retained	1	1	1	1	0	1
8	Top three leaves retained	1	1	1	0	0	1
9	Top two leaves retained	1	1	0	0	0	1
10	Flag leaf retained	1	0	0	0	0	1

[a] A value of 1 or 0 indicates the presence or absence, respectively, of a particular part of the tiller.
[b] The stem, leaf sheaths, ear, and awns constituted the nonfoliar parts.
[c] Defoliations were made after Feekes growth stage 5 (13) as soon as the corresponding leaves unfolded.

TABLE 2. Analysis of variance for tiller grain weight (g), tiller grain number, and 1,000-grain weight (g) in 10 defoliation treatments on leaf rust-inoculated and uninoculated tillers of wheat cultivar McNair 1003

Source of variation	df	Mean squares[a]		
		Grain weight	Grain number	1,000-grain weight
Model	49	0.787**	331.245**	49.122**
Year (Y)	1	11.075**	4824.309**	202.452**
Rep[b] (Y) Error A	5	0.040[ns]	148.813**	41.156**
Leaf rust (LR)	1	2.535**	869.010**	200.162**
LR × Y	1	0.245**	33.068[ns]	11.241[ns]
LR × rep (Y) Error B	5	0.021[ns]	67.617[ns]	14.919[ns]
Treatment (T)	9	2.557**	932.171**	162.494**
T × Y	9	0.206**	39.242[ns]	6.901[ns]
LR × T	9	0.079**	53.262[ns]	9.049[ns]
LR × T × Y	9	0.040[ns]	37.386[ns]	12.936[ns]
Error C	90	0.030	46.514	8.292
Total	139			
Coefficient of variation %		12.27	14.05	10.34

[a] ns = not significant at $P = 0.05$ and ** = signficant at $P = 0.01$.
[b] Replication.

The multiple regression model presented in this paper assumes an additive effect for different plant organs. Previous work (7,12,14,23,24,28,30,32) on defoliation also is based on this assumption. Compensation or interaction, both in diseased and nondiseased conditions in cereals, has been reported by several workers (6,24,31,32). If compensation exists, it may be confounded either in the experimental error in our model or in interaction effects.

The results demonstrate that the nonfoliar parts and F and F-1 leaves primarily determine the tiller grain weight. Most plant physiologists agree that the grain weight is largely affected by the photosynthesis in the two topmost leaves and the ear (26). Opinions differ, however, as to the quantitative contributions of F, F-1, and the ear. In our experiments, the grain yield of treatments with all leaves defoliated and treatments with top four leaves defoliated were not significantly different from each other in rusted and control wheat tillers (Table 2), indicating that the leaves below F-3 are not significant photosynthate sources for the tiller grain yield. Treatments with F and F-1 leaves and treatments with F alone in rusted and control tillers generally had either equal or higher yields compared with treatments with F and F-1 leaves defoliated and treatments with the F leaf defoliated (Table 2), indicating that removal of F-2 and F-3 leaves may not adversely affect the grain yield or that other leaves compensated for the losses. Defoliating the top three leaves adversely affected the yield (Table 2) because only the top three leaves are photosynthetically active during anthesis and early grain filling (18). The removal of the flag leaves from tillers in 1986-87 accounted for 44, 33, and 53% of the total reduction in grain weight, grain number, and 1,000-grain weight, respectively (Table 3). In 1987-88, the plots were not top-dressed, and the plant yields were perhaps nitrogen limited rather than source limited per se, which may have masked the effect of F-leaf removal. Singh et al (24) reported yield losses of up to 50% of the total losses after removal of flag leaves.

Defoliation techniques have been used as a means of quantifying the contributions of different plant parts towards grain yield in cereals. These estimations can be made with reasonable accuracy and precision. In our experiments, the F, F-1, and F-2 leaves accounted for 29, 15, and 1% contribution, respectively, towards

TABLE 3. Yield components[a] of wheat cultivar McNair 1003 in different rusted and control treatments during 1986-87 and 1987-88

	1986-87						1987-88					
	Grain weight/tiller (g)		Grain number/tiller		1,000-grain weight (g)		Grain weight/tiller (g)		Grain number/tiller		1,000-grain weight (g)	
Treatment	Rusted	Control	Rusted	Control	Rusted	Control	Rusted	Control	Rusted	Control	Rusted	Control
1 No leaves	0.92*[b]	1.12*	36.9*	40.7*	23.9*	25.9*	0.73*	0.78*	32.3*	32.9*	23.2*	23.5*
2 Top four defoliated[c]	0.96*	1.19*	37.6*	46.2*	25.3*	25.9*	0.76*	0.79*	34.0*	35.2*	22.5*	22.0*
3 Top three defoliated	1.09*	1.11*	45.0*	49.1*	22.6*	23.4*	0.78*	0.90*	37.1*	34.0*	21.7*	26.5*
4 Top two defoliated	1.34*	1.48*	52.8*	57.7*	26.9*	25.6*	0.89*	1.01*	43.2	40.3*	20.8*	25.1*
5 Top one defoliated	1.54*	2.08*	53.5*	63.8*	28.1	32.2*	1.21	1.29*	46.4	46.8	26.2	27.6*
6 All leaves retained	2.19	2.71	68.9	69.6	32.2	39.0	1.21	1.58	45.2	51.8	27.0	32.0
7 Top four retained	2.04	2.51*	67.8	65.0*	29.6	38.7	1.36	1.61	47.7	55.5	28.5	29.5
8 Top three retained	1.97*	2.68	61.1*	69.8	29.7	37.1	1.39	1.74	46.8	58.9	29.8	30.8
9 Top two retained	1.91*	2.38*	61.6*	64.2*	29.9	35.7	1.33	1.63	46.8	49.9	28.6	32.6
10 Top one retained	1.64*	2.20*	54.9*	59.4*	28.1	36.9	1.13	1.35*	38.1	49.5	29.8	27.7*
Least significant difference ($P = 0.05$)	0.15		4.3		4.5		0.18		8.0		4.3	

[a] Mean of three replicates in 1986-87 and four replicates in 1987-88.
[b] Significantly ($P = 0.05$) different from treatment 6.
[c] Defoliations were made after Feekes growth stage 5 (13) as soon as the corresponding leaves unfolded.

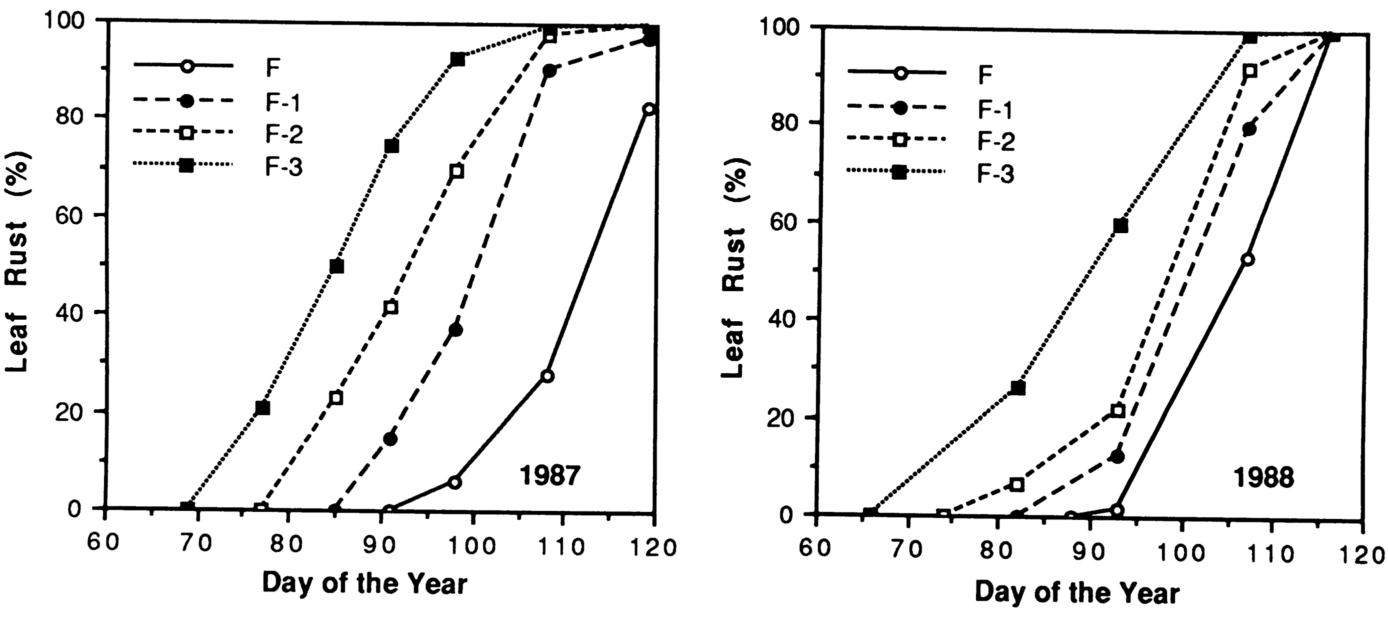

Fig. 1. Disease progress curves for flag (F), F-1, F-2, and F-3 leaves of wheat cultivar McNair 1003 during the 1987 and 1988 growing seasons. Each point is the mean of three replicates each in five rusted treatments in which the respective leaves were present. Disease severity was scored on the modified Cobb's scale.

TABLE 4. Losses due to leaf rust in three yield components of wheat cultivar McNair 1003 in 10 defoliation treatments during 1986-87 and 1987-88

		Percentage loss[a] in:					
		Grain weight/tiller		Grain number/tiller		1,000-grain weight	
Treatment		1986-87	1987-88	1986-87	1987-88	1986-87	1987-88
1	No leaves	17.9 ± 12.2	6.4 ± 20.3	9.3 ± 20.9	1.8 ± 19.0	7.7 ± 1.4	1.3 ± 27.2
2	Top four defoliated[b]	19.3 ± 10.5	3.8 ± 26.5	18.6 ± 10.3	3.4 ± 24.7	2.3 ± 4.1	−2.3 ± 10.2
3	Top three defoliated	1.8 ± 10.5	13.3 ± 5.4	8.4 ± 11.8	−9.2 ± 9.0	3.4 ± 5.3	18.1 ± 13.9
4	Top two defoliated	10.8 ± 7.7	11.9 ± 8.8	8.5 ± 10.2	−7.2 ± 11.9	−5.1 ± 12.8	17.1 ± 8.2
5	Top one defoliated	26.0 ± 11.8	6.2 ± 5.2	16.1 ± 13.1	0.9 ± 10.4	12.7 ± 1.6	5.1 ± 9.9
6	All leaves retained	19.2 ± 15.1	23.4 ± 6.3	1.0 ± 6.9	12.7 ± 9.2	17.4 ± 7.7	15.6 ± 8.9
7	Top four retained	18.7 ± 3.9	15.5 ± 7.0	−4.3 ± 7.6	14.1 ± 10.9	23.5 ± 8.4	3.4 ± 9.3
8	Top three retained	26.5 ± 4.1	20.1 ± 9.5	12.5 ± 15.6	20.5 ± 18.9	19.9 ± 1.9	3.2 ± 8.5
9	Top two retained	19.7 ± 23.3	18.4 ± 7.6	4.0 ± 2.4	6.2 ± 6.1	16.2 ± 15.6	12.3 ± 8.5
10	Top one retained	25.5 ± 18.6	16.4 ± 14.5	7.6 ± 8.3	23.0 ± 22.3	23.8 ± 2.6	−7.6 ± 24.7

[a] Plus or minus standard error.

[b] Defoliations were made after Feekes growth stage 5 (13) as soon as the corresponding leaves unfolded.

TABLE 5. Absolute and relative contributions of the top four leaves and the nonfoliar parts of wheat cultivar McNair 1003 towards the tiller grain weight in rusted and control treatments in 1986-87 and 1987-88 as indicated by the regression analysis of variance[a]

	1986-87						1987-88					
	Parameter estimate ± standard error		*P*		Relative contribution		Parameter estimate ± standard error		*P*		Relative contribution	
Part of the tiller	Rusted	Control	Rusted	Control	Rusted	Control	Rusted	Control	Rusted	Control	Rusted	Control
Nonfoliar parts	0.98 ± 0.08	1.21 ± 0.07	0.0001	0.0001	0.36	0.47	0.80 ± 0.05	0.87 ± 0.04	0.0001	0.0001	0.53	0.51
Flag (F)	0.78 ± 0.13	0.79 ± 0.11	0.0001	0.0001	0.29	0.30	0.42 ± 0.09	0.44 ± 0.06	0.0001	0.0001	0.29	0.26
F-1	0.41 ± 0.19	0.42 ± 0.13	0.0423	0.0031	0.15	0.16	0.22 ± 0.09	0.28 ± 0.07	0.0120	0.0003	0.15	0.17
F-2	0.23 ± 0.27	0.34 ± 0.13	0.4147	0.0165	0.08	0.13	0.14 ± 0.14	0.12 ± 0.07	0.3220	0.0985	0.10	0.07
F-3	0.32 ± 0.56	−0.17 ± 0.53	0.3052	0.7443	0.12	−0.07	−0.11 ± 0.30	0.02 ± 0.06	0.7103	0.0675	−0.08	−0.01

[a] Regressions in both rusted and control treatments were significant ($P = 0.0001$) with an adjusted R^2 of 0.83 and 0.91, respectively, in 1986-87 and 0.67 and 0.88, respectively, in 1987-88.

the tiller grain weight in rusted tillers. In control tillers, the contributions of F, F-1, and F-2 leaves were up to 30, 17, and 1%, respectively. Seck et al (22) reported similar figures. Others (8) have reported slightly higher figures for flag leaves. The nonfoliar parts including the stem, ear, and leaf sheaths together contributed 36–51% towards the tiller grain weight. Ibrahim and Elenein (8) reported 43–48% contribution of the nonfoliar parts. Seck et al (22) indicated that the nonfoliar parts contributed approximately 60% towards the final grain weight. Consequently, the maximum losses due to foliar infections of leaf rust in wheat may not exceed 40–60% based on these two studies. Because leaf rust rarely infects stem, ear, and awns, their contributions towards grain yield may be expected to be constant and may be amenable only to the fertility levels in different years. The maximum losses in our experimental conditions were less than 30% (Table 4). The model indicated that the estimation of leaf rust on the top two or three leaves may be sufficient to determine the losses associated with leaf rust; Yang and Zeng (30) indicated the same for stripe rust-infected plants. The yield loss model developed by Burleigh et al (2), however, accurately predicted losses due to leaf rust based on sequential leaf rust severity estimates on flag leaves. It should be noted, however, that in our experiments the defoliation treatments and use of the single-tiller method allowed greater light penetration and may have inflated the contribution of lower leaves somewhat.

Yang and Zeng (30) reported that the relative contributions of individual plant parts remain the same in control and stripe rust-infected plants. The relative contributions of the different plant parts in our experiments were also not influenced by the presence of leaf rust (Table 5) and, hence, the losses caused by leaf rust on different leaves appear to be additive and are a function of the amount of photosynthetic tissue destroyed. This is consistent with the 1:1 relationship between leaf rust severity and yield losses observed by others (1,22). The use of healthy area duration and the use of healthy area light absorption suggested by Waggoner and Berger (29) and Johnson (9) are therefore important in the study of disease effects on yield. In other studies on the wheat-leaf rust system, however, the pathogen, apart from destroying the photosynthetic area, acted as metabolic sink, indicating more than a 1:1 relationship (26).

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