Reaction of Canadian Spring Wheats to *Septoria nodorum* and the Relationship Between Disease Severity and Yield Components

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ABSTRACT

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Twelve cultivars of wheat were tested two ways: in a controlled environment for reaction to *Septoria nodorum* based on lesion type at seedling and adult stages of development; and in the field to assess the relationship between disease severity and two yield components, kernels per head and thousand-kernel weight. The four durum wheats were moderately resistant to *S. nodorum* at both stages; cultivars of other wheat types were moderately susceptible to susceptible at the seedling stage, but more resistant as adults. In the field, kernel number per head generally was not affected by *S. nodorum* infection. However, significant reductions of 6.8–15.6% in thousand-kernel weight occurred in half the cultivars in 1989, despite dry conditions which led to only moderate disease development. Higher disease severities were associated with minimal yield reductions in several cultivars; such cultivars may be tolerant to Septoria leaf blotch. In 1990, abundant early-season rainfall resulted in rapid and extensive disease development, and significant yield reductions occurred in all cultivars. The inconsistent relationship between disease severity and yield loss suggest that kernel weight may be a more reliable predictor of cultivar performance than foliar disease severity.

Septoria nodorum leaf and glume blotch of wheat (*Triticum aestivum* L.), caused by *Leptosphaeria nodorum* E. Müller (anamorph *Septoria nodorum* (Berk.) Berk. in Berk. & Broome), has been increasing in importance in recent years in many wheat-growing areas of the world (10). In Manitoba, *S. nodorum* appeared in 32% of fields in 1989, in 47% in 1990, and in 62% in 1991 (12,13,14). No clear relationship has been demonstrated between foliar disease severity and yield loss following infection by *S. nodorum* (25). Many workers, however, continue to evaluate lines on the basis of severity of foliar symptoms (20). Jenkins and Morgan (15) associated reduced weight of grain with the premature death of photosynthetic tissue, finding that this premature death accounted for nearly all the yield loss. Bronnimann (3), however, found that susceptible cultivars are more severely damaged by infection than by defoliation, while with tolerant cultivars the opposite is true. These findings suggest that the pathogen not only reduces the production of carbohydrates in leaf and other tissue, but also interferes with the translocation of carbohydrates to the grain and/or produces a phytotoxin. Therefore, total yield loss may not be associated directly with the loss of photosynthetic tissue. Verreet and Hoffmann's (32) studies confirmed the negative effect of *S. nodorum* infection on carbohydrate production; moreover, they showed that translocation of nitrogen from vegetative parts to reproductive organs during grain filling is inhibited. Tolerance to *S. nodorum* has been reported in wheat; however, successful breeding for tolerance has proved elusive (9). Reduction in thousand-kernel weight appears to be the most sensitive measure for evaluation of wheat lines (11).

The resistance to *S. nodorum* of spring wheat cultivars currently recommended for production in western Canada is generally unknown. The objectives of this study were to compare 12 spring wheat cultivars for foliar disease reaction induced by inoculation with *S. nodorum* at two growth stages in a controlled environment, and to assess the relationship between foliar symptoms, kernels per head, and thousand-kernel weight in field experiments.

MATERIALS AND METHODS

Twelve wheat cultivars were tested: four amber durums (Kyle, Medora, Sceptre, and Wakooma) and eight hexaploid wheats grouped as three types; common (Columbus, Katepwa, Laura, Pasqua, and Roblin), Canada prairie spring (Genesis and Biggar), and soft white (Fielder). These are the similarities in the backgrounds of the selected wheat cultivars. Medora and Sceptre have either Coulter or Macoun, two closely related cultivars, as one of their parents. Wakooma, crossed with breeding line DT322, is a parent of Kyle. The common wheats Columbus, Katepwa, and Pasqua are all Neepawa derivatives. Laura, without a Neepawa background, is more divergent. Roblin has both a Neepawa background and some of the parent lines of Laura. The Canadian prairie spring wheat Biggar is the hard red component of HY320, a cross of which is also a parent of Genesis. In 1991, these cultivars were grown on 73–93% of the land sown to these types in the Canadian prairie provinces (1).

Plants were grown in a controlled environment at 20 ± 1 C with a 16 hr photoperiod. For seedling tests, eight seeds of each cultivar were planted in groups of four cultivars per 15-cm-diameter clay pot. We used an incomplete block design (6) with pots as blocks, adding a 13th wheat as a dummy. Cultivars were randomly assigned to pots. Four scores per cultivar were obtained for each repetition, and the experiment was repeated twice. For adult-stage tests, cultivars were sown at five seeds per 15-cm clay pot and thinned to three seedlings per pot following emergence; they were replicated three times. Soil mix for all experiments was 2 parts loam, 1 part sand, and 1 part peat. For the 1989 and 1990 field experiments, the cultivars were sown in single rows at Glenlea, Manitoba. The plots were 3 m long and bounded on each side by a row of Robert oat. Cultivars were arranged in a randomized complete block design with three replications in 1989 and six in 1990. Cultivated strips 1.5 m wide separated the cultivar plots. A 30-cm strip of plants was removed to divide each row in half. In 1989, the western half of each row was inoculated with a conidial suspension of *S. nodorum*; in 1990, the eastern half. The noninoculated half of each row served as a control. Prior to seeding, plots were fertilized as per soil-test recommendations.

Inoculum production. With minor modifications, inoculum was produced and applied according to published practice (10). Conidia from seven single pycnidia from infected leaf tissue originating in Manitoba and Saskatchewan were streaked across plates of 15% V8 agar (150 ml of V8 juice, 3 g of $CaCO_3$, 20 g of agar, and 850 ml of distilled water) to produce isolates of *S. nodorum* (WRS 1722, 1730–1735). Cultures were grown for 7–10 days under continuous cool-white fluorescent light, until pink spore masses were readily visible. In 1990, cultures were also grown under continuous near-ultraviolet light,

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which promoted sporulation in 5–7 days. Cultures were flooded with sterile distilled water, and the conidia were dislodged with a sterile wire loop. The resulting conidial suspensions were combined and mixed in an Eberbach 8580 blender at low speed for 30 sec, filtered through two layers of cheesecloth, and adjusted to 1×10^6 conidia per milliliter using a hemacytometer.

Inoculation and incubation. For controlled-environment tests, inoculum was applied using a DeVilbiss atomizer connected to an electric air pump adjusted to provide a pressure of approximately 69 kPa. Plants were sprayed until runoff, utilizing about 15 ml per pot. Seedlings were inoculated at the two- to three-leaf stage (GS 13 in the decimal code devised by Zadoks et al [34]) and at the adult stage following heading (GS 53–59). In the first experiment (light/dark), plants were either covered with polyethylene bags or placed in a humidity chamber and incubated in 100% relative humidity (RH) with a 16 hr photoperiod for 2 days. In a second experiment (dark), plants were incubated in darkness at 100% RH for 24 hr. Light was then provided for 2 hr, and plants were air-dried and then misted and incubated in darkness for a further 24 hr. In both light/dark and dark experiments, leaves remained wet during incubation. In the field, a spray nozzle pressurized at approximately 92 kPa with CO_2 was used to apply 35 ml of conidial suspension per meter of row to test plants at four stages: jointing (GS 30–32), flag-leaf emergence (GS 37–43), booting (GS 45–51), and heading (GS 51–59). The control half of each row was protected with a single application of mancozeb (Dithane M-45) at a rate of 1.8 kg a.i./ha at flag-leaf emergence (GS 37–43). To test for possible independent yield increases due to the fungicide, in 1990 the cultivars were also planted in a randomized complete block with three replications as a nonsprayed and noninoculated control. At maturity, 25 heads were harvested at random from each row, and kernels per head and thousand-kernel weights were determined. An analysis of variance (ANOVA) (22) was performed on the differences in kernels per head and thousand-kernel weight between the fungicide-sprayed and nonsprayed, noninoculated control plots to test the effect of the application of mancozeb. The mean difference for each cultivar was compared to 0.

Evaluation. In the laboratory, plants inoculated with *S. nodorum* were rated 7–10 days after inoculation for lesion type using a 1–5 scale, where 1 = small lesions with no chlorosis (resistant); 2 = small lesions with minimal chlorosis (moderately resistant); 3 = moderate to large lesions, not coalescing, with some chlorosis (moderately resistant to moderately susceptible or intermediate); 4 = large lesions (≥10 mm in length), some coalescing (moderately susceptible); and 5 = large, coalescing lesions affecting >50% of leaf area (susceptible). Seedling data were analyzed as a mixed linear model using the SAS mixed procedure (23). Where the F test was significant at the 0.05 probability level, individual class and cultivar-within-class differences were tested using contrasts. An analysis of variance was performed on the adult data using the SAS general linear model (GLM) procedure. Class cultivars and means were compared using Ryan's Q test (Ryan-Einot-Gabriel-Welsch multiple range test [22]), as recommended by Day and Quinn (8) where the F test was significant at the 0.05 probability level. In the field, foliar symptoms of disease were assessed 7–14 days after the last application of inoculum by sampling five flag and five second-youngest (F-1) leaves per replicate for the percent total necrosis. In 1989, this corresponded to kernels watery-ripe to milky-ripe (GS 65–75); in 1990, milky-ripe to doughy-ripe (GS 75–85). The difference in the percent necrosis between flag and F-1 leaves of control and inoculated plants was calculated for each cultivar. Twice each year, after the second and third inoculations, several leaves were placed in moisture chambers to confirm that the lesions were the result of infection by *S. nodorum*.

RESULTS

Controlled-environment experiments. At the seedling and adult stages, humidification in the dark resulted in a shift to more susceptible reactions in all wheat types and cultivars (Tables 1–3). Seedlings of durum wheats were moderately resistant to intermediate in reaction when humidified in light/dark; under dark humidification, all types of wheat were moderately susceptible or susceptible (Tables 1 and 2). Common wheats were more susceptible than other types when humidifed in light/dark. The cultivar Laura was significantly better than other common cultivars tested (Table 1).

Analysis of variance of adult plants indicated that significant differences existed among types, but not among cultivars within types (Table 3). Flag leaves from adult plants incubated in

Table 1. Reactions of seedlings of spring wheat to *Septoria nodorum* after postinoculation humidification with a 16-hr photoperiod or in the dark

Wheat type / Cultivar	Humidification: Light/dark Range	Light/dark LS means	Dark Range	Dark LS means
Durum				
Sceptre	2.0–3.4[y]	2.63 a[z]	2.5–4.5	3.65 a
Medora	1.7–3.6	2.63 a	2.8–5.0	3.74 a
Kyle	1.6–3.7	2.65 a	3.0–4.9	3.82 ab
Wakooma	2.0–3.4	2.80 a	3.4–4.8	4.20 b
Canada prairie spring				
Genesis	2.8–3.9	3.34 a	4.0–5.0	4.50 a
Biggar	3.0–4.1	3.64 a	4.2–5.0	4.57 a
Common				
Laura	3.1–4.0	3.55 a	3.4–4.7	3.85 a
Roblin	3.3–4.8	4.20 b	3.7–5.0	4.44 b
Katepwa	3.4–4.6	4.04 b	4.0–5.0	4.76 bc
Columbus	3.4–4.5	4.06 b	4.0–5.0	4.65 bc
Pasqua	3.8–4.7	4.33 b	4.7–5.0	4.96 c
Soft white				
Fielder	3.0–4.0	3.27	4.0–4.9	4.37

[y] Reactions based on a 1 (resistant) to 5 (susceptible) scale, 7 days postinoculation.
[z] Within classes, least-squares means followed by the same letter are not significantly different at 0.05 probability level on a comparison-wise basis.

Table 2. Reactions of seedling plants of four wheat types to *Septoria nodorum* after post-inoculation humidification with a 16-hr photoperiod or in the dark

Wheat type	Humidification: Light/dark	Dark
Durum	2.68 a[z]	3.85 a
Soft white	3.26 b	4.37 b
Canada prairie spring	3.49 b	4.53 b
Hard red	4.04 c	4.53 b

[z] Least-squares means followed by the same letter are not significantly different at 0.05 probability level on a comparison-wise basis.

Table 3. Reactions of adult plants of four wheat types to *Septoria nodorum* after post-inoculation humidification with a 16-hr photoperiod or in the dark

Wheat type	Humidification: Light/dark	Dark
Durum	1.35 a[z]	2.08 a
Canada prairie spring	1.48 a	2.00 a
Soft white	1.46 a	2.67 ab
Common	2.45 b	3.37 b

[z] Means followed by the same letter are not significantly different at 0.05 probability level on an experiment-wise basis according to Ryan's Q test.

light/dark displayed resistant to intermediate-type (mainly moderately resistant) reactions; reactions in the dark were moderately resistant to intermediate (Table 3). Lower leaves usually displayed more susceptible reaction types than did flag leaves.

Field experiments. *S. nodorum* was isolated consistently from lesioned leaf tissue sampled from the plots in both years; other foliar pathogens were rarely observed. In the cultivar Genesis a significant difference was found in kernels per head and thousand-kernel weight between the control plots sprayed with mancozeb and the nonsprayed, noninoculated plots. Because of this apparent independent yield increase resulting from fungicide application, the analyses do not include the data for Genesis.

In most inoculated cultivars, the number of kernels per head did not differ from the noninoculated controls; the difference was significant only in Medora in 1989, and in Wakooma, Laura, and Katepwa in 1990 (Table 4). The mean decrease in kernels per head was 3.8% in 1989 and 6.0% in 1990. Thousand-kernel weights in 1989 were reduced significantly in Kyle, Wakooma, Fielder, Biggar, and Pasqua, despite arrested disease development due to the lack of precipitation after 8 July. However, thousand-kernel weight reductions were not always related to more necrosis on flag and F-1 leaves. Both Kyle and Medora had little necrosis (Table 4), the result of relatively few lesions of moderately resistant and moderately susceptible type, respectively. However, Kyle had a significant reduction in thousand-kernel weight, whereas Medora did not. Conversely, no common wheat cultivar except Pasqua showed significant differences in thousand-kernel weight despite moderate levels of necrosis (Table 4) and susceptible lesion types.

In 1990, above-average rainfall in June (172.5 mm vs. a normal 88.4 mm) promoted severe disease development, and it was not possible to differentiate among cultivars for disease severity. Thousand-kernel weights of all wheats were significantly reduced, and necrosis on flag and F-1 leaves was very severe (Table 4).

In general, reductions in thousand-kernel weights were smaller in the durum wheats than in wheats of other types, excepting cultivars Columbus and Laura in 1989, and Biggar in 1990.

Table 4. Disease severity, kernels per head, and thousand-kernel weight in spring wheats inoculated with *Septoria nodorum*[y]

Wheat type / Cultivar	Disease severity (%)		Kernel number per head		Thousand-kernel weight (g)	
	F	F-1	C	I	C	I
1989						
Durum						
Kyle	1.1	16.1	43.8	41.8	41.31	38.50*[z]
Medora	0.6	9.4	47.7	44.2*	41.89	40.16
Wakooma	0.9	10.9	40.0	39.7	40.63	37.68*
Sceptre	4.0	43.0	43.1	40.9	38.30	35.89
Canada prairie spring						
Biggar	3.1	41.3	44.4	42.6	30.49	27.10**
Genesis	0.7	5.2	54.3	54.7	33.17	30.57*
Common						
Laura	5.1	38.4	40.2	39.1	30.14	28.65
Columbus	2.3	27.0	30.1	29.2	32.36	31.59
Roblin	4.0	33.4	29.5	30.1	34.90	32.56
Pasqua	7.9	41.9	31.0	28.4	31.59	28.63*
Katepwa	9.7	30.5	29.9	28.7	31.96	29.74
Soft white						
Fielder	1.6	20.27	39.5	37.8	33.79	28.51**
1990						
Durum						
Kyle	50.4	84.1	39.78	39.98	47.87	53.57*
Medora	86.3	89.5	42.85	41.73	48.63	44.52*
Wakooma	56.3	68.1	40.04	35.59*	48.53	44.72*
Sceptre	50.3	86.2	41.61	39.94	46.97	43.49*
Canada prairie spring						
Biggar	69.2	91.8	42.06	44.06	35.59	33.82*
Genesis	67.0	83.0	50.86	46.43*	43.22	35.52**
Common						
Laura	84.5	75.0	44.70	39.36*	35.99	31.70**
Columbus	65.9	70.1	31.75	28.85	39.20	35.47*
Roblin	87.9	89.2	28.55	25.89	40.61	34.68**
Pasqua	63.7	58.3	27.25	25.47	35.97	30.30**
Katepwa	68.6	78.9	32.32	28.22	37.76	33.78*
Soft white						
Fielder	70.0	61.6	37.02	36.67	38.63	31.91**

[y] Disease severity rated at watery-ripe to milky-ripe (1989) and milky-ripe to doughy-ripe (1990) growth stages on flag (F) and second-youngest (F-1) leaves. Values represent percent necrosis of inoculated leaves (I) less necrosis of control leaves (C).

[z] * = Significant difference at the 0.05 probability level; ** = significant difference at the 0.01 probability level on a comparison-wise basis. Test based on least-squares means from analysis of differences (control–inoculated) in kernel number per head and thousand-kernel weight.

DISCUSSION

Leaf spot development was more rapid and severe when postinoculation humidification took place in the dark than in light/dark. This has been observed by others (L. Lamari, *personal communication*) and may be the result of plants being more susceptible to infection in continuous darkness than in alternating light and dark periods. Seedlings were generally more susceptible than flag leaves of adult plants, on which the lower (older) leaves were always more damaged by inoculation with *S. nodorum* than were the upper leaves. At both stages of plant development, the durum wheats were most resistant, and the common wheats were generally most susceptible. In both glasshouse and field experiments, Jonsson (16) reported the mean disease severity of a group of wheat cultivars tested at the adult stage to be the lowest on the flag leaf and to increase on leaves F-1 and F-2. He also noted a clear relationship between seedling resistance and adult-plant resistance.

Field ratings in 1989 confirmed the results of controlled-environment tests showing that durum wheats were generally more resistant to Septoria nodorum blotch (Tables 2–4). There was no correlation between reduction in thousand-kernel weight and disease severity on flag and F-1 leaves (R values equal 0 and 0.064 respectively). The common wheats, the durum cultivar Sceptre, the Canada prairie spring cultivar Biggar, and the soft white cultivar Fielder all had high levels of necrosis, but these levels were not consistently related to reduction in thousand-kernel weights (Table 4). The yield of Sceptre was not significantly reduced, despite its having the highest level of necrosis among the durums. In contrast, thousand-kernel weights in Kyle and Wakooma were significantly reduced at considerably lower levels of necrosis. Although the common wheats had the highest levels of necrosis, and were likewise the most susceptible in controlled-environment tests, only Pasqua showed a significant decrease in thousand-kernel weight. Fielder, which generally rated as less susceptible than common wheats in controlled-environment experiments, showed highly significant reductions in thousand-kernel weight in field experiments. Host-tissue susceptibility to *S. nodorum* increases with age and is maximum at heading and flowering (3,11). In our study, inoculations were timed to include this sensitive

period, but there was necessarily some variation in the stage of growth between different cultivars at the time of simultaneous inoculation. This could have influenced some of the cultivar reactions observed.

In 1990, abundant precipitation enhanced disease development, resulting in severe necrosis on flag and F-1 leaves. Cultivars that were tolerant under moderate disease pressure in 1989 suffered significant reductions in thousand-kernel weight. Both Jonsson (16) and Scharen et al (27) reported considerable variation in damage caused by *S. nodorum* among years and regions. Scharen et al (27) concluded that specific methodologies to relate leaf blotch severity to yield reduction may be appropriate and useful only for the location in which they were developed. They concluded that for multilocation testing of wheat germ plasm, the measurement of yield and of the critical components of yield is a better method of identifying superior genotypes.

As for 1989, there was a lack of correlation between thousand-kernel weight reduction and disease severity on either flag or F-1 leaves (R values equal 0.252 and 0.478, respectively). Other studies have concluded that there is a strong positive correlation between levels of leaf and head infection, and yield loss (28,29). Scott (28), however, excluded the spring wheat cultivar Sterling from parts of his analysis because it sustained a low yield reduction with high disease-severity ratings. Cooke and Fozzard (7) investigated the relationship between foliar disease severity and yield loss and found that the developmental stage showing the clearest correlation with depressed thousand-kernel weight differed for the two cultivars tested. Based on glume blotch symptoms, however, both cultivars showed a strong disease severity/yield relationship at GS 75. Glume blotch development was noted in our study in both 1989 and 1990, but this was sporadic, and any discoloration/necrosis observed on heads was generally minimal. However, differential responses to glume blotch may have had some influence on the yield parameters measured. Scott and Benedikz (29) found that yield loss is positively correlated with Septoria nodorum blotch, but they concluded it is better to measure disease severity than yield because of the high random variation in yield often found in rows or small plots. While not always reliable indicators of crop performance, single-row experiments can be useful for comparing cultivars.

Karjalainen (17) found a high correlation between seedling and field resistance, and Rufty et al (21) reported a high correlation in the percentage of leaf necrosis between seedlings and mature plants. However, both studies reported anomalous results indicating the presence of resistance genes which may be effective only in seedling or in later growth stages. Mullaney et al (19) reported that the seedling resistance of the durum wheat cultivar Giorgio 396 is lost in adult plants. Of the cultivars screened in this study, only one-third showed a positive relationship between foliar disease severity and yield loss.

There were no consistent significant differences in the number of kernels per head in the cultivars tested. This is in agreement with Scharen et al (27) and Bronnimann (4), who found that the number of kernels per head is usually affected to a lesser degree than thousand-kernel weight, because floret numbers are mainly established before disease stress occurs. Other workers have reported a relationship between kernel number and foliar symptoms (31). The reductions observed in our study were generally lower than those reported elsewhere (18,26,33), although Scott (28) observed a mean decrease of 6.5% for one year of data, which is similar to that found here for 1990. A reduction in the number of kernels by 34.8% following five inoculations between GS 13 and GS 59 was found on single-stemmed spring wheat plants, but on tillers the kernels per head increased by 10% (33). The likely mix of tiller and main-stem heads collected randomly at harvest in this study may explain the lack of consistency in the data for this variable.

The phenomenon reported by Bronnimann (4) and others (5,25,27,30), by which some cultivars sustain little or no yield loss despite high levels of necrosis, was also found in our study in cultivars Sceptre, Columbus, Katepwa, Laura, and Roblin. These cultivars may be tolerant as defined by Schafer (24).

In 1989, when disease pressure was moderate, the decrease in thousand-kernel weights in Kyle and Wakooma was not consistent with the relatively light disease severity on flag and F-1 leaves. This decrease appeared to be the result of something other than the loss of photosynthetic tissue, and was possibly a reaction to a toxin produced by *S. nodorum* (2). Additionally, Canadian spring wheat cultivars appear to have low levels of resistance to *S. nodorum,* as evidenced in 1990 when conditions favored disease. The relationship between infection by *S. nodorum* and damage, as measured by reduction in thousand-kernel weight, is complex. Therefore, even those cultivars which exhibit partial resistance may not retain high thousand-kernel weight. If this is generally true, screening for *S. nodorum* in the field and measuring reduction in kernel weight may provide more useful information to the breeder than disease-severity ratings alone.

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