Effect of Moisture on Septoria tritici Blotch Development on Wheat in the Field

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ABSTRACT

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The relationship between occurrence and duration of moisture in the field and development of Septoria tritici blotch (caused by *Mycosphaerella graminicola*) on wheat was investigated. In a wet year (1983), when weather favored natural disease development and release of spores from pycnidia within lesions, moist period duration was more important than inoculation in enhancing disease increase. In a dry year (1984), when conditions were unfavorable for disease development and spore dispersal, moist periods after inoculation enhanced disease spread more than equivalent moist periods without inoculation. By assessing disease on individual tagged plants at 2- to 4-day intervals, we were able to associate disease increase with periods of rainfall 14–16 days earlier. Disease severities on the spike, flag leaf, and penultimate leaf of individual plants at the early dough stage of growth reflected the vertical nature of disease spread and were related to reduction in thousand seed weight and crop yield. The inoculation technique developed was successful even in weather ill-suited to natural infection.

Prolonged periods of wet weather and cool temperatures favor the development of Septoria tritici blotch of wheat caused by *Mycosphaerella graminicola* (6,9,17,21), but there is a dearth of information specifically relating epidemics to weather. Experimental evidence indicates that moisture is important at all stages of the infection cycle (2,6,8,12,13,15). In the field, a moist period of 15 hr was found to be a minimum condition for infection, whereas 35 hr of moisture followed by 2 days of high humidity favored heavy infection (16). Pycnidia form within a relative humidity range of 35 to 100%, but significant reduction of pycnidial density results when plants are held at relative humidities below 85% (15). High relative humidity also favors lesion growth (13) and release of spores from pycnidia (6). Pycnidiospores exuded through the ostiole are embedded in a mucilaginous cirrhus, which serves to prevent germination in situ but promotes it when water is available (15).

Despite the recognition of the association between moisture and Septoria tritici blotch development, the amount and distribution of moisture needed in the field for an epidemic requires further quantification (17). Our experience at the Purdue Agronomy Farm has been that when disease initiated by natural inoculum fails to develop, it also develops poorly on inoculated wheat regardless of frequency or timing of inoculation, implying that inoculum is not a limiting factor.

The objectives of this study were to investigate the effects of increasing postinoculation moist periods and supplemental inoculum on Septoria tritici blotch development in the field and to relate disease severity to reduction in yield parameters.

MATERIALS AND METHODS

The experiment was conducted in two successive years at the Purdue Agronomy Farm. The wheat cultivar Arthur was sown at a rate of 4.3 g/m in rows 16 cm apart. Plantings for the respective experiments were made on 14 October 1983 and 29 September 1984. In previous years, oats had been planted in both fields. Plots were rectangular, 1.2 by 1.8 m, with 1-m alleys on all sides. Nine plots were included in each of four replicates.

In early spring, when seedlings were at growth stages (GS) 14–15 (four to five leaves unfolded) (23), notes were taken on the incidence of infection by *M. graminicola* in the plots. Observations were made on 3 March 1983 and 26 April 1984.

Development of leaf rust (*Puccinia recondita* Rob. & Desm. f. sp. *tritici*) was controlled with butrizol (Indar LC70, Rohm and Haas Co., Philadelphia, PA), applied at 556 ml/ha. In 1983, applications were made on 21 April and 29 May. In 1984, a single spray on 8 June provided adequate control because of the late rust epidemic.

Efforts were made to inoculate plots with *M. graminicola* at the beginning of prolonged periods of cool weather and precipitation. There were nine treatments. Plots of treatments 1 through 5 were inoculated and subsequently received 0, 16, 40, 64, and 88 hr of postinoculation moisture, respectively. Treatments 6 and 7 were inoculated twice at an interval of 11–14 days and subjected to respective 16- and 88-hr postinoculation moist periods after each inoculation. Plant growth stages at the first and second inoculations were, respectively, GS 30-31 (one node, penultimate leaf blade emerging) and GS 38-39 (flag leaf blade emerging). Plots of treatments 8 and 9 were not inoculated but were exposed to moist treatments of 0 or 88 hr. Four blocks were included in the experiment. Inoculum preparation has been described (7), but the spore concentration was increased to 3.3×10^6 spores per milliliter. The surfactant Tween 20 (polyoxyethylenesorbitan) was added to the inoculum at a rate of one drop per 50 ml.

On 29 April 1983, at the beginning of a 4-day period of rain, the first inoculation of plots was carried out. In 1984, rain was not in the extended forecast, so the first inoculation was made on 7 May to coincide with a period of cool weather. Plots to be inoculated were misted with 150 ml of inoculum suspension using a Polyspray compressed air sprayer (E. C. Geiger, Harleysville, PA). Plots to receive a moist period were immediately covered with clear polyethylene supported by a wire frame. Temperatures were recorded within one of the moisture tents by means of a maximum-minimum registering thermometer. Mean maximum and minimum temperatures in 1983 were, respectively, 28 and 9 C at the first inoculation and 42 and 12 C at the second inoculation. Corresponding temperatures during the 1984 experiment were 27 and 6 C at the first inoculation and 27 and 15 C at the second inoculation. Inoculum prepared for the second inoculation contained approximately 3.5×10^6 spores per milliliter. Plots were misted with 215 ml of inoculum suspension before being covered with polyethylene tents. Treatment 6 plots were uncovered the

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following morning (after 16 hr). Because of partly sunny conditions in the afternoon of 13 May 1983, treatment 7 plots were subjected to extremely high temperatures (52 C) and upper leaves sustained sunscald. This was avoided in 1984 by slitting open the tops of the plastic tents at 0800 hours on sunny days. In the late afternoon (1700 hours), 7 L of water were poured into each tent to wet the soil, plants were misted with water, and the slit was closed with duct tape. In addition, shades of black polyethylene were installed above the treatment 7 plots.

After the second inoculation, five plants were randomly selected and tagged within each plot and disease notes were taken on each leaf at 4-day intervals. One of the five plants within each plot was observed more frequently (at 2- to 4-day intervals). From the same day and at 4- to 8-day intervals thereafter, disease on 10 randomly chosen plants in each plot was estimated as the percentage area of the upper four leaves affected and an average obtained for each plot. In 1984, plot ratings were taken at four-day intervals.

Disease severities were averaged over replications for each treatment and disease progress curves were plotted. For each plot area under the disease progress curve (AUDPC) was calculated as:

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

in which Y_i severity (per unit) at the ith observation, X_i = time (days) at the ith observation and n = total number of observations.

Notes were taken of disease on spikes, flag leaves, and penultimate leaves of randomly chosen plants in each plot and recorded on a small tag attached to the respective spike. On 15 June 1983 notes were taken from 15 random plants in each plot of block 1. Notes for block 2 were taken on 17 June and for blocks 3 and 4 on 18 June. In 1984, 25 random plants per plot were tagged on 21 June. Tagged heads were harvested on 5 July 1983 and 4 July 1984 and dried before counting of nodes and spikes and threshing by hand. Kernels from each spike were counted (KER) and weighed and single kernel weight (KWT) was determined. Multiple regression analysis was used to investigate the effect of increasing disease in the different plant organs on seed number and total and individual kernel weights. Disease was absent from spikes in 1984, so this factor was dropped from analysis. Plot centers were harvested with a Hege small plot combine to obtain treatment yields.

Multiple regression analysis was used to investigate the relationship among hours of postinoculation moisture (HRS), resulting disease within field plots as measured by area under the disease progress curve (AUDPC), total plot yield (YLD), and thousand seed weights (TSW). Data for sunscalded treatment 7 plots were not included in the analysis of the 1983 results.

Trends among the three inoculation treatments were investigated for both years by simple regression analysis. AUDPC, YLD, and TSW were regressed on HRS for each treatment (no inoculation, treatments 8 and 9; single inoculation, treatments 1–5; and double inoculation, treatments 6 and 7) and regression lines were tested for equality using a general linear approach (14). Factorial analysis of variance was also used for the same purpose.

RESULTS

Incidence of natural infection by *M. graminicola* in experimental plots was high in the spring of both 1983 and 1984. Disease incidence on 3 March 1983 and 26 April 1984 was 92 and 100%, respectively.

The importance of rainfall to development of Septoria tritici blotch is shown in Figure 1, in which the disease progress curves for individual plants show two distinct plateaus (at 22 and 35 days after April 30) where disease progress ceases. The resumption of disease progress corresponds in each case to periods of rainfall occurring 14–16 days before. This detail is not apparent when disease notes were taken at longer intervals from random plants and plotted as severity averaged over plants and replications (Figs. 2–4). As postinoculation moisture increased, a corresponding increase in mean percent disease severity on the upper four leaves of wheat resulted (Fig. 2).

In both 1983 and 1984, inoculation had no effect where postinoculation moisture was lacking (Fig. 3). In 1983, little difference occurred between inoculation treatments followed by 88 hr of moisture. Disease within plots developed to similar high levels by the end of the season. In 1984, inoculation of plots that received a moist period of 88 hr produced consistently higher disease levels than occurred in uninoculated plots receiving an equivalent moist period.

In 1983, similar levels of disease resulted from single or double 16-hr inoculations, whereas no comparison could be made between the single and double 88-hr inoculations (Fig. 4). In 1984, however, second inoculations resulted in higher disease levels.

In both 1983 and 1984 and for all inoculation treatments, AUDPC increased with increasing duration of postinoculation moisture (Table 1), confirming that disease (as measured by AUDPC) increased in response to increased postinoculation moisture. Factorial analysis of variance of uninoculated and once-inoculated plots given equivalent postinoculation moisture treatments (Table 2) indicated that the moisture treatment alone affected AUDPC in 1983, whereas in 1984 both inoculation and moisture were highly significant with a highly significant interaction. In 1984, both inoculation frequency and increased moist period significantly enhanced AUDPC in double inoculated treatments (Table 3). Slopes obtained from regression of AUDPC on HRS showed that in plots exposed to equivalent moist periods, more disease developed in inoculated than in uninoculated plots (Tables 4 and 5).

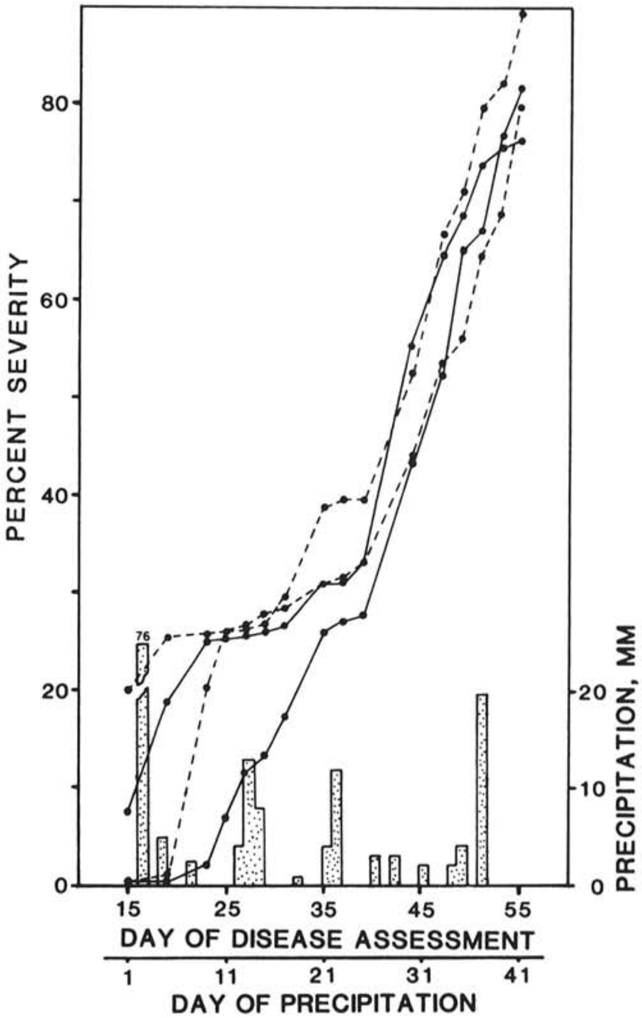

Fig. 1. Septoria tritici blotch progress on four individual plants of Arthur wheat at the Purdue Agronomy Farm in 1983. Plants were inoculated but received no moisture treatment. Disease severity was averaged for the upper four leaves. Dotted and solid lines are used to maintain distinction among individual disease progress curves. Bars represent precipitation 2 wk before disease assessment. On both time scales day 1 = May 1.

TABLE 1. Septoria tritici blotch development on wheat cultivar Arthur subjected to various moisture treatments at the Purdue Agronomy Farm in 1983 and 1984[a]

	AUDPC[c]		TSW[d] (g)		YLD[e] (g)	
Treatment[b]	1983	1984	1983	1984	1983	1984
1(I_1,0)	1,393	573	37.60	33.98	526	522
2(I_1,16)	1,578	625	36.38	34.37	544	525
3(I_1,40)	1,648	691	36.24	34.71	547	543
4(I_1,64)	1,745	791	36.25	33.11	521	503
5(I_1,88)	1,844	1,050	35.80	32.72	496	477
6(I_2,16)	1,600	951	35.78	32.44	514	493
7(I_2,88)	1,304	1,263	33.63	31.66	212	238
8(I_0,0)	1,424	538	37.16	33.92	536	555
9(I_0,88)	1,722	769	36.24	34.25	505	503

[a] Data averaged over four replications for AUDPC and three replications for TSW and YLD.

[b] I_0, I_1, and I_2 refer to no inoculation, single inoculation, and double inoculation treatments. Numbers refer to hours of postinoculation moisture.

[c] Area under the disease progress curve (15 May–24 June 1983 and 25 May–25 June 1984).

[d] Thousand seed weight.

[e] Plot yield.

For all treatments, TSW decreased as the moist period increased but correlations were very low in both years (Table 6). Factorial analysis of variance indicated that the moisture treatment was significant only in 1983 (Table 2).

As moisture duration increased, plot yield decreased (Table 6). In 1984, the regression coefficient for double-inoculated treatments was significantly more negative than coefficients for uninoculated and single-inoculated treatments (Table 5). Factorial analysis of variance showed that the moisture treatment had a significant effect on yield reduction in both years (Tables 2 and 3). In 1984, inoculation frequency and the moisture × inoculation frequency interaction were highly significant.

In 1983, TSW and YLD were negatively correlated with HRS (Table 6). Correlation coefficients were, respectively, significant ($P = 0.05$) and highly significant ($P = 0.01$). AUDPC values for the different treatments were highly and positively correlated with moist period duration. For both years of the experiment, YLD and TSW were negatively correlated with AUDPC. Results for 1984 were similar to those for 1983, but in the second year, increase in YLD was also significantly correlated with gain in TSW (Table 6).

Correlations among disease data, seed number, and single kernel weights of tagged spikes were low (Table 7). However, highly significant positive correlations did exist between disease on the spike and on the flag leaf (in 1983) and between disease on the flag

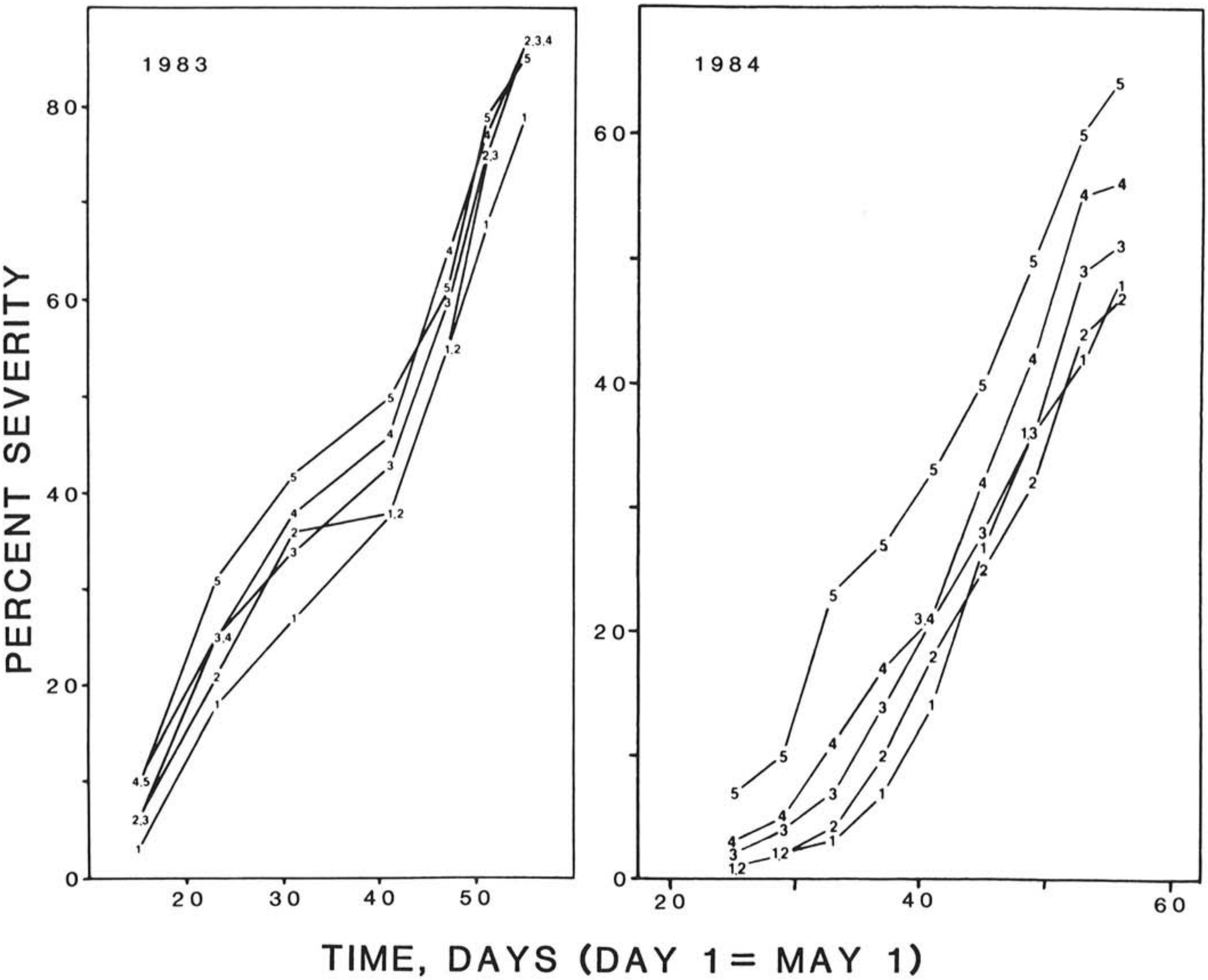

Fig. 2. Septoria tritici blotch progress on Arthur wheat subjected to different postinoculation moisture treatments at the Purdue Agronomy Farm in 1983 and 1984. Disease was averaged for the upper four leaves of 10 plants in each of four replications. Curve 1 = 0 hr moisture, 2 = 16 hr moisture, 3 = 40 hr moisture, 4 = 64 hr moisture, 5 = 88 hr moisture.

and penultimate leaves (in both years).

Kernel number was negatively correlated with disease on the spike. Kernel weight was negatively correlated with disease on the spike and flag and penultimate leaves in 1983. In 1984 the negative correlations of kernel number and kernel weight with disease on the upper two leaves were highly significant.

DISCUSSION

Field inoculation of wheat with conidia of *M. graminicola* increased Septoria tritici blotch severity over naturally occurring levels, facilitating the study of yield response to disease. AUDPC provided an accurate description of Septoria tritici blotch severity.

TABLE 2. Effect of inoculation with *Mycosphaerella graminicola* on disease progress and yield components of Arthur wheat at the Purdue Agronomy Farm[a]

		Mean squares[b]					
		AUDPC[c]		TSW[d] (g)		YLD[e] (g)	
Source of variation	DF	1983	1984	1983	1984	1983	1984
Inoculation	1	8,144	99,383**	0.000	2.266	400	588
Moisture	1	560,624**	501,618**	7.385*	0.988	3,660**	12,939*
Interaction	1	23,644	60,393**	0.789	0.930	1	10
Error	9	6,510	4,572	0.918	0.640	209	1,356

[a] Treatments 1, 5, 8, and 9 were used for analysis.

[b] Symbols * and ** indicate significant differences among treatment means at $P = 0.05$ and 0.01, respectively.

[c] Area under the disease progress curve (15 May–24 June 1983 and 25 May–25 June 1984).

[d] Thousand seed weight.

[e] Plot yield.

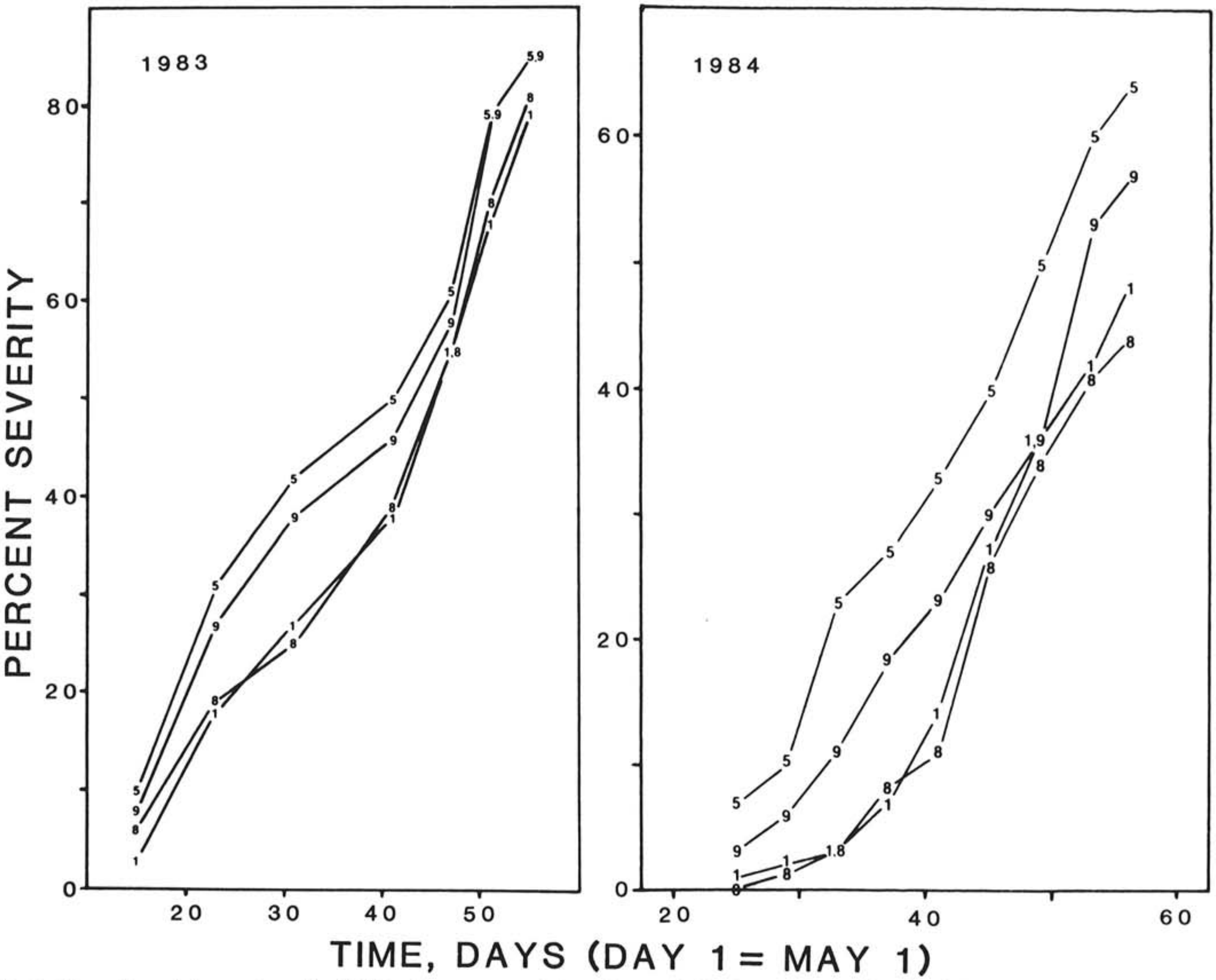

Fig. 3. Effect of inoculation on Septoria tritici blotch progress on Arthur wheat at the Purdue Agronomy Farm in 1983 and 1984. Disease severity was averaged for the upper four leaves of 10 plants in each of four replications. Curve 1 = inoculated, 0 hr moisture; Curve 5 = inoculated, 88 hr moisture; Curve 8 = uninoculated, 0 hr moisture; Curve 9 = uninoculated, 88 hr moisture.

Shaner and Finney (18) employed AUDPC as a measure of powdery mildew epidemic development because of its low error variance. Buchenau (3) reported that yield loss due to wheat stem rust and wheat leaf rust was highly correlated with AUDPC and that it is a good indicator of amount of rust on wheat cultivars.

In 1983, only moist period was significant in increasing AUDPC suggesting that natural inoculum was not limiting. Results for 1984 showed not only that disease increased with lengthening moist periods, but that natural inoculum became limiting at long moist periods. Second inoculations at a later growth stage produced more severe disease.

To interpret these results, rain data for both years were investigated. In 1983, 15 mm of rain fell the day before inoculation with an additional 101 mm falling during the 96 hr after inoculation. Conditions for natural spore dispersal preceding inoculation and for germination and infection after inoculation were therefore very

TABLE 3. Effect of frequency of inoculation with *Mycosphaerella graminicola* on disease progress and yield components of Arthur wheat at the Purdue Agronomy Farm in 1984[a]

		Mean squares[b]		
Source of variation	DF	AUDPC[c]	TSW[d] (g)	YLD[e] (g)
Inoculation	1	332,064**	6.07	75,625**
Moisture	1	601,012**	2.75	80,372**
Interaction	1	22,878	1.96	33,306**
Error	9	6,322	1.78	1,265

[a] Treatments 1, 5, 6, and 7 were used for analysis.

[b] Symbols * and ** indicate significant differences among treatment means at $P = 0.05$ and 0.01, respectively.

[c] Area under the disease progress curve from 25 May through 25 June.

[d] Thousand seed weight.

[e] Plot yield.

TABLE 4. Regression coefficients for the relation between various measurements of disease development or damage from infection by *Mycosphaerella graminicola* on Arthur wheat subjected to two inoculation treatments at the Purdue Agronomy Farm in 1983

	Treatment[a]	
Regression	No inoculation	Single inoculation
AUDPC[b] with HRS[c]	3.381 B ± 0.480	4.697 A ± 0.710
TSW[d] with HRS	−0.010 A ± 0.003	−0.016 A ± 0.008
YLD[e] with HRS	−0.349 A ± 0.171	−0.394 A ± 0.198

[a] Within each row, regression coefficients followed by a common letter do not differ significantly at $P = 0.05$ according to comparison of confidence intervals.

[b] Area under the disease progress curve from 15 May through 24 June.

[c] Hours of postinoculation moisture.

[d] Thousand seed weight (g).

[e] Plot yield (g).

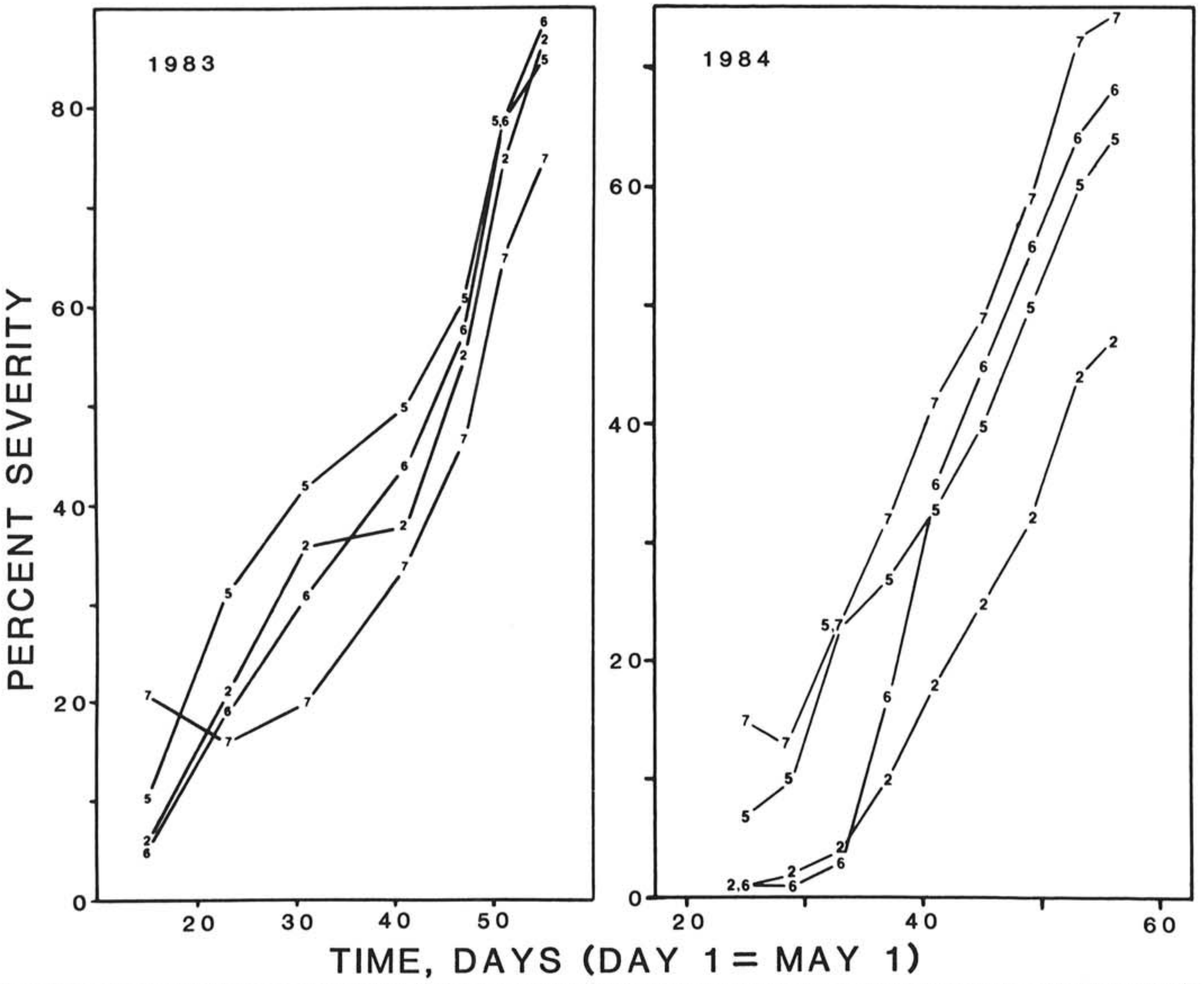

Fig. 4. Effect of inoculation frequency on Septoria tritici blotch progress on Arthur wheat at the Purdue Agronomy Farm in 1983 and 1984. Disease severity was averaged for the upper four leaves of 10 plants in each of four replications. Curve 2 = single inoculation, 16 hr moisture; Curve 5 = single inoculation, 88 hr moisture; Curve 6 = double inoculation, 16 hr moisture; Curve 7 = double inoculation, 88 hr moisture.

TABLE 5. Regression coefficients for the relation between various measurements of disease development or damage from infection by *Mycosphaerella graminicola* on Arthur wheat subjected to three inoculation treatments at the Purdue Agronomy Farm in 1984

	Treatment[a]		
Regression	No inoculation	Single inoculation	Double inoculation
AUDPC[b] with HRS[c]	2.628 B ± 0.466	5.249 A ± 0.581	4.333 A ± 0.620
TSW[d] with HRS	0.0 B	−0.014 A ± 0.008	−0.002 AB ± 0.018
YLD[e] with HRS	−0.665 B ± 0.409	−0.624 B ± 0.272	−3.236 A ± 0.500

[a] Within each row, regression coefficients followed by a common letter do not differ significantly at $P = 0.05$ according to comparison of confidence intervals.

[b] Area under the disease progress curve from 25 May through 25 June.

[c] Hours of postinoculation moisture.

[d] Thousand seed weight (g).

[e] Plot yield (g).

good. Thus, artificial inoculation was probably redundant and AUDPC responded only to moist period duration. In 1984, 19 mm of rain fell on the third and second days before inoculation, but sunny weather returned on the preceding day. Only 0.3 mm of rain fell during the 96 hr after inoculation and sunny conditions prevailed, resulting in a poor natural environment for spore germination and infection. Thus, in 1984, inoculation had a significant effect on AUDPC when there was a long moist period, but not when there was a short moist period.

Importance of a second inoculation at the time of flag leaf emergence in 1984 is also explained by considering rainfall in relation to wheat developmental stages for the 2 yr. In 1983, flag leaves emerged about 12 May and heads emerged about 26 May. Rainfall from 12 May to the 14 June cut-off date described by Shaner and Finney (17) totaled 75 mm. Rainy periods were 1–3 days long with a mean duration of 1.7 days.

In 1984, flag leaves emerged about 18 May and heads on the 30th. Rainfall from 18 May to 14 June totaled 134 mm and each rainfall period had a mean duration of 2.5 days. Drought occurred after heading with no rainfall from 31 May through 13 June. Wheat developed more slowly early in the spring of 1984 compared with 1983, but heading dates differed by only 4 days and maturity dates were the same in both years.

The prolonged growing period in 1983, combined with regular rainfall, allowed for natural disease spread and development so that the repeated 16-hr inoculation at flag leaf emergence was redundant. In 1984, however, plants grew more rapidly and, although rainfall was plentiful, it was irregular, resulting in fewer pathogen infection cycles (2) and less disease (4). Because of reduced natural inoculum spread, the second inoculations were effective for both short and long moist periods. Weather during stem elongation has also been reported to determine severity of infection of higher leaves by *Leptosphaeria nodorum* (20).

Throughout the growing season, disease spreads through spore dispersal from pycnidia formed on the lower leaves of wheat plants (1,5,6). Pycnidiospores are liberated when the atmosphere is almost saturated or when water is present on the leaf surface (12) and splashing or wind-blown rain distributes spores up the plant and between plants.

We observed that as disease progressed up the plant, lower leaves developed severe infections and died while the fungus established itself and spread on upper plant parts. This vertical disease progression is illustrated by data in Table 7. Significant correlations are found between disease levels on the spikes and flag leaves, on flag and penultimate leaves, but not on spikes and penultimate leaves.

Inoculation at boot or heading (GS 40 and 59, respectively) growth stages reduced yield substantially through severe infection of the flag leaf and sheath. The photosynthetic activity of these two organs contributes much to grain filling (19).

TABLE 6. Correlation coefficients of yield components with disease severities of Arthur wheat inoculated with *Mycosphaerella graminicola* at the Purdue Agronomy Farm in 1983 and 1984

	1983[a,b]			1984		
	HRS[c]	AUDPC	YLD	HRS	AUDPC	YLD
AUDPC[d]	0.836**			0.854**		
YLD[e]	−0.451**	−0.397*		−0.820**	−0.749**	
TSW[f]	−0.411*	−0.482**	0.122	−0.329*	−0.422**	0.412*

[a] Treatment 7 data excluded from the 1983 analysis.

[b] Symbols * and ** indicate significant differences among treatment means at $P = 0.05$ and 0.01, respectively.

[c] Hours of postinoculation moisture.

[d] Area under the disease progress curve from 15 May through 24 June 1983 and 25 May through 25 June 1984.

[e] Thousand seed weight (g).

[f] Plot yield (g).

TABLE 7. Correlations between disease severities on different plant organs or between yield components and disease severities on Arthur wheat inoculated with *Mycosphaerella graminicola* at the Purdue Agronomy Farm in 1983 and 1984[a,b]

	1983			1984	
	H	L1	L2	L1	L2
L1	0.165**				
L2	0.067	0.300**		0.397**	
KER	−0.182**	−0.081	−0.032	−0.232**	−0.177**
KWT	−0.144**	−0.205**	−0.208**	−0.134**	−0.254**

[a] L1 = disease severity (%) on flag leaf, L2 = disease severity (%) on penultimate leaf, KER = kernel number, KWT = single kernel weight, and H = disease severity (%) on spike.

[b] Symbols * and ** indicate departure from a zero relationship at $P = 0.05$ and 0.01, respectively.

Reductions in both yield and TSW resulted from increased disease favored by prolonged postinoculation moist treatment. High intensities of Septoria tritici blotch are known to produce shriveled grain (20) with resulting reduction in TSW. Head infection contributes most to TSW reduction (11). The total absence of rainfall during the first 2 wk of June 1984 halted disease spread before heads were infected.

In 1983, moisture was identified as the only significant treatment affecting TSW, reflecting the abundance of natural inoculum in that year. For single-inoculation treatments, moisture but not inoculation was found to contribute to yield reduction in 1983 and 1984. Repeated inoculation at the later growth stage reduced yield additionally but only for long moist period treatments.

Septoria tritici blotch reduces yield mainly through reduction of TSW and mean yield per head (10,22). Yield per head is least when the whole plant is infected (11), explaining the increased effect of inoculation at the later growth stage.

For disease development on the upper plant to occur, certain rainfall patterns are required. In Indiana, disease progress depends on distribution of rainfall from 1 April through 14 June (the period of stem elongation through grain filling). Disease development on upper plant organs results in economic loss through reduction in single kernel weight and mean yield per head. Quantification of environmental parameters conducive to infection by *M. graminicola* will contribute to refinement of mathematical models used in microcomputer-based disease forecasting systems (e.g., 4). A predictive system for scheduling fungicide application will aid in the economic control of Septoria tritici blotch epidemics.

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