

Effect of Light and Temperature on Expression of Partial Resistance of Maize to *Exserohilum turcicum*

M. L. CARSON, Research Plant Pathologist, USDA-ARS, and Associate Professor, Department of Plant Pathology, and C. G. VAN DYKE, Professor, Department of Botany, North Carolina State University, Raleigh 27695-7616

ABSTRACT

Carson, M. L., and Van Dyke, C. G. 1994. Effect of light and temperature on expression of partial resistance of maize to *Exserohilum turcicum*. Plant Dis. 78:519-522.

The effects of light and temperature on the expression of major gene resistance in maize (*Zea mays*) to northern leaf blight (caused by *Exserohilum turcicum*) are well documented. However, their effects on the expression of partial resistance to the disease have not been studied. Six maize inbred lines, representing a wide range in levels of partial resistance to northern leaf blight, were evaluated for three components of partial resistance (incubation period, latent period, and sporulation intensity) in controlled environmental chambers representing a factorial arrangement of three temperature regimes (22/18 C, 26/22 C, and 30/26 C, day/night) and two light intensities (full light, 639 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, or half light, 320 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Incubation and latent periods of inbred lines were consistently correlated, regardless of environmental conditions, and reflected the lines' levels of partial resistance. Although there was some relationship with partial resistance, sporulation intensity on inbred lines was highly variable, interacting with both temperature and light, and was greatly reduced at the 30/26 C temperature regime. Incubation or latent period length could be a useful measure of partial resistance of maize genotypes in greenhouse or growth chamber screenings of seedlings. Unlike major gene resistance, partial resistance expressed as an increased latent period appears to be a stable trait expressed over a wide range of temperature and light conditions, although higher temperatures tended to increase the differences among genotypes.

Additional keywords: corn, polygenic resistance, *Setosphaeria turcicum*

Northern leaf blight, caused by the fungus *Exserohilum turcicum* (Pass.) K.J. Leonard & E.G. Suggs (teleomorph = *Setosphaeria turcica* (Luttrell) K.J. Leonard & E.G. Suggs; syn. = *Helminthosporium turcicum* Pass.), is an important disease of maize (*Zea mays* L.) that occurs worldwide. The disease

can cause extensive defoliation during the grain-filling period, resulting in yield losses of 50% or more (17,22). Two types of resistance in maize to northern leaf blight are generally recognized: major gene resistance conferred by the *Ht1*, *Ht2*, *Ht3*, or *HtN* genes that are race specific (6-9,11), and partial resistance that is polygenically controlled and is not race specific (12,13,21). The *Ht1*, *Ht2*, and *Ht3* genes confer a chlorotic lesion form of resistance, whereas *HtN* results in the delay of symptoms until after anthesis. Virulence to each of these genes has been found in the *E. turcicum* population in the United States (15).

Although major gene resistance (particularly the *Ht1* gene) has been used to some extent, emphasis in most commercial maize breeding programs has been placed on exploiting forms of partial resistance to the major diseases.

Partial resistance to northern leaf blight of maize is expressed as a reduction in disease severity or progress during the grain-filling period (1,2,10,12,21). Components of partial resistance that can lead to reduced disease development include increased incubation and latent periods, reduced lesion size, reduced lesion expansion rate, reduced sporulation, and reduced infection efficiency (1,2,12,16,18). Although each of these components may contribute to partial resistance in maize to northern leaf blight, in an attempt to map components of partial resistance in the inbred line Mo17, only infection efficiency and latent period were consistently related to percent disease severity on adult (post-anthesis) plants (2). Further, components of partial resistance measured on seedlings in the greenhouse were rarely significant and were not correlated with results obtained in the field. The high coefficients of variability associated with some of these components may be due, in part, to the sensitivity of these traits to fluctuating environmental factors. We have recently developed inbred lines from the synthetic BS19 that exhibit very high levels of partial resistance expressed by seedlings in both field and greenhouse tests as a prolonged latent period. This resistance appears to be under polygenic control (3,4).

Accepted for publication 2 February 1994.

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The effects of environment on the expression of major gene resistance to northern leaf blight are documented. Virulence of race 1 (old race 2) of *E. turcicum* on seedlings of H4460H1 was expressed at a 22/18 C (day/night) temperature regime, but was suppressed at a 26/22 C regime (20). Furthermore, plants of H4460H1 grown at 22/18 C also expressed resistance if moved to a 26/22 C regime within 3 days after inoculation. This effect of temperature on expression of virulence was not seen, however, when the inbred line B37H1 was used. Virulence to Ht3 and HtN was best expressed at low temperatures (22/18 C) and intermediate light intensities (14,19).

Because of the importance of partial resistance for control of northern leaf blight and because it is desirable to know optimal conditions for expression of this resistance under a controlled environment, we conducted the following study of the effects of temperature and light intensity on three components of partial resistance: incubation period, latent period, and sporulation intensity.

MATERIALS AND METHODS

Six inbred lines of maize, representing a wide range in levels of partial resistance to northern leaf blight, were selected for this study: A632 and A619 (fully susceptible); B37 and Mo17 (intermediate level of partial resistance); and 69-1 and 92:123 (sister lines from BS19 [4], high level of partial resistance). An isolate of *E. turcicum*, Et10 (confirmed race 0, old race 1 [15]), maintained on dried infected leaf tissue collected from greenhouse studies and stored at 4 C, was used to complete this study. Inoculum was prepared by placing this infected leaf tissue in a moist chamber for 72 hr to induce sporulation. Just prior to inoculation, the tissue was flooded with water containing Tween 20 (2 drops/100 ml) and conidia were dislodged with a plastic spatula. Conidial concentrations were determined with a hemacytometer.

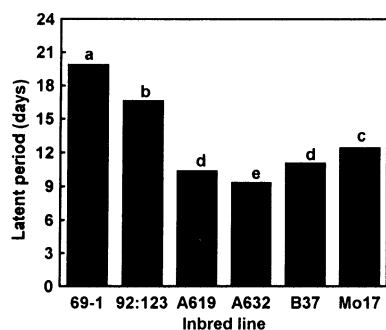


Fig. 1. Mean latent period (days to necrotic lesion formation) of *Exserohilum turcicum* on six inbred lines of maize measured across all temperature and light combinations. Columns with the same letter indicate no significant ($P = 0.05$) difference between inbred lines based on comparison of log transformed means using FLSD.

Plants of the six inbred lines were grown in the controlled environment facilities of the Southeastern Plant Environment Laboratory, Raleigh, North Carolina. Four seeds were planted in 11.4-cm-diameter pots (600 cm³ volume) in a 1:2 (v/v) mixture of peat-lite and gravel. Pots were watered twice daily with a standard phytotron nutrient solution (5). Plants were thinned to two per pot. Plants were grown for 14 days at a 26/22 C day/night temperature regime in a walk-in growth room and were provided 12 hr of light ($639 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photosynthetic photon flux density) daily. After 14 days, plants were moved to chambers providing a factorial arrangement of six temperature and light combinations. Temperature regimes consisted of 30/26, 26/22, and 22/18 C day/night controlled within 0.25 C of the setpoint. Light treatments consisted of either full light ($639 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) or half light ($320 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), provided by covering plants with nylon shade cloth. Two pots (replicates) of each inbred were randomly arranged in each temperature and light combination. The experiment was repeated three times. Plants were inoculated 21 days after planting by placing 0.5 ml of a suspension containing 10^3 conidia into the leaf whorl. Plants were placed in the dark for 16 hr in a mist chamber with a constant temperature of 26 C and misted 15 sec every 5 min. Plants were returned to the appropriate chambers for the environmental treatments. Plants were inspected daily beginning 6 days after inoculation and were rated for the presence or absence of wilting symptoms around infection points (beginning of lesion formation, incubation period) and the presence or absence of necrotic lesions (latent period). Significant sporulation of *E. turcicum* can occur whenever infected host tissue becomes necrotic. Three days after necrotic lesions were first observed, samples of

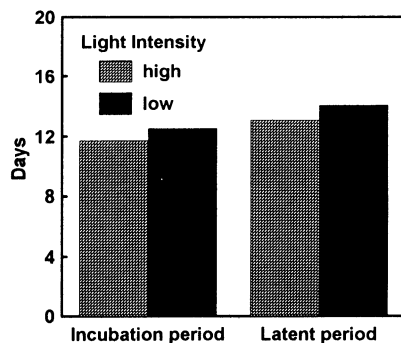


Fig. 2. Mean incubation (days to symptom formation) and latent (days to necrotic lesion formation) period of maize seedlings grown at full ($639 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and half ($320 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) light intensity in controlled environmental chambers and inoculated with *Exserohilum turcicum*. The increase in incubation and latent periods with the reduction of light intensity to half was significant ($P = 0.05$) based on analysis of variance.

leaves with lesions were taken and placed in petri dishes with moistened filter paper and returned to the environmental chamber from which they were taken. Forty-eight hours later, four leaf disks (8 mm diameter) were taken from the centers of the lesions and placed in microcentrifuge tubes containing 0.25 ml of water with Tween 20 (2 drops/100 ml). Tubes were agitated to dislodge conidia, and the conidial concentration of the resulting suspension was determined with a hemacytometer. Sporulation data were later converted to conidia per square millimeter (sporulation intensity).

Data were analyzed by analysis of variance of a split-plot design where whole plots consisted of the factorial arrangement of temperature/light treatments in a randomized complete block with three replications (repetitions) and split-plot treatments consisted of the six inbred lines. Incubation period, latent period, and sporulation intensity data were log transformed prior to analysis to normalize variances. Comparisons between transformed treatment means were made with FLSD tests using the appropriate error terms in the split-plot analysis of variance.

RESULTS

Mean incubation and latent periods on inbred lines ranged from 8.4 (A632) to 17.7 (69-1) and from 9.4 (A632) to 19.9 (69-1) days, respectively. Incubation and latent periods were highly correlated ($r = 0.99$, $P \leq 0.001$) in this experiment, indicating that they were measures of the same phenomena. Accordingly, the remainder of this discussion will focus on latent period data. The ranking of inbred lines for latent periods in this experiment did not significantly interact with either temperature or light intensity (Fig. 1). Latent periods of northern leaf blight on the six inbred lines were significantly increased ($P = 0.01$) 0.7 days by reducing light intensity to half (Fig. 2).

Sporulation intensity on inbred lines significantly interacted ($P = 0.05$) with both light and temperature in this study, although the magnitude of the mean square for the three-way interaction was small relative to the inbred line mean square (Fig. 3). Sporulation on inbred lines tended to reflect their level of partial resistance; however, there were notable exceptions. Although B37 is considered to have a moderate level of partial resistance, sporulation intensity on this inbred line was the highest of the six in four of the six environments. Sporulation on the two highly resistant inbred lines (69-1 and 92:123) was generally sparse in most environments, but sporulation on 92:123 approached that of B37 in the 30/26 C, half light intensity environment. Sporulation intensity was generally lowest in the high-temperature regimes.

DISCUSSION

Incubation and latent period on the six inbred lines consistently ranked them according to our observations of their partial resistance in the field, regardless of the temperature or light intensity. These data suggest that selection for increased latent or incubation periods could be an effective way to screen maize seedlings for partial resistance to northern leaf blight in either greenhouse or growth room conditions during the winter season, or as a substitute for disease severity ratings on adult plants in the field. Furthermore, our data indicate that these traits are stable across a range of temperature and light conditions, making precise control of environmental conditions unnecessary in these tests. This finding contradicts conventional wisdom regarding the supposed sensitivity of partial resistance to fluctuating environmental conditions. In the maize-*E. turcicum* pathosystem, partial resistance appears less sensitive to variations in light and temperature than are the major gene resistances. In a study of partial resistance to northern leaf blight in Ugandan cultivars, Adipala et al (1) also found a consistent, significant relationship between the incubation periods and lesion numbers on seedling plants in growth chamber studies and the measures of disease severity on adult plants in the field. Other components of

partial resistance measured in the study, such as lesion length and sporulation, were not consistently related to adult-plant reactions, as in the results of Brewster et al (2). The greatest range of latent periods among the inbred lines was at the high (30/26 C) temperature regime, indicating that high temperatures would be best for maximizing differences among genotypes evaluated. The half-light treatment is not recommended for this high-temperature regime because of the poor growth of plants, even though reduced light did significantly increase latent periods regardless of temperature regime or inbred line.

A previous report of the effects of temperature and light on expression of monogenic resistance to northern leaf blight indicated that infection did not occur at the high-temperature regime (30/26 C). This might partially explain the prevalence of northern leaf blight in moderate to cool climates (14). We had no difficulty in obtaining successful infection and symptom development at the high-temperature regime in our experiments. Indeed, the shortest incubation and latent periods observed in our trials were on the two susceptible inbred lines (A632 and A619) subjected to the 30/26 C temperature, full-light treatment. This discrepancy may be explained by differences in procedures between the two reports. Leath et al (14) grew their

plants at 26/22 C and full light prior to inoculation and did not expose them to the 30/26 C regime until after inoculation. In our experiment, plants were moved to the various environmental conditions 1 wk prior to inoculation. The lack of infection at 30/26 C in previous studies may have been a result of a temperature shock to the plants when they were suddenly moved to the high-temperature regime during the early stages of the infection process; whereas in our study, plants were preconditioned to the extreme temperatures before inoculation.

Sporulation intensity in our trials was highly variable, as indicated by a high coefficient of variation (25%). The significant inbred \times temperature \times light interaction indicates that the ranking of genotypes for this component of partial resistance is highly dependent on environmental conditions, although the magnitude of this interaction was still small in relation to the main effects of the inbred lines. Although sporulation intensity tended to reflect the level of partial resistance of the inbred lines, sporulation was always less on the highly susceptible inbred A632 than on the moderately resistant B37. Sporulation was generally lowest at the high-temperature regime. Although northern leaf blight does occur in the warmer climate of the coastal plain of North Carolina,

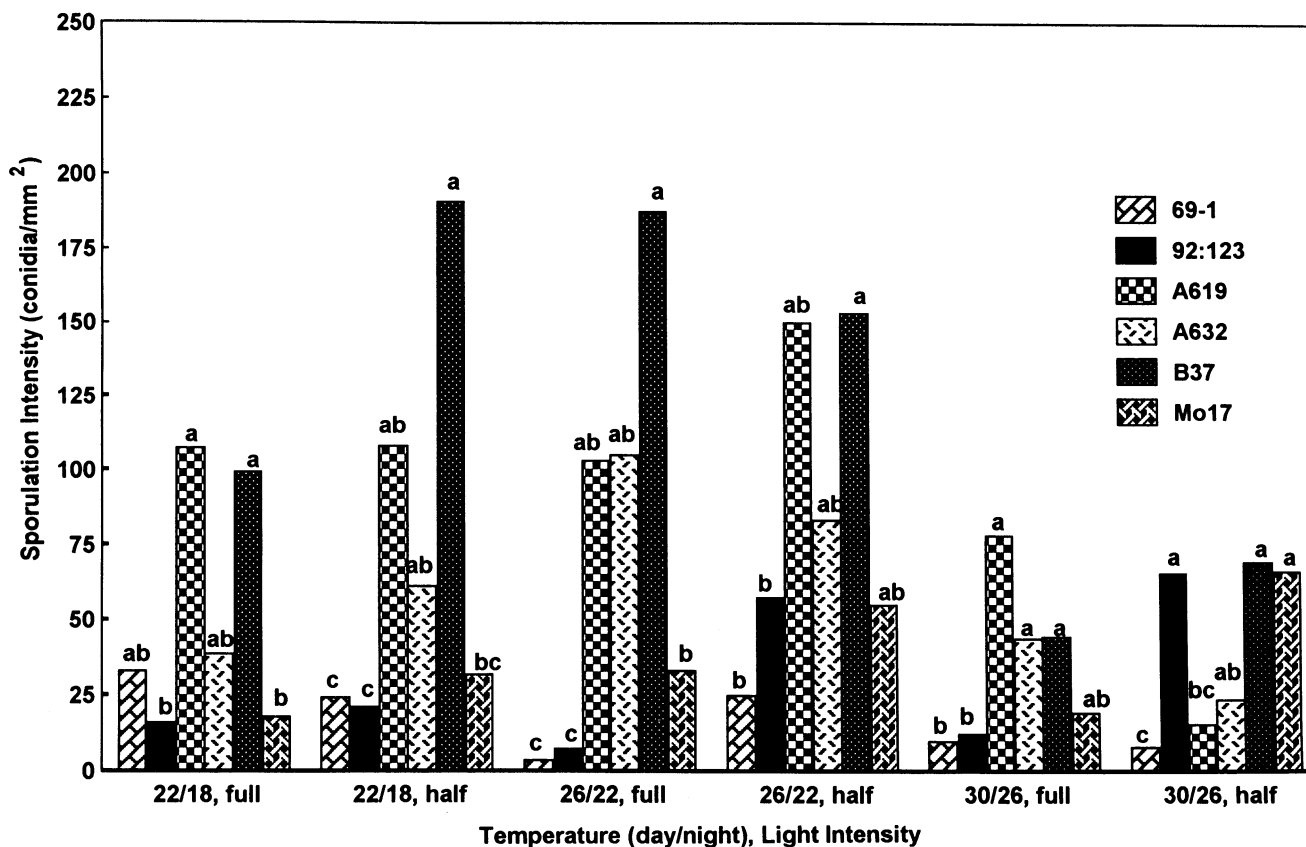


Fig. 3. Effect of temperature regime and light intensity (full = $639 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, half = $320 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) on sporulation intensity of *Exserohilum turcicum* on six inbred lines of maize. Columns with the same letter within a temperature/light regime indicate no significant ($P = 0.05$) difference between inbred lines based on a comparison of log transformed means using FLSD.

it is much more prevalent and potentially damaging in the cooler climate of the upper Piedmont and mountain regions of the state. While Leath et al (14) suggested that this distribution may be due to reduced or no infection at high temperatures, our data suggest that poor sporulation may also be a factor in restricting the development at higher temperatures. In both this study and that of Leath et al, actual inoculations were done at 26 C; therefore, it was not possible to determine the effects of temperature during the actual infection process. However, the normal nighttime low temperatures during summer on the coastal plain of North Carolina are almost always less than 26 C, so it is doubtful that high temperatures during infection periods are the factor limiting northern leaf blight development in these areas.

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ERRATUM/Volume 78, Number 1, 1994

In the article "Contribution of Four Races of *Xanthomonas campestris* pv. *vesicatoria* to Bacterial Spot in Barbados" by Leonard W. O'Garro and Simone Tudor on pages 88-90, the subhead over column 5 in Table 2 should read: Pepper group race 1 only.