Characterization of a New Race of *Exserohilum turcicum* Virulent on Corn with Resistance Gene *Ht*N

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ABSTRACT

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Isolates of a new race of *Exserohilum turcicum* collected from South Texas in 1986 were compared with isolates of race 1 and race 3 in inoculations of seedlings of corn inbred B37 and B37 backcross lines with *Ht*2, *Ht*3, and *Ht*N in controlled environment chambers. The new race resembled race 3 except for its virulence on B37*Ht*N. Race 3 has the virulence formula *Ht*1,*Ht*N/*Ht*2,*Ht*3. The new race is described as race 4 with the virulence formula *Ht*1/*Ht*2,*Ht*3,*Ht*N. Both race 3 and race 4 were virulent on B37*Ht*3 at 22 C day/18 C night temperatures but were avirulent at 26 C day/22 C night. Leaf disks were cut from lesions of races 3 and 4 on plants grown under different light and temperature conditions and incubated in moist chambers in the laboratory to compare treatment effects on sporulation. For plants grown under full light (647 $\mu E \cdot m^{-2} \cdot s^{-1}$) at 22 C day/18 C night temperatures or 26 C day/22 C night, sporulation was greater on B37 than on B37*Ht*3 or B37*Ht*N. In lesions from plants grown at reduced light intensity, sporulation on B37 was significantly decreased, but sporulation by races 3 and 4 on B37*Ht*3 and by race 4 on B37*Ht*N was significantly increased. The resistance of B37*Ht*2 to race 1 broke down at low light intensity.

Additional keywords: maize, northern leaf blight, *Setosphaeria turcica*, *Zea mays*

In 1985, severe northern leaf blight caused by *Exserohilum turcicum* (Pass.) Leonard & Suggs (teliomorph *Setosphaeria turcica* (Luttrell) Leonard & Suggs) was observed on corn in Wharton County in South Texas. A similar epidemic occurred in 1986 in Wharton and Matagorda counties. Damage was most common on the popular corn hybrids Pioneer Brand 3165 and Funks 4673A, which had no *Ht* genes for resistance to northern leaf blight. In greenhouse trials, seven single conidial isolates collected from diseased leaves in 1986 induced susceptible-type lesions in inoculated leaves of corn hybrids with *Ht*N, but not in leaves of hybrids with *Ht*1 or *Ht*2 (R. K. Jones, *unpublished*).

Recently, Leath et al (6) demonstrated that temperature and light intensity affect the expression of resistance of corn with *Ht*2 and *Ht*3 to races 1 and 2 of *E. turcicum* (virulence formulae *Ht*1,*Ht*2,*Ht*3,*Ht*N/ and *Ht*2,*Ht*3,*Ht*N/*Ht*1, respectively). They also showed that the virulence of race 3 (*Ht*1,*Ht*N/*Ht*2,*Ht*3) to corn with *Ht*2 and *Ht*3, which was first described by Smith and Kinsey (10), is expressed most clearly in controlled environment chambers at 22 C day/18 C night temperatures. The objectives of the current study, therefore, were to further characterize the expression of virulence of the new race of *E. turcicum* found in Texas and to compare its virulence with that of race 1 and race 3 under various temperature and light intensity conditions.

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MATERIALS AND METHODS

Pathogen isolates. Four isolates of *E. turcicum* (deposited in the American Type Culture Collection) were used in these studies: isolate 85-20 (ATCC 64837) is race 1 collected from Wilkes Co., NC, in 1985; R3SC (ATCC 64836) is race 3 collected from Estill, SC, in 1976 and provided by D. R. Smith, DeKalb-Pfizer Genetics; and isolates 2-5 (ATCC 64834) and 2-11 (ATCC 64835) were collected in Texas in 1986 and exhibited virulence to corn with *Ht*N in greenhouse tests. Cultures for inoculum production were initiated from conidial suspensions in 30% glycerol that were stored frozen at −70 C. The isolates were grown on lactose-casein hydrolysate agar (11). Inoculum was prepared by washing conidia from 10- to 14-day-old cultures with water to which Tween 20 (polyoxyethylene sorbitan monolaurate) had been added at a concentration of two drops per 100 ml of water. Conidial concentrations were determined in a hemacytometer and the suspensions were diluted to 10^4 conidia per milliliter.

Host plants. Seed of corn inbred line B37 and backcross lines of B37 with *Ht*2, *Ht*3, and *Ht*N were provided by W. L Pedersen, University of Illinois. Four seeds were sown per plastic pot (11.4 cm diameter, 600 ml volume) containing a 1:2 mixture of peat-lite and gravel. After plants emerged, they were thinned to three per pot. Plants were grown in controlled environment chambers in the phytotron of the Southeastern Plant Environment Laboratory, Raleigh, NC. Air temperature in the chambers was maintained within ± 0.25 C of the set point for the treatment, and the chambers were equipped with a combination of cool-white fluorescent and incandescent lamps to provide a 12-hr photoperiod with an illuminance of 49.9 klux (average photosynthetic photon flux density of 647 $\mu E \cdot m^{-2} \cdot s^{-1}$) at full light intensity (1). Reduced light intensity was obtained by turning off one-half or three-fourths of the bulbs.

The experiment consisted of four host genotypes grown in four different environments and inoculated with four pathogen isolates for a total of 64 treatments. Plants from the four growth chambers were combined and randomized for inoculation and incubation and then returned to their respective chambers. There were four replicate pots of plants for each treatment. The four environmental treatments were: 26 C day/22 C night temperatures with full light intensity (647 $\mu E \cdot m^{-2} \cdot s^{-1}$) during the day, or 22 C day/18 C night temperatures with full, one-half (324 $\mu E \cdot m^{-2} \cdot s^{-1}$), or one-fourth (162 $\mu E \cdot m^{-2} \cdot s^{-1}$) light intensity.

Inoculation. At 19 days after planting, the seedlings were inoculated by spraying the leaves to runoff with a conidial suspension of 10^4 conidia per milliliter applied with a DeVilbiss atomizer attached to an air pump. Inoculated plants were incubated 16 hr in a mist chamber in the dark at 22 C and then returned to the chambers in which they had grown before inoculation. Disease reactions were evaluated at 10 and 14 days after inoculation. A rating scale similar to that of Pedersen et al (8) was used; chlorotic lesions with little or no necrosis were rated resistant, narrow necrotic lesions surrounded by chlorosis were rated intermediate, and lesions that were wilted and necrotic without a chlorotic border were rated susceptible type.

Table 1. Effects of temperature and light intensity on reaction[a] of corn with *Ht* genes for northern leaf blight resistance to four isolates of *Exserohilum turcicum*

Corn line	Day/night temperature	Light intensity ($\mu E \cdot m^{-2} \cdot s^{-1}$)	Isolate[b] 85-20	R3SC	2-5	2-11
B37	26/22	647	0	S	S	S
	22/18	647	S	S	S	S
	22/18	324	S	S	S	S
	22/18	162	S	S	S	S
B37*Ht*2	26/22	647	R	S	S	S/R
	22/18	647	R	S	S	S
	22/18	324	S	S	S	S
	22/18	162	S	S	S	S
B37*Ht*3	26/22	647	R	R	R	R
	22/18	647	R	R/S	R/S	R/I
	22/18	324	R	R/S	S	S
	22/18	162	I	S	S	S
B37*Ht*N	26/22	647	R	R	Seg.	Seg.
	22/18	647	R	R	R/S	S
	22/18	324	R	R	S/I	S
	22/18	162	0	R	S	S

[a] S = susceptible-type lesions; R = resistant-type lesions; I = lesions intermediate between resistant and susceptible type; 0 = no lesions; R/S = range of lesion types from resistant to susceptible on the same plants, with most resembling the resistant type; S/R = range of lesion types with most resembling the susceptible type; R/I = range of lesion types from resistant to intermediate, with most lesions resembling the resistant type; S/I = range of lesion types from intermediate to susceptible, with most lesions of the susceptible type; Seg. = plants segregating for reaction type, some plants with only resistant-type lesions and others with only susceptible-type lesions.

[b] Isolate 85-20 is race 1, R3SC is race 3, and isolates 2-5 and 2-11 are of a new race found in 1985 in Texas.

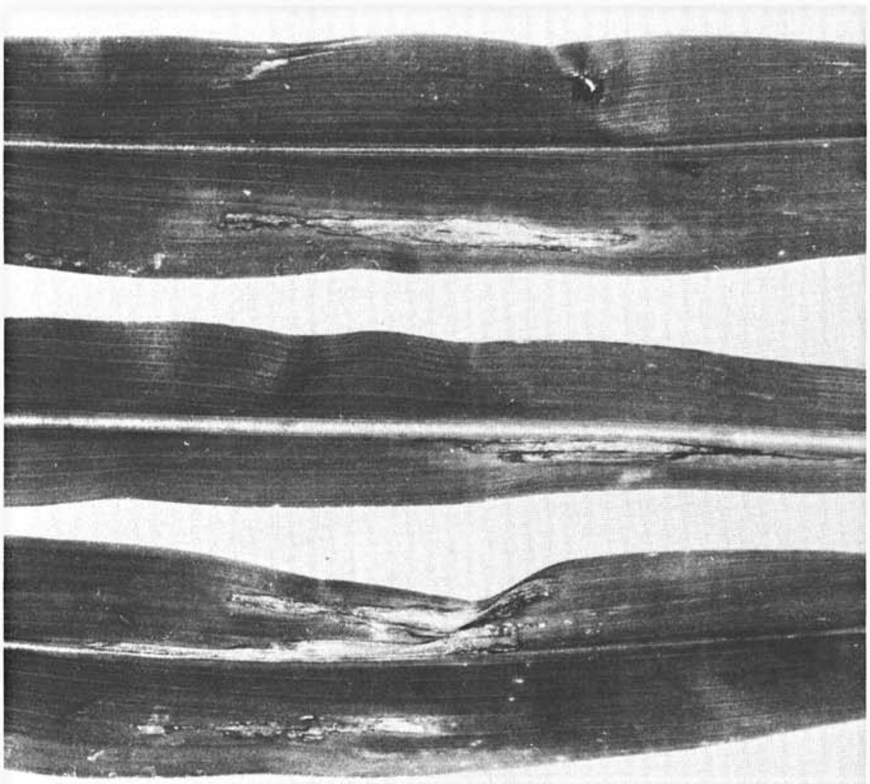

Fig. 1. Susceptible disease reactions of corn inbred B37*Ht*2 to race 3 (top leaf) and race 4 (middle and lower leaves) of *Exserohilum turcicum*. Corn plants were grown at 22 C day/18 C night temperatures with full light (647 $\mu E \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux density).

Sporulation. Sporulation in disease lesions was evaluated for isolates R3SC, 2-5, and 2-11, but not for the race 1 isolate 85-20. At 15 days after inoculation, 1-cm-diameter leaf disks were cut at the centers of five lesions on plants in each pot. The leaf disks immediately were placed on moist filter paper in petri dishes and transported to the laboratory where they were incubated at room temperature with a 12-hr photoperiod from fluorescent lights. After 4 days incubation, the leaf disks were transferred to test tubes and conidia were collected by shaking the leaf disks in 5 ml of water containing Tween 20 (two drops per 100 ml of water). Conidia were counted in three 2-μl droplets drawn from the resulting conidial suspension. Sporulation was expressed as number of conidia per leaf disk (i.e., conidia per 1-cm-long segment of lesion).

RESULTS

Disease reactions. Isolates 2-5 and 2-11 from Texas resembled race 3 (isolate R3SC), except for their reactions on B37*Ht*N (Table 1, Figs. 1–3). At 22 C day/18 C night temperatures, isolates 2-5 and 2-11 were virulent on B37*Ht*N, particularly at reduced light intensity, whereas isolate R3SC was avirulent on B37*Ht*N. Although the resistance of *Ht*N has been associated with greatly prolonged latent periods rather than with the production of chlorotic lesions (3,9), we observed resistant-type lesions on B37*Ht*N plants inoculated with races 1 and 3. Virulence of isolate 2-5 to B37*Ht*N appeared to be incomplete, because at full light and one-half light intensity isolate 2-5 induced a mixture of lesion types. Under these conditions, isolate 2-5 induced mostly susceptible-type lesions on the lower leaves, but many lesions on upper leaves resembled the chlorotic resistant-type lesions induced by races 1 and 3 on B37*Ht*N. At high temperatures, the distinction between race 3 and the new race represented by isolates 2-5 and 2-11 was less clear, because B37*Ht*N segregated for resistance to the new race at 26 C day/22 C night temperatures (Table 1, Fig. 3). Of the 12 B37*Ht*N plants with visible lesions of isolates 2-5 and 2-11 at 26 C day/22 C night temperatures, four had only resistant-type lesions and eight had only susceptible-type lesions.

Light intensity affected the expression of resistance conditioned by both *Ht*2 and *Ht*3 (Table 1). B37*Ht*2 was resistant to race 1 (isolate 85-20) at full light in the controlled environment chambers but not at 324 or 162 $\mu E \cdot m^{-2} \cdot s^{-1}$. B37*Ht*3 was highly resistant to race 1 at 647 and 324 $\mu E \cdot m^{-2} \cdot s^{-1}$, but less resistant at 162

$\mu E \cdot m^{-2} \cdot s^{-1}$. The *Ht*3 resistance also appeared to be partially effective against race 3 and the Texas isolates when the plants were grown under full light at 22 C day/18 C night temperatures (Fig. 2). Under these conditions, lesions of race 3 and the Texas isolates on lower leaves of B37*Ht*3 resembled susceptible-type or intermediate-type lesions, while those on the uppermost leaves more often resembled resistant-type lesions.

As reported by Leath et al (6), race 3 of *E. turcicum* was avirulent on plants with *Ht*3 at high temperatures. Both R3SC and the Texas isolates 2-5 and 2-11 induced resistant-type lesions on B37*Ht*3 at 26 C day/22 C night temperatures (Table 1). Thus, Smith and Kinsey's (10) race 3 virulence formula of *Ht*1/*Ht*2,*Ht*3 applies to conditions of moderate, but not high, temperatures. At high temperatures the virulence formula would be *Ht*1,*Ht*3/*Ht*2. When the reaction of race 3 to *Ht*N is added, the virulence formula is *Ht*1,*Ht*N/*Ht*2,*Ht*3 at 22 C day/18 C night temperatures or *Ht*1,*Ht*3,*Ht*N/*Ht*2 at 26 C day/22 C night.

Sporulation. The analyses of variance for effects of host lines, pathogen isolates, and temperature or light intensity are shown in Tables 2 and 3. At full light intensity in the chambers, the main effects of temperature and inbred lines were statistically significant. At 22 C day/18 C night temperatures, only the interaction effect of inbred lines × light intensity was statistically significant, indicating that light intensity affects sporulation of the isolates on B37, B37*Ht*2, B37*Ht*3, and B37*Ht*N differently. For further analysis of the effects of temperature and light on sporulation, the combination of isolate R3SC on B37*Ht*N, which gave only resistant reactions, was removed from consideration. Sporulation by isolates R3SC, 2-5, and 2-11 on plants grown at full light intensity was significantly ($P < 0.05$) greater on B37 than on B37*Ht*3. Similarly, sporulation by isolates 2-5 and 2-11 was significantly ($P < 0.05$) greater on B37 than on B37*Ht*N. Temperature did not significantly affect sporulation of isolates B3SC, 2-5, and 2-11 on B37 or B37*Ht*2, but sporulation on B37*Ht*3 was reduced at 26 C day/22 C night temperatures (Fig. 4). B37*Ht*3 was resistant to the isolates at 26 C day/22 C night temperatures, but moderately susceptible at 22 C day/18 C night under full light intensity. Sporulation of isolates 2-5 and 2-11 on B37*Ht*N was not significantly affected by temperature.

Leaf disks taken from lesions on B37 plants grown at 22 C day/18 C night temperatures at full light intensity supported greater sporulation than those from plants grown at reduced light intensity (Fig. 5). The reverse was true for B37*Ht*3 and B37*Ht*N. For B37*Ht*2, sporulation was not significantly affected by light intensity.

DISCUSSION

Our results confirm the observations of Jones (*unpublished*) that the Texas isolates are virulent on corn with *Ht*N and, thus, constitute a previously undescribed race of *E. turcicum*. In other

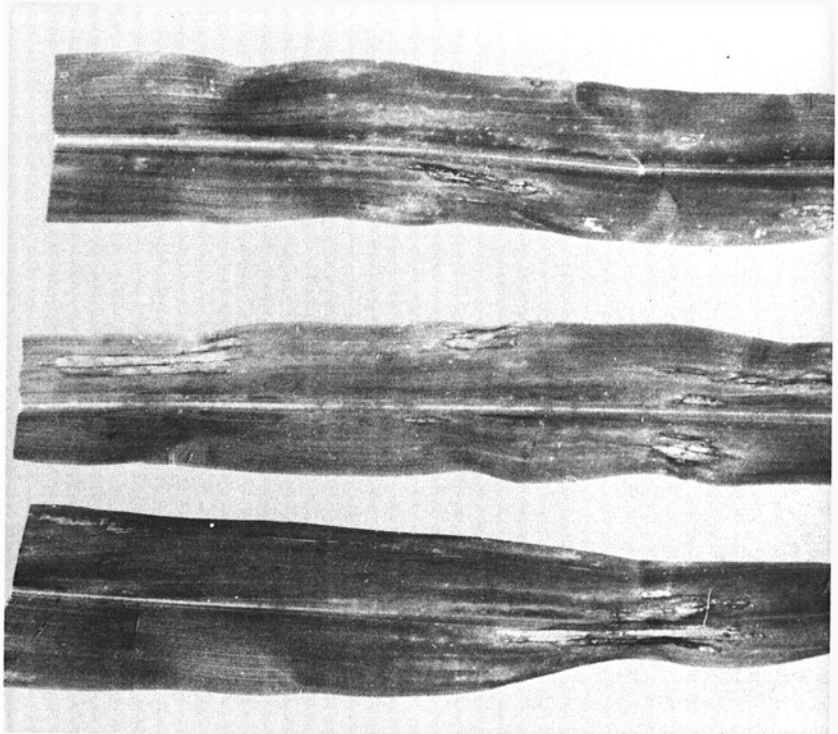

Fig. 2. Disease reactions of corn inbred B37*Ht*3 to race 3 (top leaf) and race 4 (middle and lower leaves) of *Exserohilum turcicum*. Corn plants were grown at 22 C day/18 C night temperatures with full light (647 $\mu E \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux density). The lesions are typical of intermediate types of lesions that often formed on B37*Ht*3 plants grown at full light intensity. At reduced light intensity, lesions of races 3 and 4 on B37*Ht*3 were more typically susceptible type.

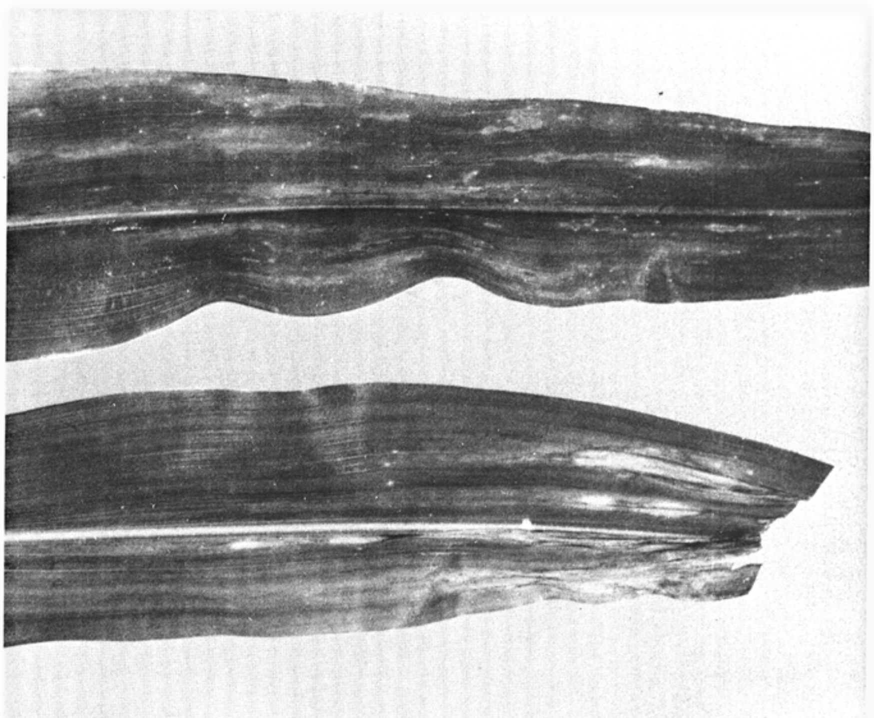

Fig. 3. Disease reactions of corn inbred B37*Ht*N to race 4 of *Exserohilum turcicum* on plants grown at 26 C day/22 C night temperatures. Under these conditions, B37*Ht*N segregated for reaction type to race 4. Some plants developed only resistant-type lesions (top leaf), and some developed only susceptible-type lesions (lower leaf). The lesions appeared within 10 days after inoculation. Races 1 and 3 induced resistant-type lesions on B37*Ht*N similar to those shown in the upper leaf on plants grown at 22 C day/18 C night temperatures as well as 26 C day/22 C night, whereas race 4 induced susceptible-type lesions on all B37*Ht*N plants at 22 C day/18 C night.

experiments (Thakur and Leonard, *unpublished*), we determined that the new race, like race 3, is avirulent on corn inbreds H4460*Ht*1 and B37*Ht*1. Therefore, we now designate isolates 2-5 and 2-11 from Texas as race 4 with the virulence formula *Ht*1/*Ht*2,*Ht*3,*Ht*N.

Gevers (2) reported that *Ht*N appeared to be ineffective against *E. turcicum* in tests conducted in India. He suggested that biotypes capable of overcoming the resistance conferred by *Ht*N may be present in India. The natural occurrence of race 4 in Texas before the commercial use of corn hybrids with *Ht*N makes Gever's hypothesis seem quite likely.

Resistant-type lesions have not been reported previously for corn genotypes with *Ht*N. Instead, according to Gevers (2), plants with *Ht*N usually remain free of lesions, although in some genetic backgrounds a few susceptible-type lesions may eventually appear on the lower leaves. Others (3,9) described the resistance of *Ht*N as resistance that extends the latent period for the development of susceptible-type lesions. This increased latent period varies for different genetic backgrounds, but in B37 the resistance of *Ht*N was effective enough to completely prevent disease development in inoculated field plots (9). Under the conditions of our experiments in controlled environment chambers, race 1 and race 3 induced numerous chlorotic streaks on B37*Ht*N plants similar to those shown in Figure 3. These streaks were small and less conspicuous than the chlorotic lesions that appeared on B37*Ht*2 or B37*Ht*3 plants inoculated with race 1. We did not observe any susceptible-type lesions on lower leaves of B37*Ht*N inoculated with race 1 or race 3, but because we discarded the plants 15 days after inoculation, lesions with extended latent periods would not have had time to be expressed.

Our data suggest that a second gene for resistance is present in B37*Ht*N. The source of B37*Ht*N provided to us by W. L. Pedersen segregated for reaction to race 4 in the high temperature treatment. The number of segregating plants in our test was too small to provide good estimates of the segregation ratio, but it seems likely that the segregation was due to a single gene for resistance that was not expressed at 22 C day/18 C night temperatures. Pedersen et al (8) indicated that B37*Ht*N segregated for reaction to race 2 in field plots in Pennsylvania, but it is not clear whether the phenomenon that they reported is connected with our observation of segregation for reaction type at high temperatures.

Our results confirm the conclusion of Leath et al (6) that the resistance of *Ht*2 breaks down at low light intensities. This loss of resistance to race 1 of *E. turcicum* has now been demonstrated for *Ht*2 in two genetic backgrounds, H4460 (6) and B37. Shading of lower leaves of corn plants might cause a similar breakdown of the *Ht*2 resistance in the field. This may account for the observation of Pataky et al (7) that *Ht*2 failed to retard epidemics of races 1 and 2 in field plots; the epidemics in hybrids with *Ht*2 were not significantly less severe than those in the same hybrids without *Ht*2.

Our results also confirm the observation of Leath et al (6) that the virulence of isolate R3SC to plants with *Ht*3 is not effective at high temperatures. This was

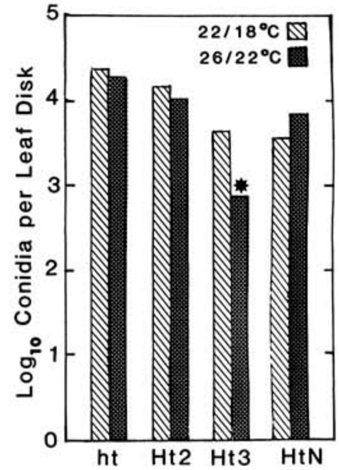

Fig. 4. Sporulation by *Exserohilum turcicum* races 3 and 4 on leaf disks taken from lesions on seedlings of corn inbred B37 and backcross lines of B37 with *Ht*2, *Ht*3, and *Ht*N grown under full light intensity at 22 C day/18 C night or 26 C day/22 C night temperatures. Values are means of three isolates, one of race 3 and two of race 4, except that values for B37*Ht*N are means of only the two race 4 isolates, which are virulent on B37*Ht*N. The * indicates a significant difference ($P < 0.05$) for the two temperature treatments.

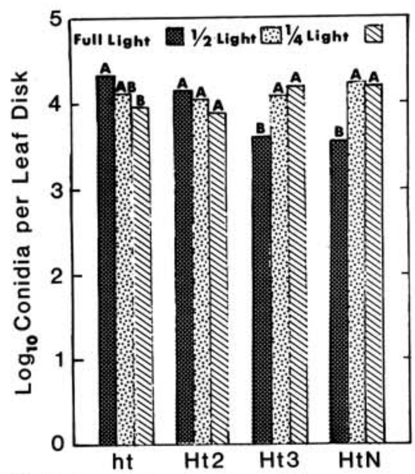

Fig. 5. Sporulation by *Exserohilum turcicum* races 3 and 4 on leaf disks taken from lesions on seedlings of corn inbred B37 and backcross lines of B37 with *Ht*2, *Ht*3, and *Ht*N grown at 22 C day/18 C night temperatures with full, one-half, and one-fourth light intensities (647, 324, and 162 $\mu E \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux density, respectively). Values are means of three isolates, one of race 3 and two of race 4, except that values for B37*Ht*N are means of only the two race 4 isolates, which are virulent on B37*Ht*N. Within inbred lines, means for different light intensities that are indicated by the same letter are not significantly different ($P < 0.05$).

Table 2. Analysis of variance of sporulation by isolates R3SC, 2-5, and 2-11 of *Exserohilum turcicum* on corn inbred line B37 and backcross lines of B37 with the *Ht*2, *Ht*3, or *Ht*N genes for resistance at 26 C day/22 C night and 22 C day/18 C night temperature treatments with full light intensity

Source	df	Sum of squares	F
Replicates	3	3.35	3.13*[a]
Inbred lines	3	16.29	15.22**
Isolates	2	1.20	1.68
Temperature	1	1.92	5.37*
Lines × isolates	6	1.81	0.85
Lines × temperature	3	2.03	1.89
Isolates × temperature	2	0.16	0.22
Lines × isolates × temperature	6	7.16	3.34**
Error	66	23.55	

[a] * = Significant at $P < 0.05$, ** = significant at $P < 0.01$.

Table 3. Analysis of variance of sporulation by isolates R3SC, 2-5, and 2-11 of *Exserohilum turcicum* on corn inbred line B37 and backcross lines of B37 with the *Ht*2, *Ht*3, or *Ht*N genes for resistance at normal and reduced light intensity in a 22 C day/18 C night temperature regime

Source	df	Sum of squares	F
Replicates	3	0.16	0.49
Inbred lines	3	0.50	1.54
Isolates	2	0.49	2.26
Light	2	0.17	0.79
Lines × isolates	6	1.41	2.17
Lines × light	6	3.45	5.31**[a]
Isolates × light	4	0.17	0.40
Lines × isolates × light	12	2.05	1.58
Error	96	10.38	

[a] ** = Significant at $P < 0.01$.

more apparent in our study with *Ht*3 in the B37 background than in the study of Leath et al with *Ht*3 in H4460. Leath et al (6) found that race 3 was able to induce some intermediate-type lesions on H4460*Ht*3 at 26 C day/22 C night temperatures, but we observed only resistant-type lesions on B37*Ht*3 at 26 C day/22 C night.

Results of the sporulation analyses confirm the susceptibility or moderate susceptibility of B37*Ht*2 and B37*Ht*3 to races 3 and 4 of *E. turcicum* and the susceptibility of B37*Ht*N to race 4 at 22 C day/18 C night temperatures. Although the pathogen sporulated well in these lesions that were designated susceptible types, the level of sporulation was sometimes less than that on B37. The moderately reduced sporulation of races 3 and 4 on B37*Ht*3 and race 4 on B37*Ht*N under full light intensity at 22 C day/18 C night temperatures could be due to residual effects of the defeated genes for resistance, or the differences may be due to the presence of linked genes for low levels of quantitative resistance. Both possibilities were considered by Leath and Pedersen (4,5) for apparent residual effects of *Ht*1 against race 1 of *E. turcicum*. They pointed out that it is difficult to rule out effects of closely linked genes for quantitative resistance even in near-isogenic lines derived from a series of up to six backcrosses.

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