

# Effect of Temperature and Growth Stage of Wheat on Development of Leaf and Glume Blotch Caused by *Septoria tritici* and *S. nodorum*

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## ABSTRACT

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Severity of leaf blotch caused by *Septoria tritici* and leaf and glume blotch caused by *S. nodorum* was assessed on two soft red winter wheat cultivars (AGRA GR855 and Caldwell) at three temperatures (19, 24, and 29 C) and four growth stages (GS 6 or first node visible, GS 10 or boot, GS 10.5 or preflowering, and GS 11 or postflowering). The percentage of leaf and glume area with symptoms, density of pycnidia in lesions, and number of conidia per pycnidium were determined. Analysis of variance (ANOVA) for area under the disease progress curve (AUDPC) indicated that *S. tritici* caused similar levels of disease at 19 and 24 C but very low levels of disease at 29 C. Growth stage had no effect on disease severity caused by *S. tritici* ( $P = 0.05$ ). *S. nodorum* caused relatively high levels of disease at each temperature tested, but no significant differences for AUDPC were detected for temperature ( $P = 0.05$ ). AUDPC values for *Septoria nodorum* leaf blotch were significantly higher ( $P = 0.05$ ) at each succeeding growth stage tested for AGRA GR855, and AUDPC values for Caldwell were significantly greater at GS 11 than GS 6 or 10. The density of pycnidia and numbers of conidia per pycnidium on leaf lesions were higher for *S. tritici* than for *S. nodorum*. *S. tritici* caused only low levels of glume blotch at 19 and 24 C and none at 29 C, whereas *S. nodorum* caused relatively high levels of glume blotch at each temperature tested. Results indicated the level of leaf blotch incited by *S. tritici* was more influenced by temperature than growth stage at time of inoculation, and leaf blotch incited by *S. nodorum* was affected more by plant growth stage at time of inoculation than temperature. This suggests an explanation for the seasonal occurrence of these two pathogens. The cooler temperatures of early spring favor development of leaf blotch caused by *S. tritici*. The greater prevalence of *S. nodorum* later in the season may be a consequence of increasing susceptibility of the wheat plant to this pathogen as it matures.

The two major pathogens comprising the *Septoria* disease complex on wheat (*Triticum aestivum* L.) are *Septoria tritici* Roberge. in Desmaz. (teleomorph *Mycosphaerella graminicola* (Fuckel) J. Schröt. in Cohn), causing *Septoria* leaf blotch or speckled leaf blotch, and *S. nodorum* (Berk.) Berk. in Berk. & Broome (synonym: *Stagonospora nodorum* (Berk.) Castellani & E. G. Germano) (teleomorph *Leptosphaeria nodorum* E. Mueller), causing *Septoria* leaf and glume blotch. Both pathogens are economically important worldwide, although *S. tritici* is more prevalent in cooler climates and more active during cooler portions of the growing season than *S. nodorum* (26).

Natural infection by *S. tritici* occurred on winter wheat in each of 3 yr of a Minnesota study, but no infections were observed on spring wheat planted in late April. *S. nodorum*, however, occurred on spring and winter wheat all 3 yr of the experiment (25). In a 2-yr study conducted on winter wheat in commer-

cial fields in Michigan, the number of fields with new lesions caused by *S. tritici* decreased as the season progressed, whereas new lesions caused by *S. nodorum* increased in 1 yr and remained relatively constant the next year (8). In the same Michigan study, both pathogens were present on the lower leaves of plants in early May, but by late May, lesions caused by *S. nodorum* were on leaves higher on the plant than those caused by *S. tritici*. By July, *S. nodorum* was isolated from lesions on the heads of mature plants in all fields surveyed, but *S. tritici* was not observed. Head infection by *S. tritici* has rarely been reported under natural conditions (13), whereas glume blotch caused by *S. nodorum* has been widely reported (3,6,10,15). Furthermore, disease severity caused by *S. nodorum* has been reported to increase with plant age (11).

Many reasons have been suggested to explain the occurrence of these two *Septoria* species on different plant parts and at different times during the wheat growing season. It has been suggested that the two species require different moisture periods (9,10) or temperatures (4,9) for infection. However, recent studies have identified virtually the same optimum temperature range for disease development by both species: 18–25 C

for *S. tritici* (9) and 20–24 C for *S. nodorum* (4). The objective of this study was to determine the effect of growth stage and temperature on the relative pathogenicity of *S. tritici* and *S. nodorum* on wheat leaves (leaf blotch) and heads (glume blotch).

## MATERIALS AND METHODS

### Isolation and inoculum production.

An isolate of *S. tritici* was cultured from infected wheat leaves obtained from G. Shaner (Purdue University, West Lafayette, IN). Conidia were released from pycnidia by immersing a leaf in approximately 5 ml of sterile distilled water, and the resulting conidial suspension was streaked onto the surface of yeast-malt agar plates (1 g of yeast extract, 10 g of malt extract, and 15 g of agar in 1 L of distilled water) (9). Cultures were grown at 22 C for 10 hr under UV and white fluorescent lighting ( $22 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). After 3–5 days, several creamy, pink-colored colonies from each plate were transferred to flasks with 2% malt broth (20 g of malt extract in 1 L of distilled water). The flasks were shaken on a rotary shaker (Fermentation Design Inc., Allentown, PA) at 150 rpm at 20 C in continuous light from 13 fluorescent light bulbs ( $47 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). Approximately 1 ml of broth containing conidia was pipetted onto the surface of yeast malt-agar plates and grown for 3–5 days under the conditions described earlier.

Six isolates of *S. nodorum*, obtained from diseased leaves collected from different wheat fields in Ohio, were cultured on V8 juice agar (V8A) plates, as described by Eyal et al (5). Cultures were also grown in 2% V8 juice broth (20 ml of Campbell's V8 juice and 0.04 g of  $\text{CaCO}_3$  in 980 ml of distilled water) under the same conditions as described for *S. tritici* in liquid culture. Aggregates of mycelium with pycnidia that formed were removed and plated onto V8A plates and allowed to dry. Resulting cultures were maintained at 21–23 C until pycnidia developed on the agar surface.

Immediately before plant inoculation, conidial suspensions of each species were prepared by flooding petri plate cultures with distilled water and scraping the agar surface. Suspensions were adjusted to approximately  $1 \times 10^7$  conidia per milliliter with a hemacytometer.

**Hosts.** Two soft red winter wheat

cultivars, AGRA GR855 (PI 508286) and Caldwell (CI 17897), were used throughout this study. AGRA GR855 and Caldwell were chosen for their known susceptibility to *S. tritici* and *S. nodorum*, respectively (17,20). Seeds of each cultivar were planted in flats, grown to the two-leaf stage in the greenhouse, and then vernalized for 8–12 wk at 4 C under fluorescent light ( $3 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) for 12 hr per day. Seedlings were then transplanted to 11-cm clay pots, one plant per pot, in a potting mix of peat moss/composted steam disinfested Wooster silt loam soil (1:5, v/v) and grown to the growth stage required for testing in the greenhouse at a temperature range of 15–27 C. Karathane (dinocap, 0.55 kg a.i./ha) was applied weekly to control powdery mildew. Malathion (1.4 kg a.i./ha) or methomyl (0.5 kg a.i./ha) were used, as necessary, to control aphids. Plants were fertilized two to three times as needed with a dilute nutrient solution (0.5 g/L each of N, P, and K, approximately 25 ml per pot).

Plants were inoculated at four different growth stages (GS) described according to the Feekes' scale (16): GS 6 (beginning stem elongation at first node visible), GS 10 (boot stage, when the wheat head had formed a swelling in the flag leaf sheath), GS 10.5 (preflowering, when the entire head had emerged from the flag leaf sheath), and GS 11 (post-flowering, when kernels were one-half to three-fourths formed and anthers were protruding from all florets of the head).

The leaf chosen for disease assessment (third or fourth leaf for GS 6; flag leaf for other growth stages) was marked with a nonphytotoxic permanent marker before inoculation. The spore suspension was atomized (513 KPa) with a Sure Shot Sprayer (Milwaukee Sprayer, Milwaukee, WI) onto leaves and heads until the surface was covered with droplets but before runoff. Immediately after inoculation, plants were placed in controlled environment chambers at 19, 24, or 29 C. Plastic bags were placed on individual plants for 96 hr to maintain high humidity. Relative humidity was not regulated and a 12-hr photoperiod was provided by 10 40W incandescent and 20 fluorescent light bulbs, providing an average light intensity of  $240 \pm 17 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for the three growth chambers.

**Disease assessments.** Disease assessments were made at 11, 16, and 21 days after inoculation. Disease on leaves was evaluated as percent leaf area occupied by pycnidia-bearing lesions for *S. tritici* or percent leaf area covered with necrotic blotches for *S. nodorum*. The difference in disease assessments was attributable to the lack of pycnidial development by *S. nodorum* on leaves in the growth chamber and the similarity of lesions caused by *S. tritici* to physical damage. The third or fourth leaf below the flag

leaf was rated on plants inoculated at the growth stage where the first node was visible (GS 6), and the flag leaf was rated for plants inoculated at the other three growth stages (GS 10, 10.5, and 11). Only the adaxial side of the leaf was assessed. Disease on glumes was evaluated as percent head area covered with black streaks for *S. tritici* or brown to black blotches for *S. nodorum*. Glumes were rated on plants inoculated at the preflowering (GS 10.5) and post-flowering (GS 11) growth stages only. In cases where entire flag leaves or heads treated with *S. nodorum* at GS 11 died before the last disease assessment, the previous disease assessment was used to determine head or leaf area covered with blotches.

**Pycnidial density and conidia per pycnidium.** After the 21-day disease assessment, plants were returned to the greenhouse. The leaf that was used for the disease assessment and two glumes with symptoms were collected and stored dry in paper bags. In cases where glumes with symptoms caused by *S. tritici* were not available, two glumes were chosen at random. Treatments of *S. tritici* at 29 C were not included because disease did not develop at this temperature. After the leaves and glumes had dried, 1-cm segments were cut from lesions covered with pycnidia of *S. tritici* or blotches caused by *S. nodorum*. The leaf segments and glumes were surface-sterilized in 70% alcohol and 1.05% sodium hypochlorite (1:1, v/v) for 2 min and rinsed in distilled water for 2 min. Five replicate tissue segments were placed on a marked glass slide in a petri dish lined with wet filter paper. Leaf segments infected with *S. tritici* and *S. nodorum* were incubated in the moisture chamber for 3–4 days and 7–10 days, respectively. All glumes were kept in the moisture chamber for 2 wk.

The number of pycnidia per square millimeter of leaf lesion were counted with a dissecting microscope ( $\times 10$ ). Ten pycnidia per leaf segment or glume were excised from tissue with a fine-pointed scalpel and put in a 5-cm-diameter petri dish with 0.5 ml of distilled water. The leaf or glume tissue was macerated with a glass coverslip, and the number of conidia per milliliter in the resulting spore suspension was determined with a hemacytometer.

**Data analysis.** A split-plot experimental design was used to determine the effect of temperature and growth stage on disease development caused by the two fungi and an uninoculated control. Whole plots were the three temperatures and subplots were the four growth stages and the two cultivars. All treatments were replicated five times, with one plant per replication. All tests were conducted twice. Statistical analyses were conducted with the SAS computer program. The general linear model

analysis of variance test and Tukey's separation of means test were used to separate treatment means. Values for area under the disease progress curve (AUDPC) were calculated according to Shaner et al (22) and used for comparisons, unless stated otherwise. A square-root transformation was performed on disease assessments for leaves and glumes because of the high variability in the data and the relationship between the variance and the mean. Disease assessments of *S. tritici* and *S. nodorum* were not compared statistically because of the different rating criteria used for each.

Data for pycnidia per square millimeter of leaf or glume lesion and conidia per pycnidium were analyzed to determine the effects of cultivars, plant growth stages, and temperatures on fungal sporulation. The statistical tests and experimental design were identical to those for the leaf and glume disease assessment studies. A log transformation was performed on all pycnidia and spore enumeration data. The analysis for number of pycnidia per square millimeter of leaf lesion and number of conidia per pycnidium was conducted separately for each fungal species.

## RESULTS

***S. tritici* on leaves.** *S. tritici* produced elongated tan-colored necrotic lesions on wheat leaves. Lesions were typically bordered by veins and contained black pycnidia. The necrotic areas with no pycnidia were indistinguishable from possible mechanical damage, thus percent leaf area occupied by pycnidia-bearing lesions was used to assess *S. tritici* on leaves. Some necrosis or flecks in the leaf were often visible at the 11-day assessment, and pycnidia were generally first visible at the 16-day assessment. Percentage leaf area affected increased over time, and by the last assessment at 21 days postinoculation, Caldwell and AGRA GR855 had 32 and 45% leaf area affected, respectively, at 19 C when inoculated at GS 10.5 (Fig. 1). Percent leaf area affected was never greater than 1% on either cultivar at 29 C when inoculated at any growth stage (Fig. 1).

Significant differences were detected between cultivars for disease assessment ( $P = 0.05$ ). Transformed AUDPC values were 8.4 for Caldwell and 4.4 for AGRA GR855. Interaction effects of temperature by cultivar and growth stage by cultivar were significant for AUDPC ( $P = 0.05$ ). The two-way interaction of temperature by cultivar was attributable to significant lower AUDPC values for Caldwell at 19 and 24 C but not at 29 C (Fig. 2). Also, the mean AUDPC value for Caldwell was larger at 19 C than 24 C, and AUDPC values were not significantly different ( $P = 0.05$ ) at 19 and 24 C for AGRA GR855. The two-

way interaction of growth stage and cultivar occurred because of a significant difference ( $P = 0.05$ ) between the two cultivars at GS 10 (Fig. 3). Plants of AGRA GR855 inoculated at GS 10 had significantly higher levels of disease than plants of this cultivar inoculated at other growth stages. No other significant differences in the AUDPC values calculated for the different growth stages were detected.

Pycnidia were often quite dense within leaf lesions. Conidia were expelled through the ostiole in the form of pink cirri. A significant difference ( $P = 0.05$ ) between cultivars was detected for the number of pycnidia per square millimeter of leaf lesion and number of conidia per pycnidium. Caldwell had fewer pycnidia per square millimeter on leaf tissue than AGRA GR855 (Table 1). Neither the growth stage at inoculation nor postinoculation temperature had an influence on the density of pycnidia in lesions ( $P = 0.05$ ). *S. tritici* produced significantly more conidia per pycnidium on leaves of AGRA GR855 than on Caldwell (Table 1).

*S. nodorum* on leaves. *S. nodorum* produced irregular light brown necrotic lesions with a chocolate-brown border or chocolate-brown spots within the lesion on leaves. Pycnidia were not produced on the leaves in the controlled environment chambers or greenhouse. Because symptoms caused by *S. nodorum* were distinct and pycnidia were not distinguishable, disease was assessed as percent leaf area covered with blotches. Symptoms were usually evident at the 11-day assessment time and percent leaf area affected increased steadily from the first to the last disease assessment (Fig. 1).

Analysis of variance for disease assessment data indicated a significant main effect of cultivar and a significant interaction effect between growth stage and cultivar ( $P = 0.05$ ). Caldwell had a significantly higher ( $P = 0.05$ ) level of leaf blotch than AGRA GR855. Transformed AUDPC values for *S. nodorum* were 21.2 for Caldwell and 18.0 for AGRA GR855. There was a significant difference in AUDPC values between Caldwell and AGRA GR855 at GS 10 but not at the other growth stages tested (Fig. 4). Significant differences in AUDPC values were also detected among each growth stage for AGRA GR855 and among only three of the four growth stages tested for Caldwell. A greater percentage of leaf area became infected when plants were inoculated at the later growth stages than earlier growth stages. No significant differences were detected for temperature or the temperatures by growth stage interaction ( $P = 0.05$ ).

*S. nodorum* produced amber-colored pycnidia within leaf lesions, and conidia erupted from the ostiole in an amber-

colored ooze. No significant differences were detected for the number of pycnidia per square millimeter of leaf produced by *S. nodorum* for cultivar, temperature, or growth stage (Table 1). Significant differences were detected between cultivars for number of conidia per pycnidium on leaves. Pycnidia on the leaves of AGRA GR855 contained more conidia than those on the leaves of Caldwell (Table 1).

*S. tritici* on glumes. *S. tritici* caused black streaks along the veins on the tips of the glumes. This species caused only low disease severity on glumes of both cultivars (Fig. 5). There were no significant differences for cultivar, tempera-

ture, or growth stage on pathogenicity of *S. tritici* on glumes ( $P = 0.05$ ). However, the interaction of growth stage by cultivar and the interaction of growth stage by temperature and cultivar was significant ( $P = 0.05$ ). The highest severity of glume blotch obtained in these tests with *S. tritici* was 17% glume area affected on AGRA GR855 by the 21-day assessment inoculated at GS 10.5 and incubated at 19 C. On plants maintained at 29 C, percent glume area affected was 1% or less on both cultivars.

Black pycnidia of *S. tritici* formed in the darkened streaks along the veins of the glumes. The mean number of pycnidia per glume was 20.3 at GS 10.5

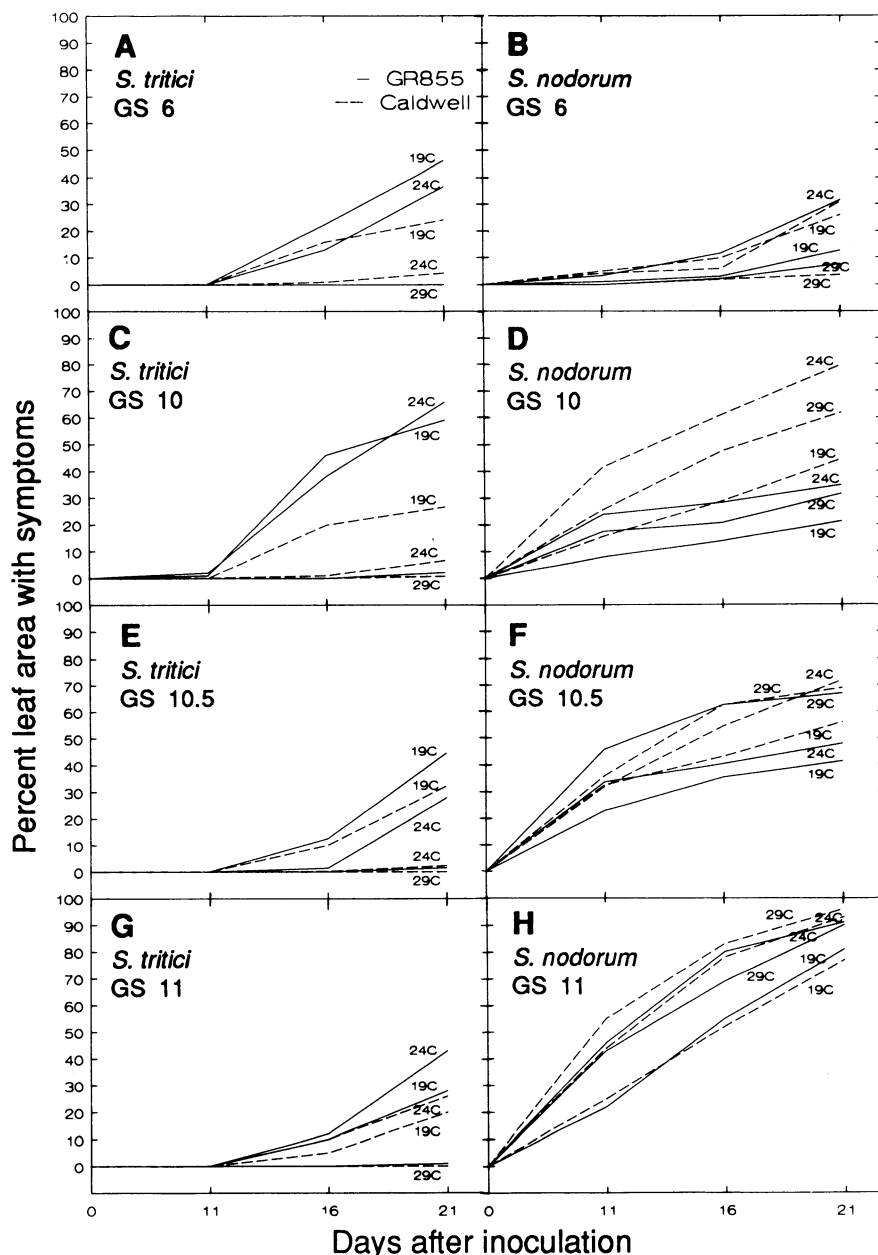


Fig. 1. Disease progress curves for percentage of leaf area occupied by pycnidia-bearing lesions for *Septoria tritici* or blotches for *S. nodorum* at 19, 24, and 29 C. Leaves were inoculated at growth stages (GS) 6, 10, 10.5, and 11. Disease severity assessed at 11, 16, and 21 days after inoculation and data points represent means of two experiments on wheat cultivars AGRA GR855 and Caldwell.

and 1.0 at GS 11 (nontransformed data). The data used to calculate the analysis of variance for the number of pycnidia per glume and number of conidia per pycnidium on glumes were not complete because of the lack of pycnidial development on glumes within some treatments. The mean number of conidia per pycnidium on glumes was 151 for glumes inoculated at GS 10.5 and 475

for glumes inoculated at GS 11 (nontransformed data).

***S. nodorum* on glumes.** *S. nodorum* caused brown-black blotches starting at the tips and spreading to the base of the glumes. *S. nodorum* caused high levels of glume blotch at both growth stages and each of the three temperatures tested (Fig. 5). The highest mean percentage of glume area affected by 21 days

postinoculation was 89.5% for plants inoculated at both GS 10.5 and 11, and the lowest was 52% for plants inoculated at GS 10.5. No significant differences were detected for percent glume area affected by *S. nodorum* for cultivar, temperature, or growth stage ( $P = 0.05$ ). However, the interaction of temperature by cultivar was significant ( $P = 0.05$ ). There was a significant difference in AUDPC values between 19 and 29 C on AGRA GR855 (13.6 and 22.4, respectively).

Pycnidia on glumes were generally located on the tips of the glumes within blotches. There was a significant cultivar and growth stage by cultivar effect on the number of pycnidia per glume ( $P = 0.05$ ). The growth stage by cultivar interaction occurred because numbers of pycnidia on glumes were similar on both cultivars inoculated at GS 11 (3.5 pycnidia per glume), whereas at GS 10.5, there were significantly more on AGRA GR855 (13.8 pycnidia per glume) than on Caldwell (2.95 pycnidia per glume) (nontransformed data). The mean number of conidia per pycnidium of *S. nodorum* on glumes was 1,264 and 5,307 (nontransformed data) for plants inoculated at GS 10.5 and 11, respectively, however, this difference was not significant.

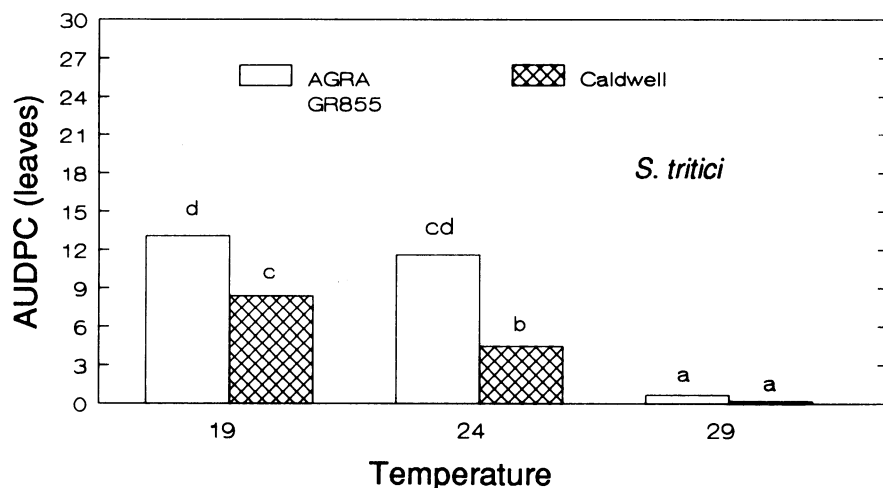


Fig. 2. Effect of temperature and cultivar on the square root of area under the disease progress curve (AUDPC) calculated from 11-, 16-, and 21-day assessments for percentage of leaf area affected by *Septoria tritici*. Means with the same letter were not significantly different according to Tukey's studentized range test ( $P = 0.05$ ).

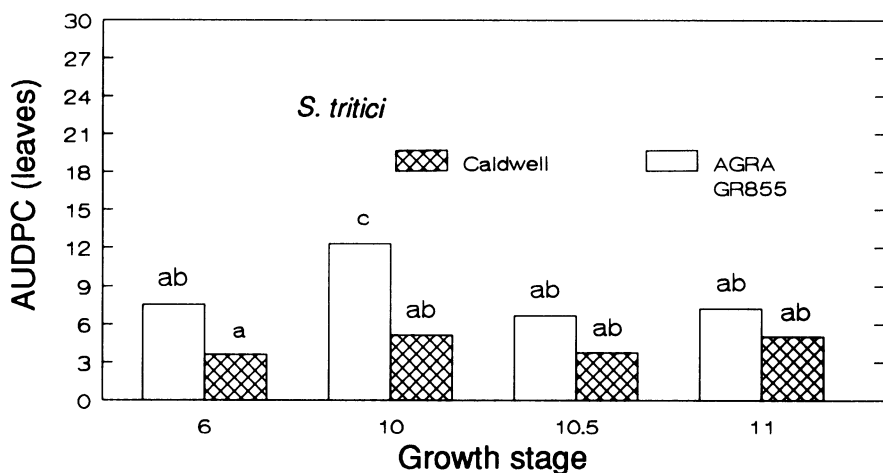


Fig. 3. Effect of plant growth stage and cultivar on the square root of area under the disease progress curve (AUDPC) calculated from 11-, 16-, and 21-day assessments for percentage of leaf area affected by *Septoria tritici*. Means with the same letter were not significantly different according to Tukey's studentized range test ( $P = 0.05$ ).

## DISCUSSION

Several factors have been shown to influence disease development by *S. tritici* and *S. nodorum*, including high humidity or precipitation at time of infection (9,10,24), temperature (4,9,10), plant growth stage (11,14), and cultivar (2,9,17). In this study, the effects of temperature, plant growth stage, and cultivar on disease development were investigated during a constant high-humidity period (96 hr postinoculation). *S. tritici* and *S. nodorum* responded differently to growth stage, temperature, cultivar, and inoculated plant part. Growth stage at time of inoculation had essentially no effect on disease severity caused by *S. tritici*. In a study to evaluate resistance in 10 wheat cultivars, Shaner and Finney also reported little effect of growth stage at time of inoculation on disease severity (23).

Growth stage at time of inoculation significantly influenced disease development on leaves caused by *S. nodorum*. Leaf blotch caused by this pathogen increased with increase of plant age at time of inoculation. This trend occurred at all temperatures tested and may partially explain why *S. nodorum* is more active in the field during the latter part of the wheat growing season during maturation of the wheat plant (8,25,26). Mullaney et al (18) recorded an increase of disease severity of *S. nodorum* on the spring wheat cultivar Giorgio 396 inoculated at GS 10 as compared with GS 1 and proposed that the late boot

Table 1. Effect of wheat cultivar on mean number of pycnidia per square millimeter of lesion and number of conidia per pycnidium on leaves produced by *Septoria tritici* and *S. nodorum*

Species and cultivar	Pycnidia/mm <sup>2</sup> leaf lesion	Conidia/pycnidium
<i>S. tritici</i>		
AGRA GR855	5.66 a <sup>z</sup>	3,011 a
Caldwell	4.47 b	935 b
<i>S. nodorum</i>		
AGRA GR855	1.83 a	1,214 a
Caldwell	1.65 a	425 b

<sup>z</sup>Means followed by the same letter within columns for each species are not significantly different according to Tukey's separation of means test ( $P = 0.05$ ).

stage may be the point in the development of cultivar Giorgio 396 at which increased susceptibility to *S. nodorum* commences. Our results indicate that disease development is greater on plants inoculated at the later growth stages than earlier growth stages, and the increase in susceptibility may be influenced by plant maturity.

In contrast with results obtained with *S. nodorum*, only temperature had an influence on disease development by *S. tritici*. Percent leaf area affected was consistently negligible at the warmest temperature tested (29 C). Hess and Shaner (9) reported that disease severity was significantly greater at 25 C than at 18 C on plants inoculated with *S. tritici*

at the postflowering growth stage. In our study, AUDPC values for plants inoculated at 24 and 19 C were not significant. The lack of disease development at the postinoculation temperature of 29 C was consistent with other studies (1,5).

Temperature, on the other hand, did not significantly influence disease development by *S. nodorum*. This pathogen caused disease at all three temperatures tested, and there were no significant differences in AUDPC values among temperatures tested. Results at the 11-day disease assessment on plants inoculated at GS 10 were consistent with those of da Luz and Bergstrom (4), who reported 18–24 C as the optimum

temperature for disease development at a similar disease assessment time and inoculation growth stage. The minimum temperature for parasitism by both *S. tritici* and *S. nodorum* has been reported as 7 C (10,21). Our results indicate that *S. nodorum* appears to be able to infect at a higher temperature than *S. tritici*, and, therefore, higher temperature may limit the parasitic activity of *S. tritici* to a greater extent than *S. nodorum* in nature.

There were significant differences in the level of disease development on the two cultivars tested for each *Septoria* species. Caldwell was more resistant than AGRA GR855 to *S. tritici* as determined by percent leaf area covered with pycnidia, density of pycnidia in leaf lesions, and number of conidia per pycnidium on leaves. Because of the greater capacity of *S. tritici* to produce both pycnidia and conidia on AGRA GR855 than on Caldwell, disease could be expected to increase more rapidly on this cultivar in the field. Caldwell has been reported as susceptible to *S. nodorum* (17,27) and resistant to *S. tritici* (20).

*S. nodorum* was consistently pathogenic on glumes and caused glume blotch on plants inoculated at both postheading growth stages and at all three postinoculation temperatures tested. *S. nodorum* also produced pycnidia on glumes, and the number of conidia per pycnidium on glumes was only slightly less than on leaves. The level of glume blotch caused by *S. tritici* in this experiment was similar to that found by Jones and Odeumni (14). The symptoms (black streaks along the veins of the glumes) matched those described by Jones and Cooke (12). Results from these and other studies with glumes (12,14), and the fact that natural infection by *S. tritici* on glumes has been reported so rarely (12–14), indicate that *S. tritici* may not be capable of causing appreciable levels of disease on wheat glumes at any temperature or post-heading growth stage. However, after incubation in a moist chamber, pycnidia did form on glumes in our study, which supports the findings of Jones and Cooke (12) and confirms that *S. tritici* is able to infect the glumes of wheat under optimal conditions.

Lower levels of glume blotch developed on heads of plants inoculated at postflowering than at preflowering. This is consistent with the results of Williams and Jones (28), who reported that glume blotch induced by *S. nodorum* was greatest on plants inoculated at one-half to three-fourths head emergence and declined steadily on plants inoculated at later growth stages. One possible reason for this phenomenon is that the glume tissue inoculated at the later growth stages actually senesced before symptoms had a chance to develop. Kernels

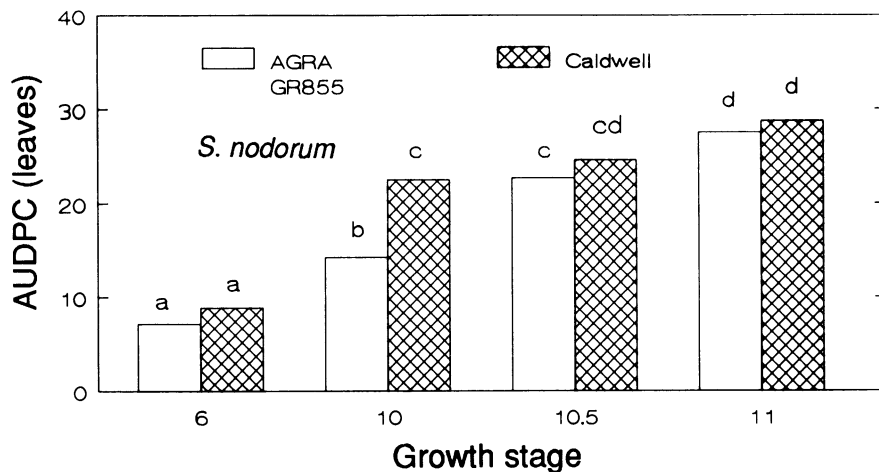


Fig. 4. Effect of plant growth stage and cultivar on the square root of area under the disease progress curve from 11-, 16-, and 21-day assessments of percentage of leaf area affected by *Septoria nodorum*. Means with the same letter were not significantly different according to Tukey's studentized range test ( $P = 0.05$ ).

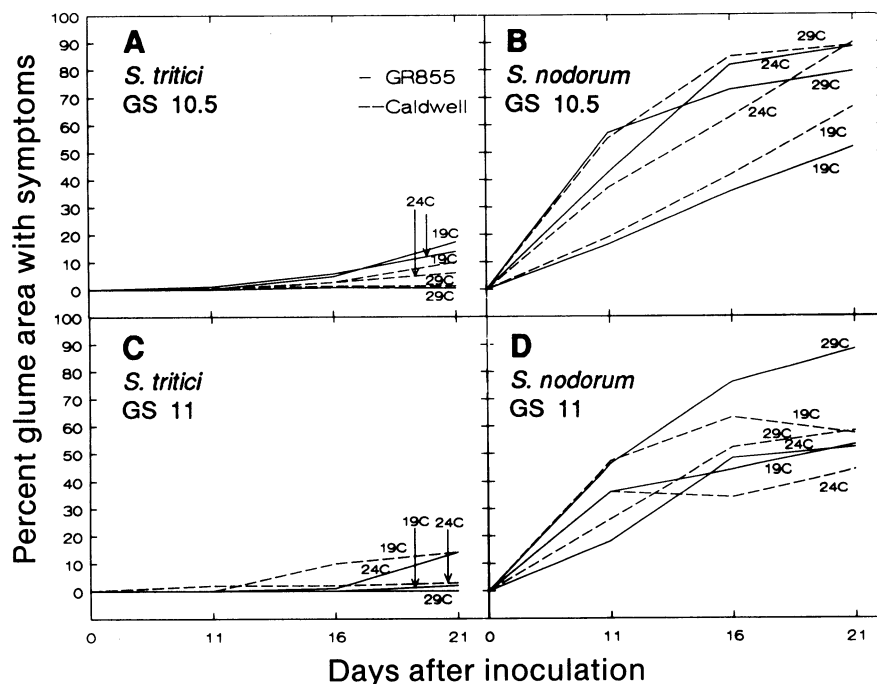


Fig. 5. Disease progress curves for percentage of glume area covered with blotches caused by *Septoria tritici* or *S. nodorum* at 19, 24, and 29 C. Leaves were inoculated at growth stages (GS) 10.5 and 11. Disease assessed at 11, 16, and 21 days after inoculation and data points represent means of two experiments on wheat cultivars AGRA GR855 and Caldwell.

were one-half to three-fourths formed at GS 11 and plants were beginning to senesce. Perhaps symptom development would have been greater had the glume tissue not been senescing after inoculation.

Host cultivar was the only treatment that had a significant effect on density of pycnidia of *S. tritici*. The number of pycnidia per square millimeter of leaf lesion for *S. tritici* was similar to numbers previously reported, but the number of conidia per pycnidium was somewhat higher than those reported by Hess and Shaner (9). The difference in recovery could be attributable to different methods used for harvesting conidia from the leaf. Hess and Shaner used the method of Gough (7), which involved dipping the leaf segments in water rather than crushing them. According to our preliminary trials, crushing pycnidia in water resulted in approximately 20% more conidia harvested.

The number of pycnidia per square millimeter of leaf lesion produced by *S. nodorum* was not influenced by any of the treatments tested in this experiment, so it appears that temperature and growth stage have little effect on the density of pycnidia within blotches on the cultivars tested.

*S. tritici* produced substantially greater numbers of pycnidia per square millimeter of leaf lesion and more conidia per pycnidium than *S. nodorum*. This occurred practically without exception in all treatments. The apparent ability of *S. tritici* to produce more conidia per square millimeter of leaf tissue relative to *S. nodorum* indicates that under favorable environments, *S. tritici* may have greater parasitic fitness (19) than *S. nodorum* if conidia of the two species had similar infection efficiencies (24,29). *S. nodorum* appeared to have other fitness attributes, including the ability to cause disease over a wider temperature range, the tendency to cause greater amounts of disease as the plants mature, and the ability to cause disease on glumes as well as leaves. The influence of temperature on pathogenicity of *S. tritici* and the ability of *S. nodorum* to cause

disease on older plants at higher temperatures may explain why leaf blotch caused by *S. tritici* appears more common in early spring and leaf blotch caused by *S. nodorum* in late spring after flowering of the wheat crop.

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