Reduction in Yield of Winter Wheat in North Carolina Due to Powdery Mildew and Leaf Rust

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ABSTRACT

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The relationships between yield reductions and severity of powdery mildew and leaf rust were examined on winter wheat cultivars Saluda and Coker 983. Plots were established in central and eastern North Carolina in the fall of 1987 and 1988. Triadimefon and/or benomyl were applied to wheat foliage for control of powdery mildew and leaf rust. Significant differences in disease development resulted from fungicide treatments, from differences in resistance of the cultivars, and from different environments. Differences in 500-kernel weight and grain yield were observed even when upper leaves had little disease in some environments. At one location in both years, tillers per meter row and kernels per head were reduced, apparently due to early-season powdery mildew epidemics. Both powdery mildew and leaf rust can reduce yield of winter wheat to a similar degree in the southeastern United States by occurring both before and after stem emergence.

Additional keywords: *Blumeria graminis* f. sp. *tritici*, crop losses, *Puccinia recondita* f. sp. *tritici*, *Triticum aestivum*.

Epidemics of powdery mildew, caused by *Blumeria graminis* (DC.) E. O. Speer f. sp. *tritici* Em. Marchal (= *Erysiphe graminis* DC. f. sp. *tritici* Em. Marchal), occur yearly in the southeastern United States on winter wheat (*Triticum aestivum* L. em. Thell). These epidemics are conspicuous, but powdery mildew is only one of the foliar diseases that often occur simultaneously on winter wheat. Recently, several authors have described the effects of powdery mildew, Septoria leaf and glume blotch (*Leptosphaeria nodorum* Muller), leaf rust (*Puccinia recondita* Rob. ex Desm. f. sp. *tritici*), and tan spot (*Pyrenophora tritici-repentis* (Died.) Drechs.) (4,5,13–15,19,20) on yield of winter wheat. Losses of 10–15% can occur from natural inoculum in winter wheat due to powdery mildew (6,15). There are, however, some contradictory results regarding the effects of powdery mildew on yield in the Southeast (10,13). Kingsland (10) did not detect significant crop losses in South Carolina, whereas Leath and Bowen (13) attributed significant crop losses (17%) to powdery mildew in North Carolina in one of two cultivars in their study. The second cultivar was moderately resistant to powdery mildew and had lower disease severity. Leath and Bowen (13) hypothesized that leaf rust epidemics may have confounded their results by causing a larger yield reduction and masking the smaller effects of powdery mildew on the moderately resistant cultivar.

Powdery mildew can be observed throughout the winter in wheat grown in the southeastern United States. Researchers have reported decreased disease levels and increased yields with early-season disease control practices, such as seed treatment (2–4, 12,13). Little has been done, however, to quantify or relate the effects of early-season (that is, before Feekes growth stage [GS] 6) disease severity to yield (11). Similarly, few recent studies have attempted to explain the role of multiple foliar diseases in reducing wheat yields. Although Spadafora and Cole (18) found an inverse relationship between severity of Septoria leaf and glume blotch and leaf rust in Pennsylvania, they could not relate disease level to grain yield or kernel weight.

This study was initiated to determine the joint relationship between powdery mildew and leaf rust occurrence and severity in the southeastern United States and to quantify the relationship of early-season powdery mildew and subsequent leaf rust development to yield. Preliminary reports have been published (2,3).

MATERIALS AND METHODS

Field plots. Similar experiments were conducted during the 1987-88 and 1988-89 growing seasons at the Central Crops Research Station near Clayton, NC, and the Tidewater Research Station near Plymouth, NC. The factorial experiments were arranged in randomized complete block designs with five replications grouped within environments. Factors were cultivar, foliar fungicide application, and levels of *P. r. tritici*.

In 1987, wheat was planted on 21 October at Clayton and 4 November at Plymouth. Before planting at Clayton, 450 kg/ha of 12-6-24 (N-P-K) fertilizer was applied to the field; at Plymouth 750 kg/ha of 4-6-12 was applied. In early March, 120 and 102 kg/ha of additional nitrogen was applied as ammonium nitrate at Clayton and Plymouth, respectively. In 1988, wheat was planted on 13 October at Clayton and 27 October at Plymouth. Preplant fertilizer applications were 450 kg/ha of 12-6-24 (N-P-K) at Clayton and 2,600 kg/ha of ground limestone plus 260 kg/ha of 6-18-36 at Plymouth. Nitrogen in the form of ammonium nitrate was applied in the spring at 114 and 67 kg/ha at Clayton and Plymouth, respectively.

Wheat was planted mechanically with a small-plot grain drill. Each 2.4 × 2.4 m plot consisted of eight rows with 0.3 m between rows. The preceding crops were tobacco (*Nicotiana tabacum*) at Clayton and corn (*Zea mays*) at Plymouth. Plots were bordered on two sides with 1.2 m of barley (*Hordeum vulgare* 'Anson'), which is not susceptible to either wheat disease studied, and with 1.2-m alleys on the remaining two sides to reduce interplot interference.

Two cultivars of winter wheat were used that, relative to one another, differed in their susceptibility to foliar diseases over the last five seasons (S. Leath, *personal observation*). Saluda (PI 480474) was moderately susceptible to powdery mildew and susceptible to leaf rust; Coker 983 was moderately resistant to powdery mildew but moderately susceptible to leaf rust. Powdery mildew in both growing seasons and leaf rust in the spring of 1989 were allowed to develop from naturally occurring inoculum. Different levels of the two diseases were obtained by foliar fungicide treatments and by inoculation of *P. r. tritici* in the spring of 1988.

Fungicide treatments. In 1987-88, foliar fungicides were applied to control powdery mildew (Table 1). Treatments in 1987-88 were: no spray (control); fall (23 November and 3 December at Clayton and Plymouth, respectively, GS-2 to GS-3); fall and early spring (23 and 24 March, respectively, GS-5 to GS-7); fall, early and late spring (20 and 21 April, respectively, GS-10.1); early and late spring; and late spring. Fungicides were applied within the range of label recommendations (74–222 g a.i./ha for control of powdery mildew and 148–296 g a.i./ha for control of leaf rust, applied at the first sign of disease) (1). Triadimefon (Bayleton 1.8EC, Mobay Corp., Kansas City, MO) was applied at 185 g a.i./ha in the fall and at either 125 or 250 g a.i./ha in the early spring. The late spring foliar spray at 250 g a.i./ha also was applied to leaf rust control plots (no rust). Some plots, which were inoculated with *P. r. tritici*, received a treatment of triadimefon at 125 g a.i./ha in the early spring followed by benomyl (Benlate 50 WP, E. I. Du Pont de Nemours & Co., Inc., Wilmington, DE) at rates between 165 and 250 g a.i./ha in the late spring (after rust inoculation). Triadimefon provides excellent control of powdery mildew at half the rates necessary for good control of leaf rust (1,4), whereas benomyl controls only powdery mildew.

Foliar fungicide applications in 1988-89 were: no spray (control); early fall (22 November and 1 December at Clayton and Plymouth, respectively, GS-2); mid-winter (26 and 31 January, respectively, GS-3); early spring (15 and 29 March, respectively, GS-4 to GS-6); and a conventional schedule (11 and 27 April and 13 and 28 April, respectively, GS-8 and GS-10) (Table 2). In 1988-89, triadimefon was applied at 185 g a.i./ha at Clayton. At Plymouth, triadimefon was sprayed at 125 or 185 g a.i./ha, except where early or late epidemics of leaf rust were reduced by applications of triadimefon at 300 g a.i./ha. Fungicides were applied both growing seasons with a CO_2 pressurized backpack sprayer delivering a volume of 300 L/ha at 240 kPa.

Differential levels of leaf rust. In 1987-88, three levels of leaf rust infection were achieved by no inoculation (check), inoculation at GS-10.0, or inoculation at GS-10.3 to GS-10.5 (11) (Table 1). Urediniospores used for inoculation were increased from field isolates collected in the spring of 1988. These were inoculated onto equal mixtures of Saluda and Coker 983 greenhouse-grown seedlings and collected with a vacuum pump approximately 3 wk after inoculation. In the field, plants were inoculated by mixing urediniospores of *P. r. tritici* collected in the greenhouse with talc and dusting the mixture onto plants in the center two rows of appropriate plots. The first inoculation consisted of approximately 3.8×10^6 urediniospores applied on 10 April at Clayton (6.3×10^4 spores/plot) and 5.7×10^6 urediniospores applied on 15 April at Plymouth (9.5×10^4 spores/plot). The second inoculation was made similarly on 4 May at Clayton and 12 May at Plymouth. In 1988-89, levels of rust due to natural inoculum were high, and desired levels of disease were achieved through triadimefon applications made at GS-8 and GS-10 (no leaf rust), GS-10 (early leaf rust epidemic), or GS-8 (late leaf rust epidemic) (Table 2).

Data collection. Severity of powdery mildew and leaf rust was assessed twice per month in February and March and weekly thereafter at both locations in both growing seasons. Before emergence of the flag leaf, disease severity was estimated throughout each plot by first visually estimating the severity of each disease on all leaves (7) of five to 10 individual plants. The incidence of plants in that plot with that disease severity then was approximated visually, and the individual severity and incidence values were multiplied to obtain an overall disease severity value for each plot. After flag-leaf emergence, disease severity also was assessed on the flag and the penultimate leaves with the aid of disease diagrams (7) on five and 10 randomly selected tillers per plot in 1988 and 1989, respectively.

Before harvest, the tillers per meter of row were counted, and 20 heads per plot in 1988 trials and 10 heads in 1989 trials then were collected for later determination of numbers of kernels per head. Plants were harvested at maturity from the center four rows ($2.9\ m^2$) of each plot with a small-plot combine. Yield variables measured were total grain weight (adjusted to 13% moisture), test weight, and 500-kernel weight.

Data analyses. To determine treatment effects, analyses of variance were performed on areas under the disease progress curve, yield (kilograms per hectare), and components of yield. Interaction terms that involved experimental factors and environment (year × location) were not large and were aggregated into an error term (error B) that was used to test all main effects and the

TABLE 1. Treatments, timing of inoculations with *Puccinia recondita* f. sp. *tritici*, and rates of triadimefon applications at the indicated Feekes growth stages (GS)[v] for control of *Blumeria graminis* f. sp. *tritici* and characteristics of desired epidemics in studies conducted during the 1987-88 growing season

Treatment	Fungicide rate (g a.i./ha) GS-2.5[w]	GS-6	GS-10.1	Desired powdery mildew epidemic	Leaf rust inoculation	Desired leaf rust epidemic
Control	...[x]	...	...	Fall onset, increasing through spring	None	None
	...	...	...		GS-10	Early onset[y]
					GS-10.4	Late onset
Fall	185	...	...	Early spring onset, increasing through spring	None	None
	185	...	...		GS-10	Early onset
	185				GS-10.4	Late onset
Fall and early spring	185	250	...	Late spring onset, increasing through spring	None	None
	185	125	...		GS-10	Early onset
	185	125	...		GS-10.4	Late onset
Fall, early and late spring	185	125	250	None	None	None
	185	125	125 + 165[z]	None	GS-10	Early onset
	185	125	125 + 165	None	GS-10.4	Late onset
Early and late spring	...	250	250	Fall onset, decreasing through spring	None	None
	...	125	125 + 165		GS-10	Early onset
	...	125	125 + 165		GS-10.4	Late onset
Late spring	...	...	250	Fall onset, increasing then decreasing through spring	None	None
	...	...	125 + 165		GS-10	Early onset
	...	...	125 + 165		GS-10.4	Late onset

[v] GS-2 to GS-3 = tiller formation; GS-6 = early stem elongation, first node visible; GS-8 = flag leaf beginning to emerge; GS-10 = head beginning to emerge (11).

[w] December, 25 March, and 20 April were the calendar dates of GS-2.5, GS-6, and GS-10.1, respectively.

[x] No fungicide was applied.

[y] Early onset of leaf rust is considered to occur at GS-10.

[z] When two rates are given, the second rate is the amount of benomyl (a.i./ha) used primarily for control of powdery mildew.

interactions of the three experimental factors: cultivar, fungicide application, and level of *P. r. tritici*. Areas under powdery mildew progress curves (AUPMC) and areas under leaf rust progress curves (AULRC) were calculated from disease assessment data (22). Total disease present was determined by adding severities of the two diseases for determination of area under the progress

TABLE 2. Timing (by Feekes growth stages [GS][w]) and rates of application of triadimefon for control of *Blumeria graminis* f. sp. *tritici* and *Puccinia recondita* f. sp. *tritici* and characteristics of desired epidemics in studies conducted during the 1988-89 growing season at Plymouth, NC[x]

	Fungicide rate (g a.i./ha)					Desired epidemic	
Desired treatment	GS-2	GS-3	GS-4–6	GS-8	GS-10	*B. g. tritici*	*P. r. tritici*
Control	...[y]	...	...	300	300	Fall onset, increasing through spring	None
	...	...	...	...	300		Early onset[z]
	...	...	...	300	...		Late onset
Fall	125	...	...	300	300	Winter onset, increasing through spring	None
	185	...	...	...	300		Early onset
	185	...	...	300	...		Late onset
Mid-winter	...	125	...	300	300	Early spring onset, increasing through spring	None
	...	125	...	...	300		Early onset
	...	125	...	300	...		Late onset
Early spring	...	...	125	300	300	Fall onset, increasing then decreasing through spring	None
	...	...	125	...	300		Early onset
	...	...	125	300	...		Late onset
Conventional	...	...	...	300	300	Fall onset, increasing then decreasing late spring	None
	...	...	...	125	300		Early onset
	...	...	...	300	125		Late onset

[w] GS-2 to GS-3 = tiller formation; GS-6 = early stem elongation, first node visible; GS-8 = flag leaf beginning to emerge; GS-10 = head beginning to emerge (11).

[x] No leaf rust was observed at Clayton, NC, in 1988-89, and inoculations were not done. At Plymouth, natural epidemics started early, and high (250+ g a.i./ha) rates of triadimefon were applied to achieve varying levels of this disease.

[y] No fungicide was applied.

[z] Early onset of leaf rust is considered to occur just after GS-10; late onset would occur during flowering (GS-10.5).

TABLE 3. Yield data from two cultivars of wheat for each of the applications of triadimefon and benomyl (applied at indicated Feekes growth stage ([GS[w]]) and averaged over leaf rust inoculation treatments[x]

	Saluda				Coker 983			
Location-year[y] treatment	No. tillers/ meter row	No. kernels/ head	500 kernels (g)	Yield (kg/ha)	No. tillers/ meter row	No. kernels/ head	500 kernels (g)	Yield (kg/ha)
Clayton, NC, 1988								
None	170.0 a[z]	29.7 a	16.1 a	5,118.5 a	186.9	65.6	16.6	5,971.3
GS-10	180.1 ab	30.4 ab	16.9 b	5,453.4 ab	185.2	65.8	16.4	5,797.7
GS-6, 10	193.2 b	31.6 c	16.6 c	5,640.4 b	189.3	64.8	16.3	5,798.3
GS-2.5, 6	188.1 b	31.2 bc	16.8 b	6,113.9 c	186.1	65.9	16.2	5,918.6
GS-2.5	192.2 b	31.5 bc	16.6 ab	5,805.9 bc	179.9	64.7	16.1	5,996.5
GS-2.5, 6, 10	188.1 b	31.8 c	16.5 ab	5,713.1 bc	190.3	66.3	16.4	6,111.8
					ns	ns	ns	ns
Plymouth, NC, 1988								
None	284.3	32.4	15.5 a	5,803.9 a	290.6	66.5	17.1	6,585.9
GS-10	294.8	32.6	15.9 ab	5,712.4 a	262.2	65.8	17.4	7,035.1
GS-6, 10	290.4	32.7	16.6 b	6,213.5 ab	246.9	68.3	17.3	6,960.5
GS-2.5, 6	279.0	32.9	16.4 b	6,577.4 b	280.9	66.7	17.3	7,029.6
GS-2.5	285.8	32.9	16.5 b	6,485.2 b	291.4	67.8	17.6	7,161.5
GS-2.5, 6, 10	286.3	31.5	16.3 b	6,781.2 b	251.4	65.6	17.4	7,055.8
	ns	ns			ns	ns	ns	ns
Clayton, NC, 1989								
None	173.3	32.7	14.8 a	3,248.7	208.1 ab	37.7	14.4 ab	2,919.8
GS-8, 10	180.1	34.1	15.3 b	3,511.0	204.5 a	28.0	14.5 b	2,897.2
GS-5	188.3	32.8	15.2 b	3,463.9	210.3 ab	27.3	14.4 ab	2,831.3
GS-3	176.5	34.1	15.0 b	3,356.3	189.1 a	28.1	14.7 b	2,784.7
GS-2	187.8	32.1	14.9 a	3,531.2	231.1 b	29.2	14.1 a	3,085.4
	ns	ns		ns		ns		ns
Plymouth, NC, 1989								
None	205.7	23.0	15.0 a	2,155.8 a	220.9 a	22.6	14.4 ab	1,379.3 a
GS-8, 10	207.5	23.7	17.5 c	2,978.7 c	245.1 ab	24.7	14.5 b	2,303.0 c
GS-5	215.2	24.6	15.8 b	2,912.0 c	233.7 ab	24.2	13.6 a	1,619.1 b
GS-3	207.7	24.5	15.6 b	2,531.4 b	255.9 b	24.0	13.4 a	1,532.1 b
GS-2	204.5	23.9	15.4 ab	2,421.0 b	234.6 ab	22.4	13.5 a	1,275.8 a
	ns	ns				ns		

[w] GS-2 to GS-3 = tiller formation; GS-6 = early stem elongation, first node visible; GS-8 = flag leaf beginning to emerge; GS-10 = head beginning to emerge (11).

[x] Yield data are averaged over rust inoculation treatments because significant treatment effects were absent in 1988.

[y] Growing season 1987-88 or 1988-89.

[z] Means within a column for each location-year combination were not significantly different if followed by the same letters, according to Fisher's protected least significant difference ($P = 0.05$); ns indicates that the fungicide treatment was not significant.

curve for both diseases (AUDPC). Areas under the curve also were calculated for intervals of powdery mildew epidemics between particular growth stages: eAUPMC (area under the curve for early powdery mildew), from first assessment to 1 April (about GS-8); AUPMC2, from 1 April to 15 April (GS-10); AUPMC3, from 15 April to 30 April (GS-10.3); and AUPMC4, from 30 April through the last assessment. The last three AUPMCs also were summed for a measure of "late" AUPMC (LAUPMC).

For every environment (location and year) in this study, each of the yield components and yield were regressed on all AUPMCs over particular time intervals (for example, eAUPMC, AUPMC2) using the GLM procedure developed by the SAS Institute (17). Type III sums of squares (which represent a variable's contribution to a model after all other variables have been added) were compared in each regression and used to assess the relative contribution of the AUPMCs over particular time intervals to each yield variable.

Correlation coefficients were calculated among disease variables (severity data at each assessment date and areas under the curves) and yield variables (yield components and yield) for each environment. Disease and yield variables between which correlations were greater than 0.40 were used for determining descriptive models by regressing specific yield variables on specific disease variables. Descriptive models were considered acceptable for describing the relationship between a yield and a disease variable when the probability of obtaining a greater *F*-value was less than 0.01 (21). Intercepts of descriptive models were considered the best estimates of maximum values for individual yield variables in each environment.

Percentage reduction in each yield variable for each environment was calculated using the intercepts of descriptive models. When correlation coefficients between particular disease and yield variables were greater than 0.40 in more than one environment, data from those environments were combined to develop a single loss model. Parameter estimates of the models were calculated by regressing the percentage reduction in a yield variable on a disease variable. Parameter estimates were not calculated for any yield variable that was correlated to a disease variable in only one environment. Plots of standardized residuals versus raw data and predicted values were evaluated for homogeneity, appropriateness of the model, and outliers.

TABLE 4. Analyses of variance of area under the disease progress curves for powdery mildew (AUPMC) and leaf rust (AULRC) and grain yield from two wheat cultivars grown with various triadimefon and benomyl foliar fungicide treatments at two locations in North Carolina

		Mean squares		
Year[y] and factor	df	AUPMC	AULRC	Yield (kg/ha)
1988				
Location	1	1,268,403*[z]	207,434*	5,310,629*
Error A (Rep [Env])	8	49,159	3,327	381,160
Cultivar (C)	1	2,882,842*	62,474*	903,018*
Fungicide (F)	5	630,372*	2,069*	284,493*
Rust inoculation (R)	2	87,523*	7,351*	1,764
C × F	5	925,132*	1,180	107,056*
C × R	2	106,137*	5,110*	142,282*
F × R	10	51,142*	719	79,964
C × F × R	10	51,359*	433	32,570
Error B	315	16,224	708	45,796
1989				
Location	1	5,670,023*	868,098*	7,004,119*
Error A	8	152,436	9,769	111,484
Cultivar	1	8,988,082*	877,608*	3,566,160*
Fungicide	4	17,388*	44,626*	174,084*
Rust	2	9,681	327	52,751*
C × F	4	170,705*	33,799*	39,370*
C × R	2	9,512	929	908
F × R	8	37,512	11,323*	19,687
C × F × R	8	48,135	11,140*	14,374
Error B	270	50,622	5,248	15,423

[y] Growing season 1987-88 or 1988-89.

[z] Asterisk indicates significant treatment effects at the 0.05 level of probability.

Total yield was assumed to be related to the components of yield (number of tillers, number of kernels per head, and 500-kernel weight) by the following relationship:

$$y = tkwc$$

in which y = grain yield in kilograms per hectare, t = number of tillers per meter row, k = number of kernels per head, where number of heads is assumed to equal number of tillers in a given area, w = weight of 500 kernels, and c = a constant that includes correction for differences in units. For regression analysis, this relationship was linearized by a natural logarithm transformation of the equation. Contributions of each of the yield components to total yield was determined by calculating the proportion of the total sum of squares contributed by the Type III sum of squares (17) for each yield component.

RESULTS

Environmental conditions in the 1987-88 growing season were excellent for wheat production (9). In 1988-89, however, there were unseasonable periods of warm weather and damaging freezes at GS-8, 9, and 10. Excess precipitation occurred from February through May 1989 when rainfall at Clayton and Plymouth was 183 and 203 mm above the 30-yr average (147 and 150% of normal, respectively) for these months and locations. These abnormal environmental conditions in the second growing season resulted in 36–62% lower yields in untreated plots than yields obtained in 1987-88 untreated plots (Table 3). Because of the extreme differences in the environments between the two growing seasons of the study, analyses were summarized over locations but not over years.

Overall factor effects. In the 1987-88 growing season (hereafter

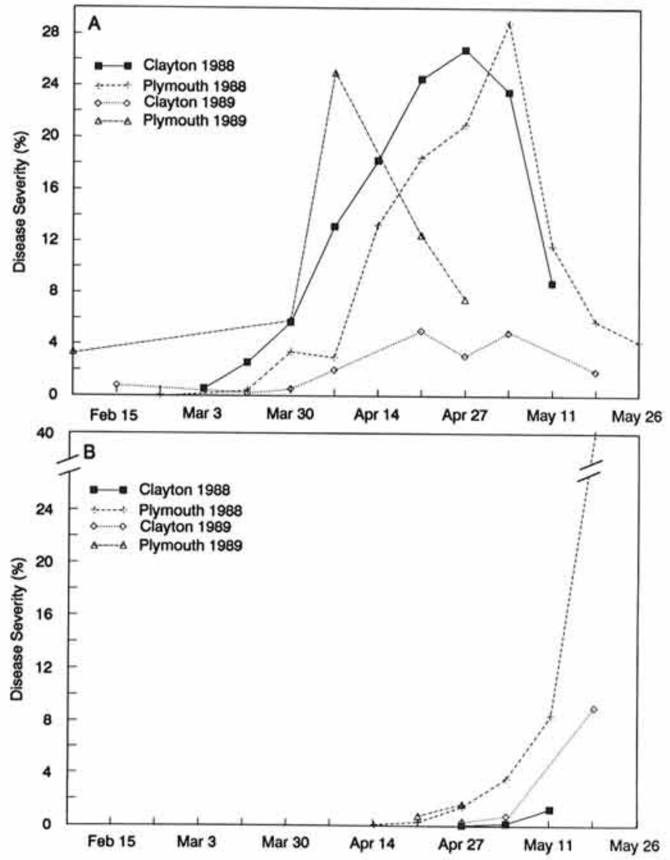

Fig. 1. Disease progress curves on winter wheat (cultivar Saluda) with no fungicides applied in the 1987-88 and 1988-89 growing seasons at Clayton and Plymouth, NC, for: **A,** powdery mildew, and **B,** leaf rust.

referred to as year 1988), AUPMC, AULRC, and yield (kilograms per hectare) were affected ($P \leq 0.05$) by location, cultivar, foliar fungicide treatment, and rust inoculation (Table 4). All interactions were significant for AUPMC; the cultivar × rust interaction was significant for AULRC; and there were significant cultivar × fungicide and cultivar × rust interactions for yield.

In the 1988-89 growing season (hereafter referred to as year 1989), AUPMC, AULRC, and yield were affected ($P \leq 0.05$) by location, cultivar, foliar fungicide treatment, and the cultivar × fungicide interaction. Yield also was affected ($P \leq 0.05$) by levels of leaf rust. In addition, fungicide × rust and the three-way interactions were significant for AULRC (Table 4). The fungicide × rust interaction was significant for only AUPMC in 1988 and AULRC in 1989, but not for yield in either year. Therefore, effects due to the rust level × fungicide interaction were not analyzed separately.

Fungicide treatment effects and disease levels. All fungicide treatments were effective in controlling mildew. Fall, midwinter, and early-spring applications of triadimefon provided powdery mildew disease control for several weeks after application. This delayed the spring onset of powdery mildew that was desired in this study (Table 1). Triadimefon rates less than 200 g a.i./ha also had some effectiveness against leaf rust. This resulted in low leaf rust epidemics, even in inoculated plots, in wheat that had been treated with triadimefon.

In plots of Saluda that did not receive fungicide applications, different disease progress curves were observed in the different locations and years (Fig. 1). In 1988, for example, both locations had similar and severe epidemics of powdery mildew, but leaf rust epidemics differed. Leaf rust severity was low (<2%) at Clayton but reached 40% on flag leaves at Plymouth (Fig. 1). The leaf rust epidemic at Clayton in 1989 was relatively severe, but the powdery mildew epidemic was not severe in that environment (Fig. 1 and Table 5). The AUPMCs on Saluda, in untreated plots, were similar in three of the four environments, yet the shape of the curves differed, with the highest disease severities occurring at different stages of plant development in each of those environments (Fig. 1).

Disease levels differed because fungicide was applied on Saluda wheat but not on Coker 983; therefore, analysis also was performed on Saluda alone. Fungicidal treatments resulted in different disease progress curves in a single environment, as typified by disease progress curves (Fig. 2) at Plymouth in 1988 and area under the curve data (Table 5). In the early stages of plant development, that is, during stem elongation from 14 March to 1 April (GS-6 to GS-8), large differences in powdery mildew severity were observed.

In 1988 at both locations on Saluda, the late, single application of triadimefon did not result in epidemics of powdery mildew that differed ($P \leq 0.05$) from those in untreated plots; however, all other treatments did differ from the untreated plots (Table 5). Similarly, at Plymouth on Saluda, the late fungicide application did not significantly reduce leaf rust epidemics compared with epidemics in untreated plots. In 1989 at Plymouth on Saluda, the epidemics in plots receiving the fungicide applications at GS-8 and GS-10 did not differ significantly from epidemics in the untreated plots, but they did at Clayton. In 1989 at Clayton, powdery mildew severity did not exceed 5%; however, the fungicide applications at GS-8 and GS-10 reduced powdery mildew from a maximum of 5 to 1.2% and also reduced leaf rust from

TABLE 5. Areas under the curves of early, late, and total powdery mildew (eAUPMC, LAUPMC, and AUPMC) and leaf rust (AULRC)[w] epidemics for each of the triadimefon treatments (applied as indicated at Feekes growth stage [GS[x]]) on two cultivars in four environments, averaged over all leaf rust inoculation treatments

Location-year[y] treatment	Saluda				Coker 983		
	eAUPMC	LAUPMC	AUPMC	AULRC	eAUPMC	AUPMC	AULRC
Clayton, NC, 1988							
None	104.8 a[z]	772.3 a	854.2 a	6.8	0.00	0.4	0.4
GS-10	72.9 ab	634.1 a	683.4 a	4.3	0.00	1.0	0.4
GS-6, 10	46.0 bc	54.9 b	93.6 b	4.9	0.00	0.2	1.5
GS-2.5, 6	1.0 c	2.6 b	3.3 b	2.8	0.00	0.0	0.1
GS-2.5	0.0 c	11.4 b	11.4 b	2.6	0.00	0.5	0.0
GS-2.5, 6, 10	0.2 c	4.6 b	4.8 b	1.8	0.00	3.0	0.0
				ns	ns	ns	ns
Plymouth, NC, 1988							
None	42.3 b	480.9 a	523.2 a	180.0 a	0.00	6.9	99.5
GS-10	78.2 a	399.8 a	478.0 a	179.3 a	0.00	2.2	62.8
GS-6, 10	0.9 c	3.7 b	4.6 b	52.7 b	0.00	0.1	46.6
GS-2.5, 6	0.2 c	8.7 b	9.0 b	45.8 b	0.00	0.1	58.2
GS-2.5	11.0 bc	6.5 b	17.5 b	46.2 b	0.00	0.1	47.7
GS-2.5, 6, 10	0.0 c	7.2 b	7.2 b	55.5 b	0.00	0.1	50.0
					ns	ns	ns
Clayton, NC, 1989							
None	17.9	149.5 a	167.5 a	76.5 a	0.00	0.1	1.6
GS-8, 10	30.5	44.7 b	75.2 b	12.4 b	0.00	0.0	0.1
GS-5	27.5	30.7 b	58.2 b	53.5 a	0.00	0.0	0.9
GS-3	1.8	48.4 b	50.2 b	51.0 a	0.00	0.0	1.8
GS-2	6.9	46.6 b	53.5 b	64.2 a	0.00	0.0	3.0
	ns				ns	ns	ns
Plymouth, NC, 1989							
None	266.8 ab	503.4 a	770.2 a	33.0	0.00	0.3	29.0
GS-8, 10	321.1 a	492.2 a	832.2 a	23.3	0.00	0.0	16.6
GS-5	369.3 a	239.0 b	608.3 b	25.9	0.00	0.0	17.5
GS-3	166.3 bc	205.9 b	372.2 c	26.6	0.00	0.0	21.0
GS-2	141.2 c	413.3 a	554.5 b	25.0	0.00	0.0	26.5
				ns	ns	ns	ns

[w] Areas under the curves were calculated using: powdery mildew severity up to 1 April (eAUPMC), powdery mildew severity from 1 April through the last assessment (LAUPMC), powdery mildew severity from all assessments (AUPMC), and leaf rust severity from all assessments (AULRC).

[x] GS-2 to GS-3 = tiller formation; GS-6 = early stem elongation, first node visible; GS-8 = flag leaf beginning to emerge; GS-10 = head beginning to emerge (11).

[y] Growing season 1987-88 or 1988-89.

[z] Means within a column for each location-year combination were not significantly different if followed by the same letters, according to Fisher's protected least significant difference statistic ($P = 0.05$).

9.1 to 0.7% on Saluda.

Yield differences. In all environments, with regard to Saluda, 500-kernel weights differed significantly ($P \leq 0.05$) due to fungicide treatment (Table 3). Yields were increased significantly by fungicides in all environments except at Clayton in 1989. Significant treatment effects in number of tillers per meter row and number of kernels per head were observed in 1988 only at Clayton (Table 3) where foliar fungicide application before GS-10 increased number of tillers per meter row and number of kernels per head.

Powdery mildew that occurred through 1 April (represented by eAUPMC) significantly contributed ($P \leq 0.10$) to numbers of tillers per meter row in three of four environments and numbers of kernels per head in two of four environments (Table 6). Yield was reduced when the area under the curve from GS-8 to GS-10 (during flag-leaf emergence, AUPMC2) increased in two of four environments. At Clayton, where significantly more tillers and kernels per head were observed on Saluda in fungicide-treated plots than in control plots, there was a significant negative correlation between these two yield variables and eAUPMC and AUPMC2 (Fig. 3A and B). Weight of 500 kernels from Saluda was correlated negatively with total disease severity (leaf rust plus powdery mildew) during dough stage, 18 May at Plymouth in 1988 (Fig. 3C).

Loss models. Total yield was negatively correlated with AUDPC at both locations in 1988. A yield loss model for Saluda was developed with AUDPC as the independent variable (Fig. 4) and percent maximum total yield as a dependent variable. The coefficient of determination for the loss model increased slightly from 0.52 to 0.55 when AUDPC was broken into its components, AULRC and AUPMC, such that:

$$\text{Percent maximum yield} = 103.37 - 0.01\,(\text{AUPMC}) - 0.03\,(\text{AULRC})$$

The independent variables, AUPMC and AULRC, contributed 60 and 40%, respectively, to the model's total sums of squares.

In 1989, early-season powdery mildew at Clayton was not as severe as in 1988, and no significant differences in number of tillers were observed (Table 3), but trends in data were similar to those observed in 1988. At Plymouth, however, early-season powdery mildew severity reached 24%. Number of tillers and number of kernels per head were reduced in 1989 compared with 1988 Plymouth data. However, the statistical significance of this reduction was not tested. There were no significant differences in number of tillers or number of kernels per head among treatments at either location in 1989. At both locations in 1989, plots treated with fungicides at GS-3, GS-5, GS-8, and GS-10 had differences in 500-kernel weight ($P \leq 0.05$) compared with control plots (Table 3).

Leaf rust was observed on Saluda wheat in all four environments beginning in the second or third week of April in untreated plots (Fig. 1), but it increased above 5% severity only at Plymouth in 1988 and Clayton in 1989. At Clayton in 1989, the negative correlations between 500-kernel weight and AULRC were high. Because these two variables were correlated in data from Plymouth in 1988, a loss model with 500-kernel weight as the dependent variable and AULRC as the independent variable was developed for these two environments (Fig. 5).

At Clayton, number of tillers and number of kernels together contributed 32 and 54% to the yield sum of squares in 1988 and 1989, respectively (Table 7). At Plymouth, in both years, more than 80% of total sum of squares for yield could be attributed to 500-kernel weight.

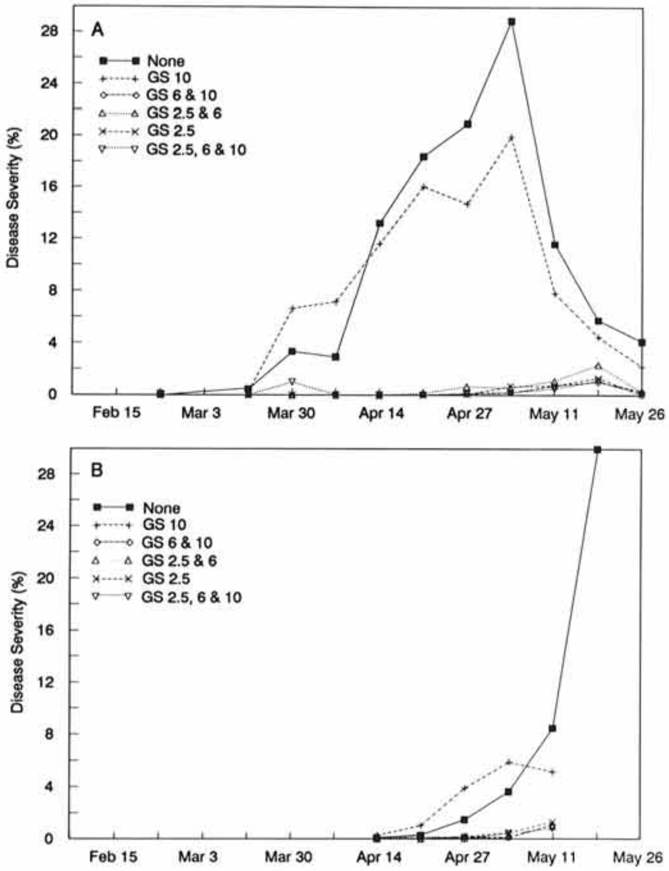

Fig. 2. Effects of fungicides applied at different growth stages on disease progress curves for powdery mildew **(A)** and leaf rust **(B)** on winter wheat (cultivar Saluda) at Plymouth, NC, during the 1987-88 growing season. Growth stage (GS) 2–3 = tiller formation; GS-6 = early stem elongation, first node visible; GS-8 = flag leaf beginning to emerge; GS-10 = head beginning to emerge (11).

DISCUSSION

Powdery mildew in the southeastern United States is found continuously on winter wheat from one month after planting until late spring. This disease is observed first on the oldest leaves

TABLE 6. Type III sums of squares contributed by areas under the powdery mildew progress curves (AUPMC) calculated between particular dates[x] for three yield components and total grain yield

Location and year[y]	Tillers/ meter row	No. of kernels/head	500-kernel weight (g)	Yield (kg/ha)
Clayton, NC, 1988				
eAUPMC	1,927.7*[z]	5,016.1*	0.2	1,707.0
AUPMC2	760.4	457.4	1.5+	2,538.1
AUPMC3	404.2	3,656.6+	0.5	12,436.2
AUPMC4	1,239.6+	5,014.9*	0.8	63,321.7
Plymouth, NC, 1988				
eAUPMC	4,298.4+	3,756.8	2.5	1,105,421.0
AUPMC2	104.5	5,236.3	0.0	88,009.8
AUPMC3	4,963.6+	332.7	3.3+	68,366.2
AUPMC4	1,368.4	1,197.4	2.0	1,246.2
Clayton, NC, 1989				
eAUPMC	2,514.4*	37.9	1.5+	1,199.3
AUPMC2	2,268.6+	470.1	0.0	117,730.7*
AUPMC3	2,246.9+	39.5	0.3	24,422.6
AUPMC4	4,132.3*	557.9	4.2*	7,095.0
Plymouth, NC, 1989				
eAUPMC	604.0	3,488.3+	0.0	190.5
AUPMC2	281.6	2,534.3	5.1+	66,826.4+
AUPMC3	353.5	4,014.0*	2.0	73,022.9+
AUPMC4	156.9	4,308.8*	0.2	2,616.5

[x] AUPMCs were calculated between the following dates: eAUPMC, from first assessment up to 1 April, approximately growth stage (GS) 8; AUPMC2, from 1 April to 15 April, approximately to GS-10; AUPMC3, from 15 April to 30 April, approximately to GS-10.3; and AUPMC4, from 15 April to last assessment. GS-8 = flag leaf beginning to emerge; GS-10 = head beginning to emerge (11).

[y] Growing season 1987-88 or 1988-89.

[z] Plus sign indicates that mean squares were significant at $P \leq 0.10$; asterisk indicates that mean squares were significant at $P \leq 0.05$.

and progresses upward with plant growth. Development of powdery mildew is inhibited when temperatures increase above 28 C during the season. Throughout the Southeast, as temperatures increase and powdery mildew epidemics decline, leaf rust epidemics often follow (Fig. 1) (13). Whereas the upper leaves contribute most to grain yield (14,16), it is possible that disease on a plant before tillering or stem elongation can affect yield by reducing the number of tillers that a plant produces or the number of kernels developing per head. Previous studies that have dealt with the relationship between powdery mildew and yields of winter wheat generally have restricted disease estimations to the disease that is assessed on the uppermost leaves, although some studies have included severity estimates on lower leaves (13–15). Even the inclusion of the third leaf below the flag leaf in disease assessments omits the possible effects of disease that occurs before GS-6.

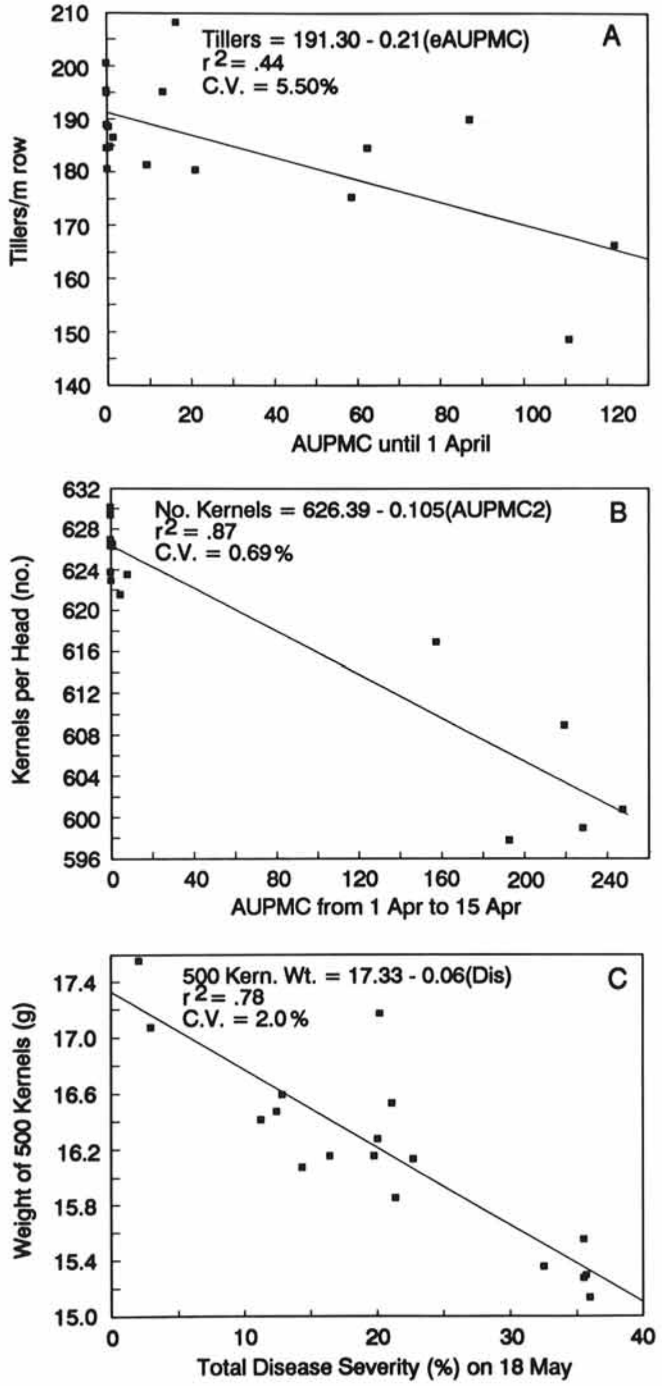

Fig. 3. Relationship between three yield components and disease levels from winter wheat (cultivar Saluda) grown at Clayton, NC, during the 1987-88 growing season. **A,** Regression of number of tillers per meter of row on area under the powdery mildew curve up to 1 April 1988 (eAUPMC). **B,** Regression of number of kernels per head on area under the powdery mildew curve, calculated from 1 April to 15 April 1988 (AUPMC2). **C,** Regression of 500-kernel weight on total disease severity (powdery mildew plus leaf rust) on 18 May 1988 (Dis).

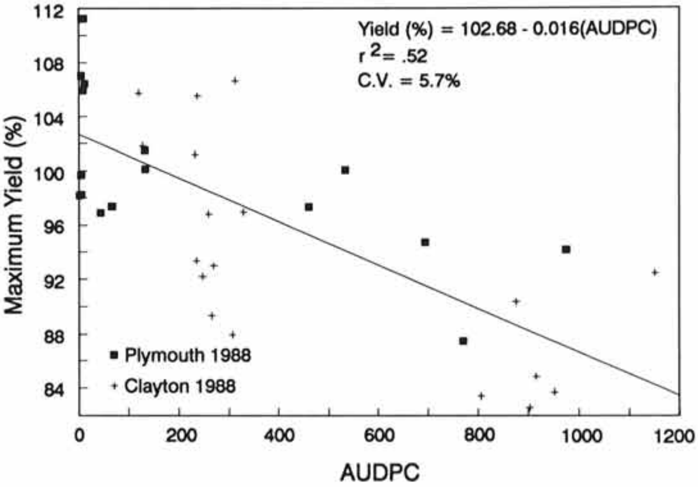

Fig. 4. Relationship between percentage of estimated maximum yield and area under the disease progress curve (AUDPC) through the end of May on winter wheat (cultivar Saluda) for two locations, Clayton and Plymouth, NC, in 1988. Line represents the predicted values from regression analysis.

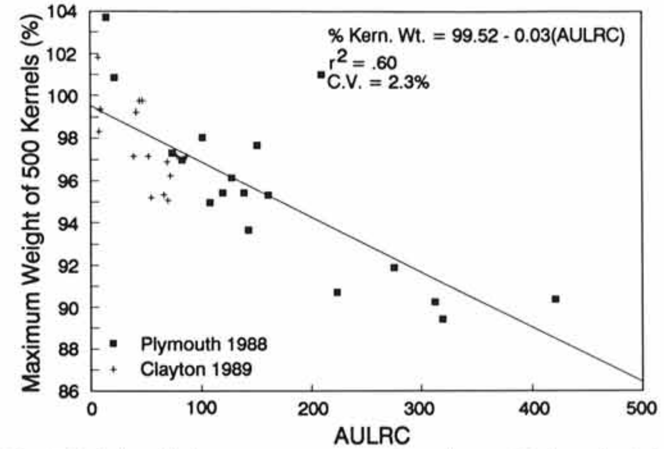

Fig. 5. Relationship between percentage of maximum 500-kernel weight and area under the leaf rust curve (AULRC) on winter wheat (cultivar Saluda) in 1988 at Plymouth, NC, and in 1989 at Clayton, NC. Line represents the predicted values from regression analysis.

TABLE 7. Contributions of individual yield components to total yield of Saluda winter wheat

Location and year[x]	Percentage of variation explained by:[y] No. tillers/ meter row	No. of kernels/head	500-kernel weight (g)
Clayton, NC, 1988	25.0*[z]	7.0	61.7*
Plymouth, NC, 1988	0.9	14.3+	82.5*
Clayton, NC, 1989	37.4*	16.7*	54.8*
Plymouth, NC, 1989	2.1	1.4	94.6*

[x] Growing season 1987-88 or 1988-89.

[y] Based on percentage of the sums of squares that each component contributes to the model. Yield = tillers per meter row × kernels per head × 500 kernel weight × *c*, where *c* is a constant that is used to correct for unit differences.

[z] Asterisk indicates significance at $P \leq 0.05$; plus sign indicates significance at $P \leq 0.10$.

Unfortunately, in most studies a treatment in which disease was controlled for the entire season was not included and estimated yield losses were based on a maximum yield from plants kept disease free only after flag-leaf emergence. This problem is magnified when mildew is present on plants throughout the winter in milder southern climates. The importance of powdery mildew that occurs before flag-leaf emergence to yield has been demonstrated in both Ohio and North Carolina (13,15). Our study provides further support for this idea because mildew declined rapidly after 7 April in 1989 when flag leaves were still emerging and losses in yield were incurred in the absence of late-season mildew or leaf rust.

Early disease control, in the form of seed treatment (4,6,12) or foliar sprays made in the fall, as in our study, has been shown to improve yields. However, the magnitude of yield loss caused by disease levels early in the growth of the crop had not been determined previously, nor had the specific yield component affected by early-season powdery mildew. We have demonstrated that amount of disease present before flag-leaf emergence may affect yields by affecting specific components that contribute to yield. Early-season powdery mildew, in certain environments, can result in decreased numbers of tillers and numbers of kernels per head (Figs. 3 and 4).

The relative contribution of individual yield components, such as number of tillers per meter row, to yield may differ among environments, as was the case in our study (Table 7). At Clayton, number of tillers was shown to have a positive ($P = 0.05$) effect on final yields. However, the primary component that accounted for total yield in wheat at Plymouth was 500-kernel weight. This may indicate that there was compensation for disease early in the season at Plymouth but that plants had no alternatives to kernel size to compensate for effects of late-season disease that was at relatively high severities. Correlations between particular disease variables and yield components, and subsequent predictive models developed from data from Clayton in 1988, also show the effect of early-season powdery mildew levels on winter wheat yields. All these data indicate that some environments may be more conducive to compensatory growth by wheat plants and that the importance of early-season powdery mildew may change from year to year.

To characterize the relationship between disease and yield, studies must include healthy treatments and treatments with various levels of disease (8). In our study, a wide range of disease levels was observed only on Saluda; the relatively high level of resistance in Coker 983 rendered it difficult to initiate different epidemics with fungicide treatments. Various levels of disease were observed in each of the four environments, and comparisons made among environments indicated relationships between disease and yield not otherwise apparent. For example, despite similar powdery mildew epidemics at both locations in 1988, severe leaf rust epidemics developed only at Plymouth; however, at both locations, 500-kernel weight and yields were higher with all fungicide treatments. At Clayton, 500-kernel weight was increased 4.7% with a single late application of triadimefon, even though there was very little leaf rust at this location. This indicates that powdery mildew may affect yield components determined late in plant development even though severity of mildew declines because of hot weather late in the season. At Plymouth, where leaf rust was substantial, a single late fungicide application resulted in only a 2.6% increase in 500-kernel weight. The smaller increase may be due to incomplete rust control with a single fungicide application and to leaf rust's masking the effects of powdery mildew and uniformly reducing yields across various treatments. The joint effects of powdery mildew and leaf rust also can be observed among the different epidemics. At Clayton in 1988, high levels of powdery mildew and low levels of leaf rust were observed (Table 5). Across treatments with these varying disease levels, yields were reduced 7.5% compared with the full-season control. At Plymouth, high levels of both mildew and rust were observed (Table 5), and yields were decreased 14.5% compared with the full-season control (Table 3). This decrease is twice that associated with powdery mildew alone, thus indicating that the levels of mildew and rust observed in this study acted equally and additively in reducing wheat yields.

In 1989 at Plymouth, powdery mildew epidemics were extremely severe and early, and decreases of up to 30% in number of tillers per meter row and number of kernels per head were observed, compared with these yield components from Plymouth in 1988. Although the decrease in these yield components could be due to environmental factors, similar decreases were not observed at Clayton in 1989, where weather was similar. Thus, early levels of powdery mildew at Plymouth in 1989 may have had a significant effect on yields in that environment not readily apparent from these data—as shown, for example, where reductions in eAUPMC in plots sprayed at GS-2 and GS-3 (Table 5) did not result in increased number of tillers per meter row (Table 3). The poor environment in 1989 was the major factor in reducing grain yields, but trends in the data and significant differences among treatments were similar in both years of the study.

The individual contributions of yield components of winter wheat are difficult to determine because they are relatively small and are influenced by many factors. Number of tillers per meter row were counted from plant crowns at crop maturity. This may or may not have been an accurate estimation of the number of grain-producing heads in the field because, in any wheat crop, there are tillers that do not produce grain. This may be due to delayed development of certain tillers from an early growth stage, with senescence occurring before completion of flowering or grain fill. A plant also may put out tillers late in the season, as various stresses are removed from the plant. The period of time in which tillers are produced by winter wheat, relative to disease levels early in the season, needs to be studied.

Powdery mildew and leaf rust, at least in the environments included in this study, appear to act additively on yields of winter wheat. The relationship between yield and AUDPC in this study, compared with the relationship between yield and AUPMC with AULRC, shows this. In much of the southeastern United States, powdery mildew rapidly declines late in the season, and leaf rust becomes the predominant disease on winter wheat during grain fill. Traditional recommendations for disease control, which are based on the amount of disease on the flag leaf, therefore ignore a major portion of the effects that powdery mildew may have on yields.

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