Development of Septoria nodorum Blotch on Winter Wheat Under Two Cultivation Schemes in Maryland

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ABSTRACT

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Field experiments were conducted on soft red winter wheat cultivars Florida 302 and Coker 916 at three locations in Maryland over two seasons to assess the effect of cultivation schemes on Septoria nodorum blotch epidemics and the need for disease control. High-input cultivation (HIC) employed half the row spacing and 1.5–2 times the nitrogen fertility of conventional input cultivation. Subplots were inoculated with *Stagonospora nodorum* at different rates to develop various epidemic levels. Septoria nodorum blotch in the field was more severe on foliage but less severe on heads of Florida 302 than on Coker 916, regardless of the cultivation scheme. HIC tended to reduce disease severity and resulted in higher yields, regardless of cultivar. However, seed infection was either not affected or increased with HIC. Fungicides effectively improved only grain quality, regardless of the cultivation scheme employed. Greenhouse experiments were conducted to quantify the relative susceptibility of cultivars to Septoria nodorum blotch at three growth stages and to determine the effect of nitrogen fertility on disease development. High nitrogen fertility tended to suppress disease in the greenhouse trials. The reduction of Septoria nodorum blotch severity on foliage by HIC in the field was apparently due to interference of splash dispersal of spores in the denser canopy and the suppressive effect of high nitrogen fertility.

Septoria nodorum blotch caused by *Stagonospora nodorum* (Berk.) Castellani & E.G. Germano (= *Septoria nodorum* (Berk.) Berk. in Berk. & Broome), anamorph of *Phaeosphaeria nodorum* (E. Müller) Hedjaroude (= *Leptosphaeria nodorum* E. Müller), is a disease that affects all aboveground parts of small grain plants and is known to occur sporadically in Maryland (19). Recent trends in agricultural practices may be leading to more frequent and severe epidemics. In particular, short-statured, early-maturing wheat cultivars are generally more susceptible to Septoria nodorum blotch. Increased susceptibility has been associated with pleiotropic effects that can be attributed to or linked with plant height (17). There has also been an increase in the production of wheat with decreased row spacing and increased nitrogen fertility, thereby altering the interaction among host, pathogen, and environment.

The effect of nitrogen on Septoria nodorum blotch epidemics is unclear. *S. nodorum* is reportedly a perthophyte, sporulating in dead or senesced tissue (9,22). High nitrogen promotes rapid culm elongation and abundant foliage that reduces splash dispersal of inoculum as well as maintain green tissue longer, thus keeping leaves in an immature and more resistant state (22). However, observations of Septoria nodorum blotch epidemics in the field have yielded contrasting results, with some noting a decrease in disease severity (7,21) and others reporting an increase (1,15,19) with increased nitrogen fertility.

The denser canopies that develop with narrow-row cropping and higher nitrogen fertility levels have been implicated in increasing the severity of several foliar diseases of wheat (1,5,15), including Septoria tritici blotch. Splash-dispersed pathogens tend to be affected more by host density, as plant-to-plant dissemination is, in part, influenced by proximity of susceptible host tissue (4). Greater development of Septoria nodorum blotch epidemics in dwarf wheat cultivars is believed to be partially a result of the shorter vertical distances between upper and lower leaves, which allows more efficient spore dispersal (17). The effect of close horizontal proximity of host tissues resulting from narrow-row cropping on spore dispersal by *S. nodorum* has not been experimentally demonstrated.

Gaps remain in our understanding of the effects of crop nutrient status and canopy (4,9) on development of Septoria nodorum blotch epidemics. Thus the objective of our study was to investigate epidemic development under currently used but contrasting strategies of wheat cultivation and to suggest disease management strategies for successful wheat production in areas prone to Septoria nodorum blotch.

MATERIALS AND METHODS

Field experiments. A four factor ($2 \times 2 \times 2 \times 4$) experiment was conducted during 1986–1987 (trial 1) at the Beltsville Agricultural Research Center in Maryland on a sandy-loam soil. Prior to planting, the field was lightly disked to a depth of 10 cm, incorporating 22.4 kg ha^{-1} of 20-20-20 (N-P-K) fertilizer in the fall. Coker 916, a short-statured, early-maturing soft red winter wheat cultivar, and Florida 302, a taller, later maturing cultivar, were planted in two cultivation schemes as whole plots in a randomized split-block design with four replications. Both cultivars were resistant to prevalent races of *Erysiphe graminis* DC. f. sp. *tritici* Ém. Marchal and *Puccinia recondita* Roberge ex Desmaz. Each cultivar was planted in strips 49×1.8 m in nine rows on 20-cm spacing (wide) at approximately 65 seeds per meter of row and in 17 rows on 10-cm spacing (narrow) at approximately 33 seeds per meter of row. Wide-row plots received a single spring application of 53 kg ha^{-1} of nitrogen from NH_4NO_3 at Feekes (11) growth stage (GS) 4–5; hereafter this combination is referred to as conventional-input cultivation (CIC). Narrow-row plots received 53 kg ha^{-1} of nitrogen from NH_4NO_3 in the spring at GS 4–5 and again at GS 6; hereafter this combination is referred to as high-input cultivation (HIC). These whole plots were split into eight 3.4×1.8 m subplots that were randomly assigned to two fungicide and four inoculation treatments.

A single-spore isolate of *S. nodorum* was obtained from infected wheat near Beltsville in the cropping season prior to the study and maintained on yeast-malt extract agar (YMA). Pathogenicity of the isolate was tested by spraying 6-wk-old wheat seedlings with 1×10^6 conidia per milliliter, then covering them with polyethylene bags and incubating them at room temperature for 10 days. Conidia were obtained by the method of Cooke and Jones (2). Conidial inoculum was prepared by flooding each sporulating YMA plate with 10 ml of sterile distilled water and gently scraping with a sterile loop. This suspension was filtered once through a single layer of cheesecloth, and spore concentrations

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were determined with a hemacytometer. Solid inoculum, produced by homogenizing cultures grown for conidial production with sterile water in a blender, was poured onto a 60 × 42 × 2.54 cm tray of sterilized wheat kernels containing 0.1% (w/w) calcium carbonate. The trays were covered with aluminum foil and incubated at room temperature for 4 days, uncovered in a laminar flow hood, and then remixed and incubated for an additional 7 days.

All inoculated plots received the solid inoculum at the rate of 30.6 g m^{-2} at GS 2–3 in December. Inoculation was repeated at GS 4–5 in March using 30.2 g m^{-2}. Additional inoculations with conidial suspensions prepared with water amended with 0.1% (v/v) Tween 80 were applied by backpack sprayer at 269 L ha^{-1} to produce the two higher inoculation levels. Inoculations were made with 2×10^4 conidia per milliliter at GS 8–9 (flag leaf unfolding) and 20 days later with 3×10^4 conidia per milliliter at GS 10–10.4 (boot to heads emerging); Florida 302 was at GS 10 and Coker 916 was at GS 10.2–10.4. Conidial suspensions were applied late in the afternoon to avoid the hottest part of the day, permitting a more favorable environment for infection. Therefore, the four inoculation levels (I_x) were: I_0, noninoculated control; I_1, solid inoculum only; I_2, solid inoculum plus conidial inoculum at GS 8–9; and I_3, I_2 plus conidial inoculum at GS 10–10.4.

Fungicide treatments were applied as a tank mix of mancozeb (2.24 kg ha^{-1} Dithane M-45 80WP) and triadimefon (0.14 kg ha^{-1} Bayleton 50WP) to one-half of the plots. The mix was applied at GS 10 and 11 with 269 L ha^{-1} water as recommended. The applications were made with a backpack sprayer at 0.12 kPa pressurized by CO_2 and equipped with hollow cone (HC12) nozzles.

Disease assessments were made on 10 tillers per plot on up to four different leaf positions and glumes throughout the growing season by visually estimating the leaf or glume area displaying necrotic or chlorotic symptoms, sensu James (6). Disease ratings began in mid-April (GS 7–8) and continued approximately every 10 days until all tissues senesced (GS 11.3). Leaves were identified by their relative positions to the heads. The uppermost is the flag leaf, and each consecutively lower leaf is identified as flag −1, flag −2, etc. Results are presented on only those leaves that were not senesced at heading. The average percentage of leaf or glume area diseased for each plot at each rating period and time from first assessment in days was used to compute the area under the disease progress curve (AUDPC) (18). The percentage of infected seed was determined for 100 seeds per plot on oxgall agar (13).

The number of fertile tillers per unit area was assessed just before harvest by counting the number of heads in a 0.12-m^2 area of each plot. Plots were machine-harvested with a small-plot combine after removal of the outer two rows of each plot to reduce border effects caused by small alleys between plots. Grain was cleaned, moisture content was determined, and yield was calculated for a 13.5% moisture content.

In the following season, the experiment (trial 2) was repeated at two locations in Maryland. One was a sandy-loam site at the Hayden Farm of the University of Maryland Central Maryland Research and Education Center (CMREC) near Beltsville, and the other was a silty-loam site at the University of Maryland CMREC near Clarksville. The same experimental design was used, with some changes. At Clarksville, nitrogen fertility was reduced to one application for CIC and two applications for HIC of 37.3 kg ha^{-1} of NH_4NO_3, because soil tests indicated high residual nitrogen levels. Only three replicates were used at the Clarksville site. Different epidemic levels at both sites were encouraged by varying the quantity of solid inoculum only. Inoculations in the fall were applied at both sites at GS 2 in November at the rate of 39.5 g m^{-2}. Additional solid inoculum was applied to plots at GS 4–5 in March at 28.2, 40.3, and 52.4 g m^{-2} for I_1, I_2, and I_3, respectively. Only one application of the fungicide tank mix was applied at GS 10.2.

Greenhouse experiments. Three greenhouse experiments were conducted to determine the effect of nitrogen and growth stage at inoculation on the epidemic components of the two cultivars independent of host density. The experimental factors were cultivar (Coker 916 and Florida 302), growth stage at inoculation (GS 3, 10, and 10.5), and nitrogen fertility (low and high). The first two trials were completely randomized with six and nine replications, respectively. The third trial was a randomized complete block design with three replicates and two subsamples per treatment combination. Noninoculated controls were included in each trial.

Two vernalized seedlings of each cultivar were planted per pot in a standard greenhouse potting mix in 10-cm plastic pots and thinned to one per pot after 3 wk. Plants were fertilized every 10 days with either 236 ppm of nitrogen from a 20-20-20 (N-P-K) water-soluble fertilizer for the low treatment or 532 ppm of nitrogen from a 30-10-10 (N-P-K) water-soluble fertilizer for the high treatment. Phosphate and potassium were balanced at approximately 205 ppm in each treatment.

The inoculum consisted of 5×10^5 conidia per milliliter of water amended with 0.1% (v/v) Tween 80. Inoculum was obtained as described previously except that conidial suspensions were filtered through three layers of cheesecloth. Plants were removed from the greenhouse at GS 3 (tillering), GS 10 (boot), or GS 10.5 (anthesis) for inoculation. An airbrush was used to spray the plants with the conidial suspension until runoff. The plants were then incubated in the dark in a growth chamber for 60 hr at 25 C with continuous misting, after which they were returned to the greenhouse, where the temperature was 22–25 C and day length was 14 hr.

Following inoculation, plants were observed daily for symptom development. The incubation period (IP) was determined as time in days from the date of inoculation until 1% of the leaf area displayed symptoms (20). Inoculated leaves were assessed visually as described for the field experiments for leaf area infected 25 days following inoculation. The latent period (LP), time in days from inoculation until conidia were produced (12), was determined on samples of detached leaves. Sample leaves were removed 12 days after inoculation and maintained on water agar amended with 0.1% (w/v) benzimidazole (8). Lesions were examined daily with a dissecting microscope for the appearance of mature pycnidia. Occurrence of sporulation was determined by observing cirrhi.

General linear model analyses of variance procedures were performed on both field and greenhouse data using the statistical analysis system (SAS Institute, Cary, NC) program.

RESULTS

Field experiments. The results of the field trials averaged over replications examining the effect of cultivation scheme, cultivar, inoculation, and fungicide on disease and yield are presented in full in Tables 1 and 2. The text presents a summary of significant main and interactive treatment effects; means for main and interactive effects are averages of these data taken over all other unnamed factors.

Mean disease development on the flag −1 leaf under CIC was significantly greater than that observed under HIC in trial 1 (57.8 and 23.3 mean AUDPC units, respectively) and also at the Beltsville site in trial 2 (125.9 and 76.3 mean AUDPC units, respectively) (Table 1). Fungicides reduced flag −1 disease development in trial 1 more effectively ($P = 0.03$, cultivation × fungicide interaction) in CIC than in HIC plots (48 and 24 mean AUDPC units reduced, respectively). Inoculation was only marginally effective at altering epidemic development on the flag −1 leaf above background; at Beltsville in trial 2, it resulted in significant changes in rank ($P = 0.03$, cultivar × cultivation × inoculation interaction) of the different inoculum levels applied to the different combinations of cultivar and cultivation.

There was no significant effect of cultivation scheme on development of disease on flag leaves in trial 1. Although disease development on flag leaves was generally

low, HIC in trial 2 at both locations significantly reduced epidemic development when compared with CIC (Table 1). Mean AUDPC values for HIC and CIC were 16.9 and 18.3 units, respectively, at Beltsville and 3.4 and 5.2 units, respectively, at Clarksville. At Clarksville there was a significant cultivation × fungicide ($P = 0.02$) interaction because the magnitude of the disease reduction with fungicides was greater (6.9 reduced to 3.4 AUDPC units) in the CIC plots where disease pressure was greater than in the HIC plots (5.3 reduced to 3.5 AUDPC units). Similarly, for the Beltsville location in both trials, cultivar × fungicide interactions were significant ($P = 0.0002$ and $P = 0.005$, respectively), as fungicides were more effective on Florida 302 than on Coker 916. Untreated Florida 302 allowed greater disease development than did untreated Coker 916.

Septoria nodorum blotch development on glumes of both cultivars was significantly reduced at the Beltsville location when HIC was used as compared with CIC only in trial 2 (3.9 and 5.2 mean AUDPC units, respectively) (Table 1). Fungicides significantly reduced disease development on the glumes at both locations in trial 2, and in trial 1 the reduction was significant at the high inoculum level ($P = 0.0001$, fungicide × inoculation interaction). Cultivar differences occurred at Beltsville in both trials. Coker 916 had significantly greater disease development on the glumes than did Florida 302 at the high inoculum level in trial 1 ($P = 0.01$, cultivar × inoculation interaction), whereas at Beltsville in trial 2 the higher level on Coker 916 occurred regardless of inoculum level.

There was a significant cultivar × cultivation interaction in trial 1 ($P = 0.05$) resulting from Coker 916 producing significantly more fertile tillers in response to HIC (538 m^{-2}) than to CIC (520 m^{-2}), whereas Florida 302 exhibited a mean difference of approximately 1 m^{-2} tiller between cultivation schemes (Table 2).

Table 1. The effect of cultivation scheme, fungicide application, and inoculation with *Stagonospora nodorum* on the area under the disease progress curve (AUDPC) for flag leaf −1, flag leaf, and glumes of two soft red winter wheat cultivars grown in Beltsville (B) and Clarksville (C), Maryland

		AUDPC								
		Flag leaf −1			Flag leaf			Glumes		
		Trial 1	Trial 2		Trial 1	Trial 2		Trial 1	Trial 2	
Fungicide	Inoculum level	B[a]	B[b]	C[c]	B[d]	B[e]	C[f]	B[g]	B[h]	C[i]
Coker 916										
Conventional input										
−	0	117.3	109.6	24.4	9.8	3.9	5.7	1.7	5.9	6.1
−	1	77.1	96.9	14.8	8.0	7.7	7.7	4.3	9.0	5.6
−	2	119.8	101.2	9.2	3.6	7.6	6.1	2.5	7.7	4.7
−	3	119.6	119.2	22.9	42.5	13.2	8.3	92.9	6.7	3.6
+	0	31.7	54.8	13.4	7.7	4.6	3.5	1.3	4.4	4.4
+	1	27.3	77.9	12.1	1.0	4.8	2.6	0.8	3.2	3.2
+	2	83.6	113.8	5.4	12.7	4.9	4.2	0.5	3.7	4.8
+	3	51.3	133.4	8.4	5.1	4.4	3.8	27.6	3.9	2.1
High input										
−	0	63.7	60.4	8.4	7.0	4.9	2.6	2.6	4.6	7.2
−	1	32.2	84.0	8.2	5.9	5.5	3.2	3.8	5.7	2.8
−	2	24.1	93.2	15.5	3.0	7.6	4.4	1.7	7.6	6.3
−	3	59.0	73.1	18.6	77.1	6.6	2.3	63.9	4.8	4.7
+	0	21.5	50.5	8.1	0.4	4.4	2.8	0.4	4.0	1.8
+	1	6.6	56.5	15.7	1.6	2.8	1.2	0.4	3.0	2.3
+	2	3.8	45.5	8.9	0.0	3.3	6.7	0.3	4.3	2.6
+	3	13.7	46.4	25.7	0.4	2.6	1.0	1.5	2.7	2.3
Florida 302										
Conventional input										
−	0	36.0	167.7	11.7	11.1	33.3	11.0	3.6	5.7	1.9
−	1	46.0	176.7	17.7	7.3	38.8	7.7	1.8	6.7	3.8
−	2	31.6	195.6	19.9	11.7	34.0	5.2	2.0	5.6	1.9
−	3	74.5	125.0	23.4	103.2	32.5	3.9	37.8	6.0	1.9
+	0	7.4	120.3	9.1	1.0	21.6	2.0	0.7	3.0	0.8
+	1	14.6	169.0	6.0	1.2	20.0	4.1	0.8	3.3	1.8
+	2	20.1	135.1	18.8	2.3	15.4	3.0	1.0	3.7	0.6
+	3	25.9	117.3	8.4	6.8	19.2	4.3	6.0	4.3	0.6
High input										
−	0	11.0	91.0	8.9	22.5	18.6	2.8	2.2	3.7	2.8
−	1	13.0	104.2	18.0	7.2	27.4	5.8	1.4	5.5	2.8
−	2	23.2	108.5	7.2	5.8	19.5	2.8	1.4	4.7	2.4
−	3	34.0	95.8	19.9	130.0	19.7	3.6	33.3	3.7	2.4
+	0	8.4	62.8	9.8	2.2	11.7	4.8	2.0	2.7	1.4
+	1	3.8	88.4	10.5	1.0	12.8	3.5	0.5	2.2	0.7
+	2	10.9	80.4	11.3	1.5	9.2	3.6	1.3	1.8	1.5
+	3	15.1	79.4	8.0	7.3	8.2	3.4	7.8	1.9	2.7

[a] Beltsville trial 1 means were based on four replicates, except that those for inoculum level three were based on eight replicates. The interactions of cultivar × fungicide ($P = 0.02$) and cultivation scheme × fungicide ($P = 0.03$) were significant.
[b] Beltsville trial 2 means were based on four replicates. The main effect of fungicide ($P = 0.0001$) and the interaction of cultivar × inoculation ($P = 0.03$) were significant.
[c] Clarksville means were based on three replicates. There were no significant differences.
[d] The interactions of cultivar × fungicide ($P = 0.003$), cultivar × inoculation ($P = 0.02$), and fungicide × inoculation ($P = 0.0001$) were significant.
[e] The main effect of cultivation ($P = 0.01$) and the interaction of cultivar × fungicide ($P = 0.0005$) were significant.
[f] The interaction of cultivation × fungicide ($P = 0.02$) was significant.
[g] The interactions of cultivar × inoculation ($P = 0.01$) and fungicide × inoculation ($P = 0.0001$) were significant.
[h] The main effects of cultivar ($P = 0.03$), cultivation ($P = 0.01$), and fungicide ($P = 0.0001$) were significant.
[i] The main effect of fungicide ($P = 0.0001$) was significant.

At Beltsville in trial 2, there was a significant cultivation effect ($P = 0.01$), as both cultivars produced more fertile tillers under HIC (796 m^{-2}) than under CIC (747 m^{-2}). There was also a significant effect of cultivar at this site, with Coker 916 producing significantly more fertile tillers (813 m^{-2}) than Florida 302 (755 m^{-2}). Statistically, the cultivation × inoculation interaction was significant at Clarksville in trial 2. However, there is no meaningful biological interpretation of these data because of confounding by the unusually high tiller survival. The high survival was a result of a very mild winter, adequate seasonal moisture, and high residual fertility from a previous crop of alfalfa.

There was no significant effect of cultivation in trial 1 on the percentage of infected seed (Table 2). Seed infection was significantly higher on Florida 302 than on Coker 916 at the high level of inoculum ($P = 0.03$, cultivar × inoculum interaction). Also in trial 1, the reduction of seed infection with fungicides was significant and much greater at the high inoculum level than at any of the other inoculum levels ($P = 0.0002$, fungicide × inoculum interaction). In trial 2 at Beltsville, there was a significantly higher mean percentage of infected seed on Coker 916 under HIC (14%) than under CIC (7.5%). However, seed infection on Florida 302 was not affected by cultivation, with 11.2 and 12.8% for HIC and CIC, respectively. This discrepancy was reflected in a significant cultivar × cultivation interaction ($P = 0.03$) (Table 2). Fungicides significantly reduced seed infection overall from 13.1 to 9.6% ($P = 0.002$). There was also a significant interaction at the Clarksville site for cultivation × inoculation ($P = 0.03$). However, the percentages of infected seed were low and the statistical difference was probably of no biological significance (Table 2).

The trial 1 crop was heavily scavenged by pigeons just prior to harvest, so yield data are not presented. Florida 302 was the significantly higher yielding cultivar of the two in the second season at both sites, and the trend was the same in the

Table 2. The effect of cultivation scheme, fungicide application, and inoculation with *Stagonospora nodorum* on fertile tiller density, seed infection, and yield of two soft red winter wheat cultivars grown in Beltsville (B) and Clarksville (C), Maryland

		Fertile tiller density (no. m^{-2})			Infected seed (%)			Grain yield (kg ha^{-1})	
		Trial 1	Trial 2		Trial 1	Trial 2		Trial 2	
Fungicide	Inoculum level	B[a]	B[b]	C[c]	B[d]	B[e]	C[f]	B[g]	C[h]
Coker 916									
Conventional input									
−	0	495.8	735.4	1,327.7	10.2	10.2	4.6	4,328	7,051
−	1	535.4	710.4	1,291.7	7.7	8.5	6.6	4,763	6,906
−	2	489.6	795.8	1,275.0	10.2	9.5	2.0	4,687	6,564
−	3	590.6	806.2	1,122.3	48.8	7.2	2.3	4,353	6,732
+	0	441.7	762.5	1,227.8	3.0	8.5	2.6	4,558	5,929
+	1	475.0	691.7	1,494.4	0.5	5.0	7.0	4,602	6,570
+	2	539.6	758.3	1,219.4	0.5	6.0	3.6	4,065	6,523
+	3	520.8	810.4	1,175.0	9.0	5.0	2.6	4,873	6,753
High input									
−	0	668.7	847.9	1,519.4	25.0	20.2	8.0	5,946	6,379
−	1	562.5	839.6	1,428.7	19.2	15.7	3.0	5,789	6,829
−	2	618.7	847.9	1,255.6	18.2	14.7	5.6	5,593	6,091
−	3	567.7	906.2	1,519.4	42.8	12.7	4.3	5,211	6,150
+	0	577.1	841.7	1,630.4	4.7	15.5	4.0	5,692	6,871
+	1	564.6	822.9	1,386.1	2.0	10.2	3.6	5,985	6,543
+	2	514.6	900.0	1,588.9	2.5	12.5	7.6	6,779	6,691
+	3	594.8	933.3	1,675.0	12.6	10.5	5.0	6,677	6,163
Florida 302									
Conventional input									
−	0	529.2	829.2	1,311.1	13.0	10.0	5.6	4,504	7,709
−	1	485.4	712.5	1,391.7	8.5	16.0	7.6	4,652	7,304
−	2	460.4	733.3	1,411.1	8.7	11.0	6.6	4,635	7,682
−	3	493.7	781.2	1,080.6	59.8	14.0	5.6	4,750	7,177
+	0	456.2	658.3	1,205.6	2.0	8.7	0.6	4,532	7,848
+	1	456.2	700.0	1,288.9	0.7	8.5	5.3	4,929	7,849
+	2	533.3	781.2	1,105.6	3.5	10.0	4.3	4,918	7,935
+	3	502.0	685.4	1,211.1	22.0	11.5	0.6	4,278	7,506
High input									
−	0	456.2	841.7	1,219.4	22.5	9.2	5.6	6,200	7,931
−	1	531.2	722.9	1,205.6	23.0	17.2	6.0	6,276	7,611
−	2	435.4	768.8	1,566.7	12.5	19.5	6.3	6,039	8,024
−	3	522.4	775.0	1,450.0	50.5	14.5	4.0	7,094	7,336
+	0	497.9	729.2	1,275.0	4.0	15.0	6.0	6,168	8,145
+	1	489.6	683.3	1,400.0	14.2	7.7	4.6	6,011	7,323
+	2	495.8	827.1	1,355.6	3.5	9.5	4.0	6,246	8,273
+	3	472.9	847.9	1,441.7	29.9	10.0	4.0	6,544	7,702

[a]Beltsville trial 1 means were based on four replicates, except that those for inoculum level three were based on eight replicates. The interaction of cultivar × cultivation × fungicide × inoculum ($P = 0.01$) was significant.
[b]Beltsville trial 2 means were based on four replicates. The main effects of cultivar ($P = 0.002$), cultivation ($P = 0.01$), and inoculation ($P = 0.01$) were significant.
[c]Clarksville means were based on three replicates. The interaction of cultivation × inoculation ($P = 0.02$) was significant.
[d]The interactions of cultivar × inoculum ($P = 0.03$) and fungicide × inoculum ($P = 0.0002$) were significant.
[e]The main effect of fungicide ($P = 0.002$) and the interactions of cultivar × cultivation ($P = 0.03$) and cultivar × inoculation ($P = 0.02$) were significant.
[f]The interaction of cultivation × inoculation ($P = 0.03$) was significant.
[g]The main effects of cultivar ($P = 0.04$) and cultivation ($P = 0.0001$) were significant.
[h]The main effect of cultivar ($P = 0.0001$) was significant.

first season (Table 2). HIC produced significantly greater total yield (6,141 kg ha^{-1}) than CIC (4,590 kg ha^{-1}) at Beltsville in trial 2. Fungicide applications did not result in significantly greater yields.

Greenhouse experiments. In the first trial, there was a significant cultivar × growth stage interaction ($P = 0.02$) for disease severity resulting from a change in rank, with Coker 916 exhibiting a lower mean disease severity at GS 3 than Florida 302 but a greater mean disease severity at GS 10 and 10.5 (Table 3). In the second trial, there was a significant interaction ($P = 0.02$) among all three factors (cultivar, growth stage, and nitrogen fertility) for disease severity (Table 3). When inoculated at anthesis (GS 10.5), only Coker 916 had a significant percentage of leaf area infected, and infection was reduced by increased nitrogen fertility. In the third trial, although lower disease severities developed, the trends in response to fertility and time of inoculation were similar to those in the first trial. Inoculation at GS 3 produced significantly lower disease severity than inoculations at the other growth stages.

In the second trial, the mean IP for *S. nodorum* was significantly longer (about 0.6 days) on Coker 916 than on Florida 302 (Table 3). On both cultivars, the mean IP was longer when inoculation was at GS 3 (6.8 days) than at the other growth stages (5.0 days). Although there were statistical differences between cultivars and growth stages in the third trial, they were due to the reduced estimate of IP on Coker 916 at GS 10, for which no comparable data on Florida 302 were available. Nitrogen fertility had no significant effect on IP in any trial.

The mean LP in the first trial was affected by a significant three-way interaction of all tested factors. This results from a change in magnitude in the dramatically longer LP associated with high nitrogen in Coker 916 at GS 3 than the lesser effect observed in Florida 302 under those treatment combinations ($P = 0.0001$, mean LP of 18.9 and 24.0 days for Coker 916 and 15.4 and 16.3 days for Florida 302) (Table 3). The significant cultivar × growth stage interaction ($P = 0.001$) in the second and third trials was due to a difference in the rank between growth stages for each cultivar. Coker 916 exhibited the longest mean LP at GS 3 and the shortest when inoculated at GS 10. Florida 302 exhibited little difference in LP between growth stages (Table 3).

DISCUSSION

The results indicate that under environmental conditions prevailing in Maryland during the trial seasons, Septoria nodorum blotch was not a serious disease of wheat in the region. However, even noninoculated plots were never disease-free, and sufficient disease developed to separate relative effects of the studied factors.

The higher field disease levels noted on Florida 302 than on Coker 916, particularly in trial 2, developed from a more natural epidemic encouraged by solid inoculum only, as opposed to direct inoculation with spore suspensions. Greater early epidemic development on Florida 302 foliage is supported by the results of the greenhouse evaluations. Florida 302 seedlings were more susceptible and had shorter or similar, but never longer, LPs and IPs than Coker 916.

Although the field disease severity on the upper leaves of Coker 916 was reduced relative to that on Florida 302, the disease severity on glumes was greater in two experiments. This may be due to the shorter stature and earlier maturity of Coker 916 and the greater importance of inoculum produced in the lower canopy than of that produced in the upper canopy for head infections (3,16). The stature and maturity characteristics have been implicated to favor Septoria nodorum blotch epidemic development by allowing inoculum produced in the lower canopy ready access to the spikes and by providing earlier senescence of tissues necessary for completion of the disease cycle (9). The later effect was observed in the greenhouse, where Coker 916 plants inoculated at GS 10.5 and treated with low nitrogen demonstrated early senescence and greater susceptibility.

Florida 302 appeared to be more susceptible to seed infection based on the results of the first field trial, where late conidial inoculations were made on the developing spikes. Under more natural epidemic conditions in trial 2 at Beltsville, Coker 916 had less seed infection under CIC than did Florida 302 but greater seed infection under HIC. The higher seed infection may be explained by the delayed maturity and longer ripening period of the spikes that are associated with HIC, allowing greater opportunity for the pathogen in infected glumes to colonize the seed (15).

Disease severity on the glumes, flag leaf, and flag −1 leaf in CIC was never less, and often was greater, than that in HIC plots. The denser canopy associated with HIC wheat under the prevailing conditions of these studies may have been

Table 3. The effect of growth stage at time of inoculation and nitrogen fertility on severity of Septoria nodorum blotch and length of incubation and latent periods on two soft red winter wheat cultivars grown in the greenhouse

Growth stage[a]	Nitrogen fertility	Disease severity (%)			Incubation period (days)			Latent period (days)		
		T1[b]	T2[c]	T3[d]	T1	T2[e]	T3[f]	T1[g]	T2[h]	T3[i]
Coker 916										
3	Low	0.2	0.3	0.2	6.0	7.9	5.2	18.9	20.7	22.3
3	High	0.2	0.4	0.4	6.0	6.9	5.0	24.0	19.8	24.2
10	Low	3.0	1.2	3.0	4.0	5.1	4.0	16.0	11.5	17.3
10	High	2.3	1.6	2.3	4.0	5.0	4.0	17.8	11.1	16.8
10.5	Low	3.4	22.2	3.3	5.0	5.4	5.0	16.0	15.1	18.0
10.5	High	1.9	11.4	1.9	5.0	5.1	5.0	17.0	14.3	19.2
Florida 302										
3	Low	1.4	2.1	1.5	5.0	6.1	5.2	15.5	16.1	17.0
3	High	0.8	0.2	0.8	5.0	6.1	5.0	16.3	15.0	18.0
10	Low	0.2	3.5	...	5.0	5.0	...	19.8	15.8	...
10	High	0.7	3.5	...	6.0	5.0	...	21.0	15.5	...
10.5	Low	2.6	1.5	2.6	5.0	4.9	5.0	18.2	13.0	19.2
10.5	High	2.1	1.8	2.1	5.0	4.4	5.0	18.3	13.0	19.2

[a] Feekes growth stage at time of inoculation.
[b] Trial 1 (T1) means were based on six replicates. The interaction of cultivar × growth stage ($P = 0.02$) was significant.
[c] Trial 2 (T2) means were based on nine replicates. The interaction of cultivar × growth stage × nitrogen ($P = 0.02$) was significant.
[d] Trial 3 (T3) means were based on three replicates. Separate analyses were done by cultivar; main effects of growth stage for Coker 916 ($P = 0.004$) and Florida 302 ($P = 0.02$) were significant.
[e] Main effects of cultivar ($P = 0.01$) and growth stage ($P = 0.0001$) were significant.
[f] The interaction of cultivar × growth stage ($P = 0.0001$) was significant.
[g] The interaction of cultivar × growth stage × nitrogen ($P = 0.004$) was significant.
[h] The interaction of cultivar × growth stage ($P = 0.0001$) was significant.
[i] The main effect of nitrogen ($P = 0.004$) and the interaction of cultivar × growth stage ($P = 0.0001$) were significant.

an important factor suppressing Septoria nodorum blotch epidemic development. High nitrogen levels and narrow-row spacing induce rapid culm elongation that elevates the upper leaves, thereby increasing the distance from the source of inoculum. Several effects of a closed canopy on the microclimate (providing shading, higher humidity, and decreased gas exchange, possibly raising oxygen levels) have been investigated in other pathosystems (10). Most of these effects tend to favor the pathogen. Although final fertile tiller density was greater under HIC, the trials were all planted at the same population per unit area, and plant density at GS 3 was similar under both cultivation schemes (14). Therefore, the reduced competition for water, light, and available nutrients resulting from more uniform distribution of plants under HIC may be important in establishing healthy stands that produce higher yields. Higher total yields were achieved with HIC than with CIC. It might be hypothesized that healthier, more productive plants are less susceptible to colonization and completion of an infection cycle by a perthophyte such as *S. nodorum*. The greenhouse data provide some support for this hypothesis. Increased nitrogen did not in any trial increase susceptibility but in several cases significantly decreased susceptibility to infection. Similarly, increased nitrogen did not in any trial reduce LP but in several cases significantly lengthened LP. Furthermore, the denser canopies and rapid growth associated with HIC inhibited splash dispersal of conidia (16,17).

Fungicide applications were effective in suppressing the epidemics in both seasons. Detection of a fungicide effect was greatest where disease severity was highest in nontreated controls. The greatest effect of fungicides was observed in the first season, when severe infections were induced in the upper canopy by inoculation with conidial suspensions. Fungicide applications did not significantly impact total yield but did improve grain quality.

In general, HIC results in higher yields and less Septoria nodorum blotch pressure. However, there may also be an increase in percentage of seed infected with HIC, apparently associated with delayed maturity. Evidence from this study suggests that fungicide applications may be recommended for seed producers utilizing HIC schemes even when disease severity on the upper foliage is reduced. Fungicide applications under such conditions could improve seed quality but may have little or no effect on yield.

The combination of increased tiller density and higher nitrogen fertility that developed under intensive cultivation suppressed the epidemics under the tested conditions. The mechanisms through which high nitrogen fertility suppresses disease development on the foliage while enhancing seed infection remain unclear. Experiments conducted under strict environmental controls, such as in growth chambers, may provide the data to separate the epidemic components affected. Further research is warranted to elucidate the mechanisms of these effects and to test the effects under conditions particularly favorable to Septoria nodorum blotch epidemics.

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