Effect of Moisture and Temperature on Development of Septoria tritici Blotch in Wheat

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ABSTRACT

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Septoria tritici blotch, caused by *Mycosphaerella graminicola*, is a major disease of wheat in many parts of the world. The effects of temperature (11, 18, and 25 C) and wetness duration (24, 48, 72, and 96 hr) on Septoria tritici blotch development were examined by inoculating four wheat cultivars that differ in susceptibility to *M. graminicola*. There was a positive correlation between increase in postinoculation moisture and postinfection temperature and disease severity. Percent necrosis on the susceptible cultivar Morocco and moderately susceptible cultivars Beau and Arthur was influenced more by change in temperature and moisture treatments than was percent necrosis on the resistant cultivar Auburn. For cultivars Morocco and Arthur, percent necrosis and pycnidial density increased with increase in temperature. For cultivars Beau and Auburn, temperature and percent necrosis were positively correlated but pycnidial densities increased only for the high temperature treatment. Necrotic leaf tissue, pycnidial volume and density, and spore production in the resistant cultivar Auburn were reduced in comparison with the susceptible cultivars.

Symptom expression of Septoria tritici blotch of wheat reflects the interaction between host and pathogen (*Mycosphaerella graminicola* (Fuckel) Schroeter) and is influenced by differential host susceptibility, fungal pathogenicity, and environment (29). Hilu and Bever (9) reported that resistance is in part a consequence of reduced postpenetration establishment of the fungus and in part a reduced rate of fungal growth following establishment. This latter component is similar to slow-rusting resistance, which has been reported in several cereal crops, including wheat (e.g., 15).

Weather influences Septoria tritici blotch development (26,27,29,31), although its effects are not thoroughly understood. Fellows (6) found that high temperature (22 C) favored infection, whereas Joshi et al (13) reported inhibition of disease with increasing temperature. Other workers have associated low temperatures with reduction in disease severity (10,22,27). The latent period is probably temperature dependent (24). Weber (31) found that latent periods in the field vary from 11 to 15 days, and are shortest during the warm days of May and June. Fellows (6) recorded that at 22 C pycnidia first appeared 21–30 days postinoculation. However, in the winter the latent period may be as long as 60 days (11). Pachinburavan (18) found that pycnidia are produced over a temperature range of 10–30 C both in culture and on diseased plants.

Moisture is important at all stages of the infection cycle (9,14,27,29). In the laboratory, conidia germinate on moist leaves within 12 hr and penetration occurs after 24 hr (9). Successful inoculation in the laboratory requires extended incubation periods in a moist chamber (26,32). Plants given a 96-hr moist treatment after inoculation with *M. graminicola* develop a more susceptible infection type than plants receiving shorter moist treatments (29). The number of spores infecting a leaf may be greater the longer the leaf surface remains moist, but postinfection moist periods may also enhance fungal development (22,25,29), thereby reducing incubation and latent periods.

Pycnidia form within a relative humidity range of 35–100%, but significant reduction of pycnidial density results when plants are held at relative humidities below 85% (18). High relative humidity also favors lesion growth (17) and release of spores from pycnidia (2). Pycnidial number usually correlates positively with the amount of leaf necrosis, with more spores produced in a susceptible host than in a resistant one (4,5,8,28).

Interactions of environmental factors are known to influence disease development (23). Although host susceptibility, wet weather, and cool temperatures are recognized to influence Septoria tritici blotch development (2,10,27,29,31), studies of their interactions are absent from the literature.

The purpose of this study was to investigate the effects and interactions of three factors: postinoculation moist period, postinfection temperature, and host cultivar on Septoria tritici blotch development in a controlled environment.

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MATERIALS AND METHODS

All plants employed in this experiment were planted in 54-× 36-× 8-cm flats filled with peat and soil (1:1, v/v). Immediately after seed was sown the flats were watered and placed in the greenhouse until the first leaf appeared, at which time they were moved to a 3 C cold chamber for the 8–10 wk vernalization period. Plants were then transplanted individually into 500-ml plastic pots containing soil mix. Plants were grown in the greenhouse where natural daylight was supplemented with incandescent and fluorescent light, resulting in a total photon flux density on the greenhouse bench of approximately 167 $\mu E \cdot m^{-2} \cdot sec^{-1}$ for 16 hr each day from transplanting to maturity.

Four cultivars of wheat (*Triticum aestivum* L. em. Thell.) with different levels of resistance to *M. graminicola* were employed. These were the susceptible spring wheat cultivar Morocco and three cultivars of soft red winter wheat developed at Purdue University (19,20,21). Cultivars Beau (CI 17420) and Arthur (CI 14425) are moderately susceptible to *M. graminicola* and cultivar Auburn (CI 17898) is resistant.

Conidia of *M. graminicola* were produced in abundance on the surface of yeast malt extract agar (1 g of yeast extract, 10 g of malt extract, 15 g of agar, 1 L of distilled water). When cultures were 6–10 days old, inoculum was prepared by scraping conidia from the agar surface and diluting them in distilled water to a concentration of 10^6 conidia per milliliter. Unflavored gelatin was added as a sticker at a rate of 0.5 g per 100 ml of inoculum suspension.

Plants were arranged in a randomized block design on a greenhouse bench and conidia were atomized onto the adaxial surface of flag (F) and penultimate (F-1) leaves with a DeVilbiss atomizer (DeVilbiss Co., Somerset, PA) operated at a pressure of about 0.35 kg · cm^{-2}. Approximately 41 conidia per square millimeter of leaf surface were applied. Plants were at the late anthesis to early seed-filling growth stages (GS 68-73) (32).

After inoculation, plants were placed in a moist chamber and

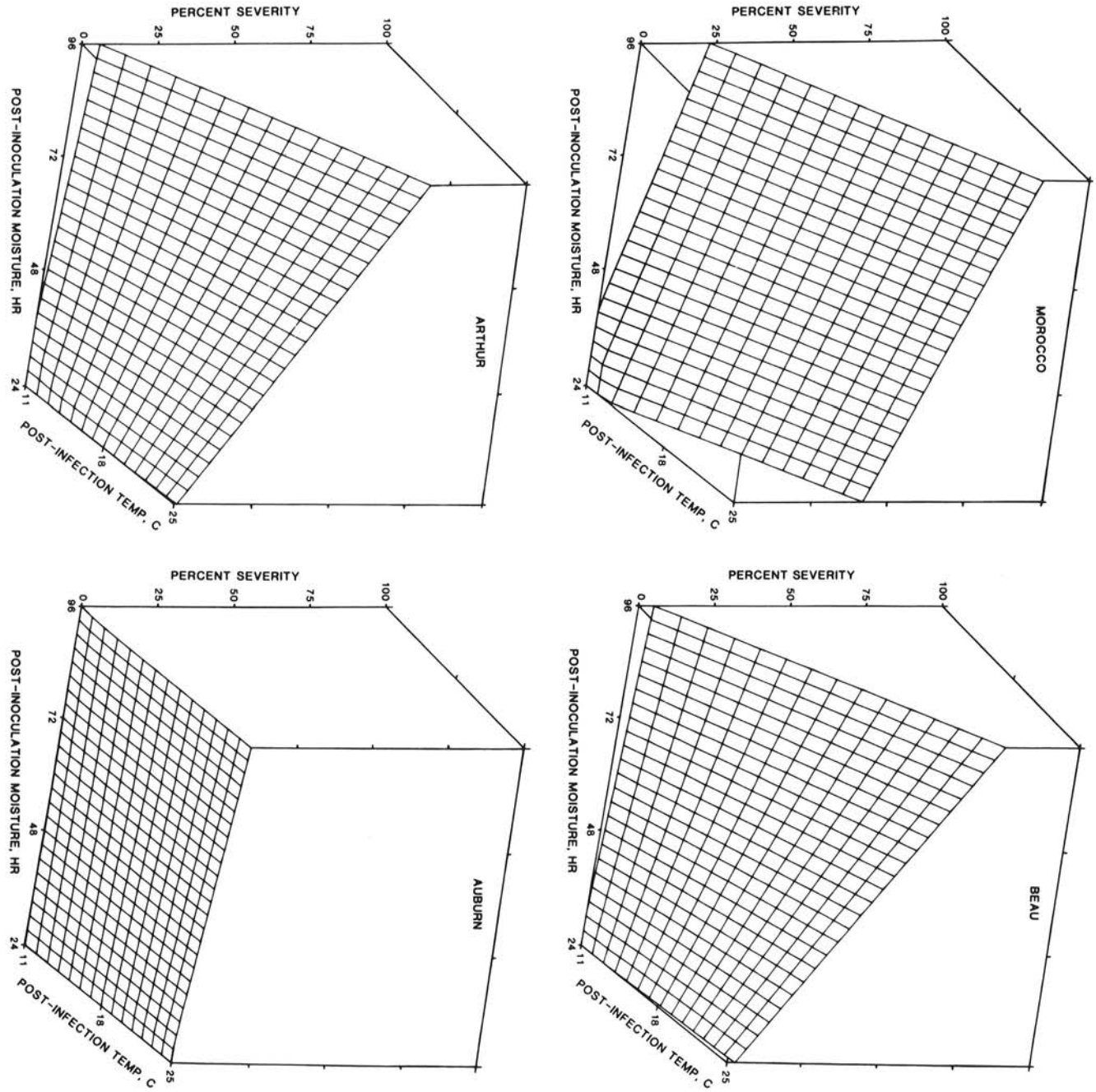

Fig. 1. Influence of postinoculation moist period (M) and postinfection incubation temperature (T) on Septoria tritici blotch severity on the flag leaves of four wheat cultivars. The response surface equations for each cultivar are: Morocco, $Y = -50.9051 + 3.1657\ T + 0.1889\ M + 0.0196\ TM$; Beau, $Y = 14.5082 - 1.5326\ T - 0.7285\ M + 0.0732\ TM$; Arthur, $Y = 11.7756 - 1.4183\ T - 0.6258\ M + 0.0660\ TM$; and Auburn, $Y = 5.0360 - 0.3843\ T - 0.1625\ M + 0.0130\ TM$.

misted for 12 sec at hourly intervals. Intervals were reduced to 30 min between 0830 hours and 1730 hours on sunny days. Temperatures within the inoculation chamber were monitored by means of a maximum-minimum registering thermometer. Fifteen plants of each cultivar were removed following 24, 48, 72, and 96 hr of moisture. After the leaf surfaces were dry (approximately 60 min), five plants were placed in each of three growth chambers set to maintain temperatures of 11, 18, or 25 C. No controls were available to regulate relative humidity (RH) within the chambers. Fluorescent and incandescent lights provided 295 $\mu E \cdot m^{-2} \cdot sec^{-1}$ at canopy level for 16 hr per day. Temperatures and relative humidity were monitored with a Hi-Q hygrothermograph model 5020 (Weathertronics, Sacramento, CA).

Disease severities were visually estimated 23 days postinoculation by which time some Morocco flag leaves were 100% necrotic. To determine pycnidial densities within lesions, a Bausch & Lomb dissecting microscope with a 10 × 10 ocular grid was used (one square = 0.0361 mm). Five counts were made at random in lesions distributed from the tip to the base of each leaf blade. The length and width of 10 randomly chosen pycnidia from each leaf were measured with an ocular micrometer in a compound light microscope. Pycnidial volumes were determined using methods described by Gough (8). Subsequently, a 1.5–2-cm segment bearing lesions with pycnidia was cut from each leaf and conidia were harvested and counted after 48–50 hr in petri dish moist chambers (8). Pycnidial density, volume, and conidial production were measured on leaves from the 72- and 96-hr moisture treatments. The experiment was performed three times, in March, April, and November of 1983. Hereafter, the respective experiments will be referred to as the first, second, and third experiments.

Analysis of variance was used to examine disease severity data, which were in a 4 × 4 × 3 factorial (four cultivars, four moisture periods, and three temperatures) with five subsamples (plants) per treatment and three trials (replications). A split-split plot design was employed where temperature treatments were whole plots, cultivars were subplots, and moisture treatments were sub-subplots. The temperature and moisture effects were partitioned into orthogonal polynomial components. Response surfaces (Fig. 1) for each cultivar resulted from fitting the model: $Y = B_0 + B_1 T + B_2 M + B_3 TM$ in which Y = percent Septoria tritici blotch severity, B_i = regression coefficient of the ith term, T = postinfection temperature (C), and M = postinoculation moisture (hr).

RESULTS

Temperatures in the inoculation chamber averaged 23 ± 7 C. Mean temperatures in the three growth chambers were 25.0 ± 1.0 C, 18.2 ± 1.6 C, and 10.7 ± 1.7 C with respective relative humidity values of 70, 66, and 67%.

Trends are recognizable by scanning Figure 1. Within each temperature and moisture treatment, disease severities increased with increasing cultivar susceptibility (Auburn, Arthur, Beau, and Morocco). Disease severity increased as postinfection temperature or as postinoculation moist period increased, and greatest severities resulted from combinations of long moist periods and high temperature (i.e., 96 hr and 25 C).

Although detailed notes were not taken on incubation or latent periods, these were observed to decrease with increasing moisture, temperature, and cultivar susceptibility. Mean incubation periods for the susceptible cultivar Morocco and moderately susceptible cultivars Beau and Arthur were approximately 13, 16, and 23 days at 25, 18, and 11 C, respectively. For these three cultivars, the incubation and latent periods were approximately equivalent. For the resistant cultivar Auburn, incubation periods averaged 21, 25, and 30 days at 25, 18, and 11 C, respectively, whereas the latent period was longer.

Factorial analysis of variance demonstrated that the temperature treatment was significant ($P = 0.05$) and moisture and cultivar treatments were highly significant ($P = 0.01$). In addition, two-way interactions between temperature and moisture, temperature and cultivar, and moisture and cultivar were highly significant. Only the linear orthogonal polynomials were significant ($P = 0.01$). Use of the arc sine-square root transformation of percent severity before statistical analysis reduced mean squares but did not affect conclusions. Interactions are illustrated graphically in Figure 1 for combined data from the three experiments.

For all moisture treatments, susceptible and resistant cultivars had consistently highest and lowest respective disease severities (Fig. 1).

At 11 C, disease development was reduced in all cultivars. At temperatures of 18 and 25 C, severity was greater, but the response to temperature varied according to cultivar resistance. The response to temperature was high, intermediate, and low for cultivars that were, respectively, susceptible, moderately susceptible, and resistant to *M. graminicola*.

Moist period duration (72 or 96 hr) did not significantly affect pycnidial density, volume, or spore production, so data from the two moist period treatments were combined before analysis of the effects of incubation temperature and cultivar. The higher the postinfection temperature, the more densely pycnidia formed in lesions on cultivars Morocco and Arthur (Fig. 2). For those two cultivars, temperature, percent leaf necrosis, and pycnidial density were positively correlated. A different trend was seen for cultivars Beau and Auburn: Pycnidial densities remained unchanged as temperature increased from 11 to 18 C, but increased as temperature rose to 25 C. Fewer pycnidia formed per square millimeter of necrotic tissue in the resistant cultivar Auburn than in the susceptible cultivars at each of the three temperatures.

As postinfection temperature increased, spore production of pycnidia on cultivar Morocco increased (Fig. 3). Spore production in cultivars Arthur and Auburn was greater at 25 C, unlike cultivar Beau in which most spores were produced at 11 C.

Pycnidial volume decreased with increasing postinfection

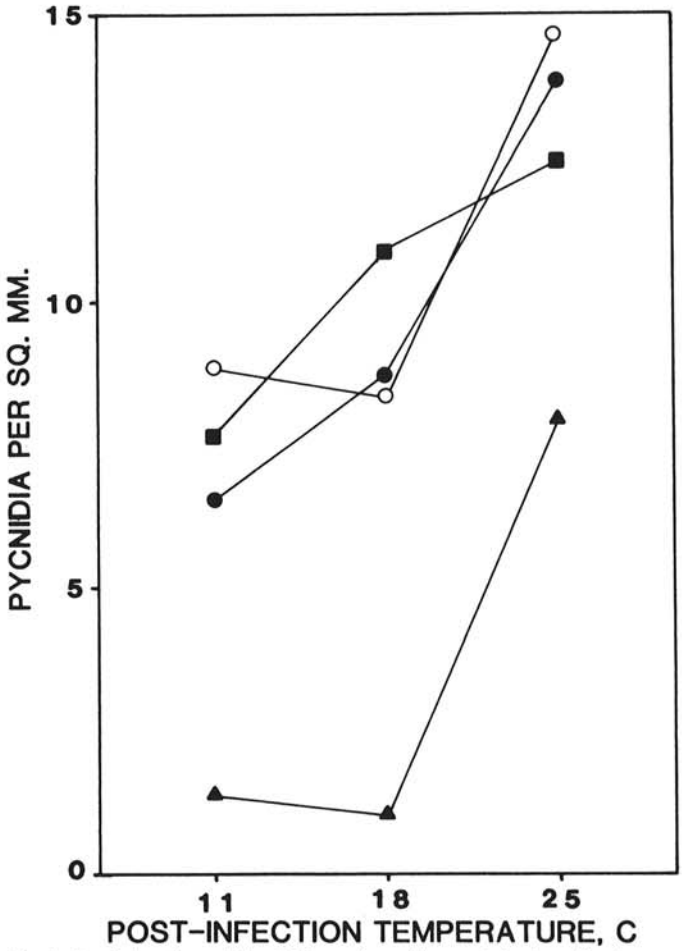

Fig. 2. Densities of pycnidia of *Mycosphaerella graminicola* on flag leaves of four wheat cultivars at three incubation temperatures. Average of three experiments. ■ = Morocco, o = Beau, • = Arthur, and ▲ = Auburn.

incubation temperature in cultivars Morocco and Beau (Fig. 4). Pycnidia from cultivar Auburn were smallest at 18 C, larger at 11 C, and largest at 25 C. In cultivar Arthur, pycnidia maintained a constant volume independent of temperature.

In susceptible and moderately susceptible cultivars, pycnidia developed quickly, were large, dark, and clearly visible. In resistant Auburn, pycnidia were smaller, lighter, more sparse, and developed more slowly. Pycnidia with ostioles were considered to be mature. The percentage of mature pycnidia increased in all cultivars with increasing temperature but was reduced in the resistant cultivar. After 23 days only 19% mature pycnidia developed on the resistant cultivar Auburn in contrast to an average of 45% mature pycnidia on the susceptible cultivars.

DISCUSSION

Variation in postinoculation moisture, postinfection incubation temperature, and cultivar susceptibility affected disease development on wheat inoculated with *M. graminicola*. Disease severity on the flag leaves of all four cultivars tested increased with increase in moist period from 24 through 96 hr. This result concurs with the report that 96 hr of postinoculation moisture produce a more susceptible reaction than do shorter moist periods (29) and observations that Septoria tritici blotch is favored by prolonged rainy weather (3,7,16,28,30). The greater severity at longer moist periods may result from increased spore germination and penetration (18). Disease development was favored by increase in incubation temperature as previously reported (1,6,25,31). A compensation appeared to exist between moisture duration and temperature in susceptible wheat cultivars, with severe disease resulting from either long moist periods followed by cool incubation conditions or short moist periods followed by warm incubation conditions. Disease on the resistant cultivar was low at all combinations of moisture and temperature.

The latent period of all cultivars increased as temperature decreased, but the latent period of the resistant cultivar appeared to increase more than those of susceptible cultivars. The same trend was reported for latent periods of the wheat leaf rust pathogen *Puccinia recondita* Rob. & Desm. f. sp. *tritici* parasitizing susceptible and resistant wheats (12).

Although latent period and percent leaf necrosis were positively correlated with incubation temperature and moist period duration, pycnidial densities varied according to cultivar. Pachinburavan (18) reported that in culture, pycnidial density increased with rise in incubation temperature through 25 C and was favored by 100% RH. The lower relative humidity in growth chambers used in this experiment may have resulted in delayed maturity and reduced density of pycnidia for some or all cultivars studied.

Hilu and Bever (9) found similar numbers of pycnidia in lesions on susceptible, intermediate, and resistant wheats, but pycnidia in intermediate and resistant cultivars were smaller than those in the susceptible cultivars. We report similar numbers of pycnidia in susceptible and moderately susceptible cultivars with fewer pycnidia in the resistant cultivar. Pycnidia were smaller in the resistant cultivar except at 25 C. Eyal and Brown (5) reported that small pycnidia were associated with a high pycnidial density. We found this association to be cultivar-dependent.

Gough (8) reported that pycnidial size and spore production were reduced in the resistant cultivar Oasis compared with susceptible cultivars and suggested a positive correlation between pycnidial volume and the number of spores released per pycnidium. We also observed reduction in pycnidial size and spore production on resistant cultivar Auburn compared with susceptible Morocco and moderately susceptible cultivars Beau

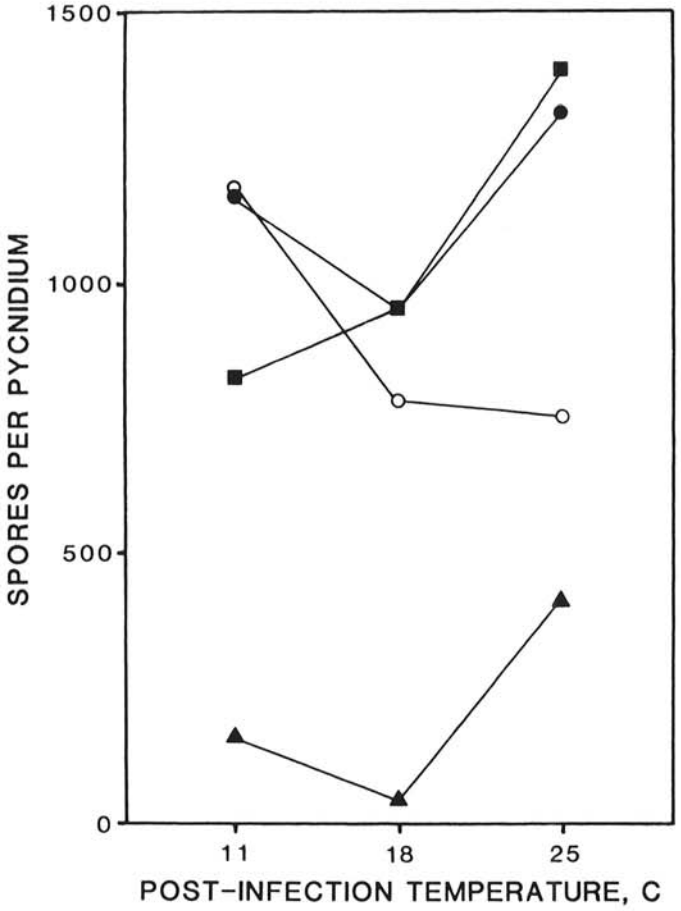

Fig. 3. Spore production in pycnidia of *Mycosphaerella graminicola* in four wheat cultivars incubated at three temperatures following inoculation. Average of three experiments. ■ = Morocco, o = Beau, • = Arthur, and ▲ = Auburn.

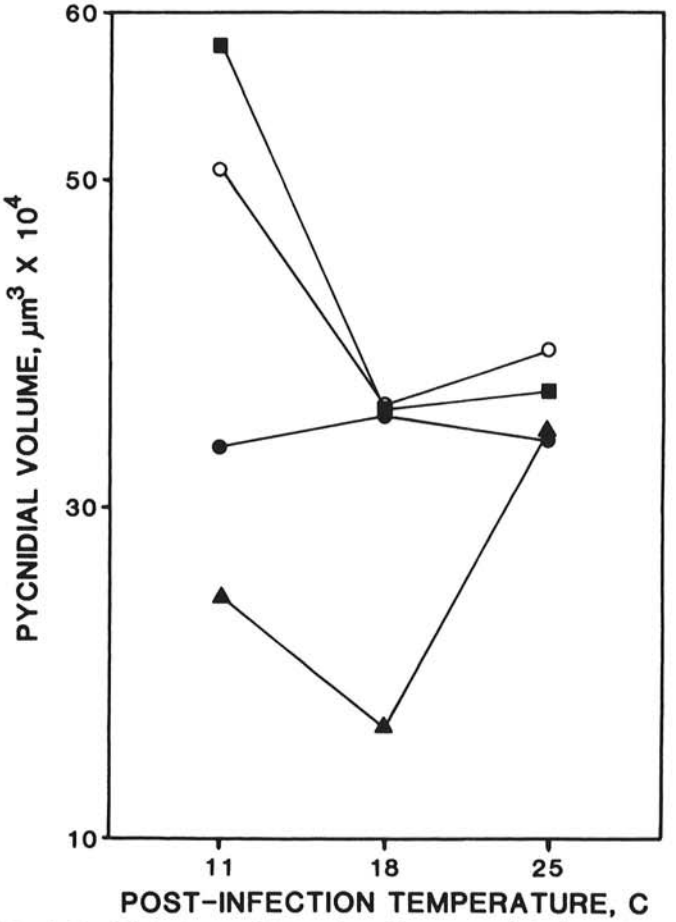

Fig. 4. Pycnidial volume of *Mycosphaerella graminicola* in four wheat cultivars incubated at three temperatures after inoculation. Average of three experiments. ■ = Morocco, o = Beau, • = Arthur, and ▲ = Auburn.

and Arthur. Environmental variation can affect pycnidial spore production in a given host cultivar (8).

These findings confirm field observations in which cultivar Auburn, in addition to developing fewer and smaller lesions, produces fewer and smaller pycnidia than susceptible cultivars. This reduced spore production is accumulated over several infection cycles and disease progress up individual plants and its spread throughout the field is dramatically reduced.

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