Partial Resistance to Northern Leaf Blight and Stewart's Wilt in Sweet Corn Germ Plasm

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ABSTRACT

Meyer, A. C., Pataky, J. K., and Juvik, J. A. 1991. Partial resistance to northern leaf blight and Stewart's wilt in sweet corn germ plasm. Plant Dis. 75:1094-1097.

Sources of partial resistance to northern leaf blight (NLB) and Stewart's wilt were identified in sweet corn germ plasm. Inbreds that were classified resistant to NLB in evaluations from 1988 to 1990 included IL545a, IL611a, IL676a, IL677a, IL685d, IL731a, and IL797a. Inbreds that were classified resistant to Stewart's wilt in both 1988 and 1989 included IL126b, IL676a, IL766a, IL772a, IL772b, IL776a, and IL797a. Inbred lines with IL677a in their pedigree tended to be more resistant to NLB and Stewart's wilt than the populations of inbreds evaluated for these two diseases. Frequency distributions of z-scores for the populations and for inbreds with IL677a in their pedigree were different when compared by chi-square contingency tests. Thus, the resistance in IL677a appears to be inherited relatively easily.

Additional keywords: Erwinia stewartii, Exserohilum turcicum, Zea mays

Northern leaf blight (NLB), caused by Exserohilum turcicum (Pass.) K. J. Leonard & E. G. Suggs, and Stewart's wilt, caused by Erwinia stewartii (E. F. Smith) Dye, are endemic in many areas of the United States where sweet corn (Zea mays L.) is grown. Epidemics of NLB on sweet corn are frequent in the spring in Florida and also occur in the summer in upstate New York and in the northern corn belt (northern Illinois, Wisconsin, and Minnesota). Stewart's wilt is prevalent on sweet corn grown in Delaware, Maryland, New Jersey, Pennsylvania, and the Ohio River Valley. Epidemics have also occurred recently in upstate New York (4) and Ontario, Canada (1). Stewart's wilt and NLB can substantially reduce yield and quality of susceptible and moderately susceptible sweet corn hybrids (16,20,21).

Host resistance provides the most efficient and effective control of NLB and Stewart's wilt. Reactions of maize genotypes to these pathogens range from resistant to susceptible, the two extremes of a continuum that is measured by the ability of the host to reduce the growth, reproduction, and/or disease-producing abilities of the pathogen. Reactions of sweet corn hybrids to *E. turcicum* and *E. stewartii* vary from highly resistant

Research supported by the Illinois Agricultural Experiment Station, University of Illinois, Urbana, as part of project 68-0323 and by the United States-Israel Binational Agricultural Research and Development Fund (BARD), project US 1213-86.

Accepted for publication 25 April 1991 (submitted for electronic processing).

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to highly susceptible (13-16). Even though single dominant genes for resistance (i.e., *Ht* genes) and partial resistance exist in some sweet corn hybrids, many popular hybrids with good agronomic characteristics are highly susceptible to both diseases. Thus, additional sources of partial resistance to NLB and Stewart's wilt need to be identified in sweet corn germ plasm.

Sources of highly heritable partial resistance to NLB (8) and single dominant Ht genes for resistance to NLB (7) occur in dent corn. Widespread use of the gene Htl applied selection pressure on the pathogen population resulting in an increased frequency of biotypes that were virulent against that resistance (19,22). Consequently, the effectiveness of the gene Htl has been greatly diminished. Resistance to Stewart's wilt is dominant, controlled by relatively few genes, and highly heritable (18). Specific virulence against sources of resistance to Stewart's wilt has not been reported.

By using sources of resistance from sweet corn rather than from dent corn, the important quality characteristics of sweet corn can be more easily maintained when incorporating resistance into elite germ plasm. This paper reports on sources of partial resistance to NLB and Stewart's wilt from sweet corn germ plasm.

MATERIALS AND METHODS

Sweet corn germ plasm was evaluated for reactions to NLB and Stewart's wilt in Urbana, IL. Germ plasm evaluated consisted primarily of inbred lines developed in the sweet corn breeding program at the University of Illinois, other elite public inbreds, and seven com-

mercial hybrids used as standards in the Illinois sweet corn hybrid disease nursery (16). The inbreds included three endosperm types, sul, sulse, and sh2. A total of 202 different inbreds were evaluated for reaction to NLB: 139 in 1988, 182 in 1989, and 116 in 1990. A total of 191 different inbreds were evaluated for reaction to Stewart's wilt: 141 in 1988 and 167 in 1989. The Stewart's wilt evaluation in 1990 was flooded. A complete listing of the materials evaluated in all five trials and their reactions to NLB or Stewart's wilt can be obtained from the second author.

Planting dates were 17 May 1988, 17 May 1989, and 31 May 1990. Stewart's wilt and NLB were evaluated in separate experiments. Inbreds were arranged in a randomized complete block design with three replications. Each experimental unit consisted of a single row of a specific inbred. Rows were 76.5 cm apart, 3 m long, and contained approximately 16 plants.

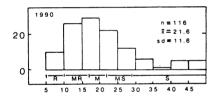
Plants were inoculated with E. turcicum or E. stewartii at the three- to fourleaf stage. Races 0 and 1 of E. turcicum, formerly designated race 1 and 2, respectively (10), were isolated originally from corn grown in central Illinois and were mixed 1:1 in a suspension of approximately 10³ conidia per milliliter and sprayed into the whorls on 14 and 29 June 1988, 20 June 1989, and 25 June and 2 and 9 July 1990. Plants were inoculated with E. turcicum more than once to ensure adequate infection. Inoculum was produced by culturing E. turcicum on lactose-casein hydrolysate agar at room temperature for 2-3 wk. Cultures were flooded with tap water, ground in a blender, and filtered through several layers of cheesecloth. Plants were inoculated with E. stewartii on 13 June 1988 and 21 and 30 July 1989 using the pinprick method (2,3). Inoculum was produced as described previously (16,20).

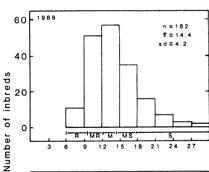
Reactions to NLB were assessed on 10 August 1988, 18 July and 1 August 1989, and 10 August 1990. Severity of NLB was estimated visually for each row as the percentage of the total leaf area infected using the standard diagram of Elliott and Jenkins (5), which was modified to include additional classes (13-15). For Stewart's wilt, a scale of 1-9, as illustrated and described by Suparyono and Pataky (20), was used to rate individual plants in each row. Ratings

for Stewart's wilt were then calculated as the mean of all plants per row. Stewart's wilt was assessed on 13 July 1988 and 8 and 26 June 1989.

Data were analyzed by ANOVA. Waller-Duncan Bayesian least significant difference (BLSD) values with K=100 were used to compare inbreds. Grand means and standard deviations were calculated from all inbreds tested each year. Standardized z-scores were calculated for each disease rating of each inbred as: $z_i = (\bar{x}_i - \bar{x})/SD$, where $z_i =$ the z-score of the *i*th inbred, $\bar{x}_i =$ the mean rating of the *i*th inbred over replications, $\bar{x} =$ grand mean rating for all inbreds in a trial, and SD = the standard deviation for all inbreds in a trial.

In each year, inbreds were classified as resistant (R), moderately resistant (MR), moderate (M), moderately susceptible (MS), or susceptible (S) according to a categorization procedure using BLSD separations and z-scores as described by Pataky et al (16). In general, z-scores of inbreds classified R were less than -0.75, and those of inbreds classified S were greater than 0.75. Z-scores of inbreds classified MR, M, and MS generally ranged from -0.25 to -0.75, -0.25 to 0.25, and 0.25 to 0.75, respectively.





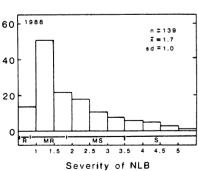


Fig. 1. Frequency distributions of inbreds for reactions to northern leaf blight (NLB) in 1988, 1989, and 1990, where n = number of genotypes sampled, $\bar{x} = sample$ mean, and SD = standard deviation. Classifications indicated are: R = resistant, MR = moderately resistant, M = moderate, MS = moderately susceptible, and S = susceptible.

Ratings and ranks of inbreds were correlated for each disease within and among years. Frequency distributions of inbreds based on z-scores for NLB and Stewart's wilt were developed for the entire population sampled and for inbreds with IL677a in their pedigree. Frequency distributions were compared by chi-square contingency tests. Frequency distributions were compared based on z-scores because the range and standard deviations of disease severity differed among years, whereas z-scores were standardized based on means and standard deviations within years.

RESULTS

Reactions to NLB. Severity of NLB ranged from 0 to 6% in 1988, 7 to 34% in 1989, and 6 to 68% in 1990. The range of severity was small in 1988 because of the lack of secondary infection during a drought. Mean severity of NLB in 1988, 1989, and 1990 was 1.7, 14.4, and 21.6%, respectively, and standard deviations were 1.0, 4.2, and 11.6, respectively (Fig. 1).

Parameters for classifying inbreds as R. MR. M. MS, and S differed among years primarily because of the extent of secondary infection. Based on multiple comparison tests and z-scores, inbreds were classified resistant when severity was less than 10% in 1989 and 1990, and inbreds were classified susceptible when severity was greater than 18 and 29% in 1989 and 1990, respectively (Fig. 1). Secondary infection was adequate in these years. In 1988, inbreds were classified resistant when severity was less than 0.8%, and inbreds were classified susceptible when severity was greater than 3.5%. Evaluations in 1988 were based principally on primary infection resulting from inoculation.

Inbreds classified resistant to NLB included IL545a, IL611a, IL676a, IL677a, IL685d, IL731a, and IL797a (Table 1).

IL685d was the most resistant in each year; however, it also was extremely late in maturity. Inbreds classified resistant in at least 1 yr included IL11d, IL442a, IL753a, IL757c, IL766a, IL767a, IL772a, IL791a, IL793a, and IL799b (Table 1). Inbreds that were consistently classified susceptible to NLB and may be useful as susceptible testers included FA56a, IL104g, IL439a, IL543c, IL665a, I453, I5125, and Ma83608b.

Correlations of severity of NLB among years were significant and were 0.52 for 1988 and 1989, 0.67 for 1989 and 1990, and 0.31 for 1988 and 1990. Rank correlations among years were also significant and were 0.49 for 1988 and 1989, 0.54 for 1989 and 1990, and 0.32 for 1988 and 1990.

Reactions to Stewart's wilt. Ratings for Stewart's wilt ranged from 1.25 to 8.75 in 1988 and from 1.52 to 5.42 in 1989. The mean rating of Stewart's wilt was 3.2 for both years. Standard deviations were 1.3 and 0.64 for 1988 and 1989, respectively (Fig. 2). Based on multiple comparison tests and z-scores, inbreds rated below 2.1 and 2.5 were classified as resistant in 1988 and 1989, respectively. Inbreds rated above 4.3 and 4.0 were classified susceptible in 1988 and 1989, respectively.

Inbreds classified resistant to Stewart's wilt in both years included IL126b, IL676a, IL766a, IL772a, IL772b, IL776a, and IL797a (Table 2). IL797a was most resistant in both years. Inbreds classified resistant in 1 yr included IL515a, IL685d, IL731a, IL767a, IL769a, IL777a, IL796a, and IL798a (Table 2). Inbreds consistently classified susceptible included IL18b, IL103a, IL110g, IL393a, IL648a, IL665a, IL673a, IL689a, IL729a, IL733a, IL775a, and P39.

The correlation of Stewart's wilt ratings between years was significant (r = 0.62). The rank correlation between years also was significant (r = 0.58).

Table 1. Inbreds classified resistant to northern leaf blight and their pedigrees

Inbred	Pedigree
Resistant in all y	rears
IL545a	$(IL11d \times P8) \times IL11d) \times IL112d$
IL611a	$(IL101t \times IL112f) \times$ open-pollinated yellow
IL676a	$(IL176a \times IL21f) \times IL325a$
IL677a	$(IL44b \times Bolivian 1035) \times IL442a$
IL685d	Self from Puerto Rican sweet
IL731a	(Golden Sensation \times IL637a \times Comp ²) \times IL677a
IL797a	$(IL304a \times IL677a) \times [(IL751a \times IL752a) \times Pa405]$
Resistant in at le	east 1 yr
IL11d	Self from open-pollinated Narrow Grain Evergreen
IL442a	$(W23 \times IL104q) \times IL104q) \times IL104c$
IL753a	$(T35 \times IL677a) \times IL677a$
IL757c	(IL14 × IL11) × Antiqua 2D
IL766a	$IL677a \times (T35 \times IL677a)$
IL767a	$IL197a \times (IL197a \times IL677a)$
IL772a	$(IL676a \times P245) \times IL11a) \times IL677a$
IL791a	$IL677a \times IL18c$
IL793a	$(IL751a \times IL752a) \times Pa405$
IL799b	(Gold Cup \times Pa405) \times {[(Hawaiian Sugar \times IL110g) \times (T35 \times
	$[L677a] \times (IL459 \times IL677a)$

² Comp = IL11a, IL27a, IL112x, IL465a, IL552a, and Y82.

Correlations between NLB and Stewart's wilt. Correlation coefficients were calculated for NLB and Stewart's wilt ratings and rankings of inbreds within and between years. The correlation between severity of NLB in 1989 and ratings of Stewart's wilt in 1989 was significant (r = 0.57), as was the correlation between NLB in 1989 and Stewart's wilt in 1988 (r = 0.45). Other correlations between NLB and Stewart's wilt were not significant. Rank correlations between NLB in 1988 and Stewart's wilt in 1989 (r =0.26), NLB in 1989 and Stewart's wilt in 1988 (r = 0.56), NLB in 1989 and Stewart's wilt in 1989 (r = 0.54), and NLB in 1990 and Stewart's wilt in 1989 (r = 0.29) were significant.

Progeny from crosses with IL677a. Inbred lines with 1L677a in their pedigree tended to be more resistant to NLB and Stewart's wilt than the population of inbreds evaluated for NLB in 1989 and 1990 and that evaluated for Stewart's wilt in 1988 and 1989. Frequency distributions of z-scores of NLB and Stewart's wilt for the entire population and for progeny from crosses with IL677a differed significantly based on chi-square contingency tests (Figs. 3 and 4). Chisquare values for the comparison of the entire population and inbreds with IL677a in their pedigree were 13.6 and

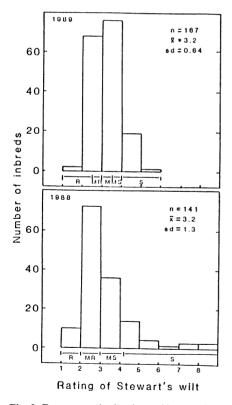


Fig. 2. Frequency distributions of inbreds for reactions to Stewart's wilt in 1988 and 1989, where n = number of genotypes sampled, $\bar{x} = \text{sample mean}$, and SD = standard deviation. Classifications indicated are: R = resistant, MR = moderately resistant, M = moderate, MS = moderately susceptible, and S = susceptible.

23.2 for NLB and for Stewart's wilt, respectively.

DISCUSSION

Additional sources of partial resistance to NLB and Stewart's wilt were identified in sweet corn inbreds developed at the University of Illinois. These sources of resistance can be used in breeding programs to improve disease resistance in sweet corn with less deleterious effects on marketable quality than sources of resistance from dent corn.

The pedigrees of resistant inbreds often had common ancestors, such as IL11d. IL11d is an inbred that was selfed from an open-pollinated population of Narrow Grain Evergreen (17). Narrow Grain Evergreen is also in the pedigrees

of IL515a, IL442a, IL676a, and IL677a, which were classified resistant to NLB and/or Stewart's wilt.

IL677a, a common ancestor of many of the inbreds resistant to NLB and Stewart's wilt, is the source of the sugary enhancer (se) gene (6). Partial resistance from IL677a appears to be highly heritable, because most of the resistant inbreds that have IL677a in their pedigrees were not selected for disease resistance. Similarly, many commercial se hybrids that are related to IL677a (e.g., Merlin, Miracle, Seneca Sentry, Sugar Buns. Tuxedo, etc.) are partially resistant to NLB and/or Stewart's wilt even though there was little selection for disease resistance in the development of these hybrids. Thus, IL677a may be an extremely useful source of resistance.

Table 2. Inbreds classified resistant to Stewart's wilt and their pedigrees

Inbred	Pedigree	
Resistant in bot	h years	
IL126b	$(IL11d \times KY corn borer) \times IL11d$	
IL676a	$(IL176a \times IL21f) \times IL325a$	
IL766a	$L677a \times (T35 \times IL677a)$	
IL772a	$(IL676a \times P245) \times IL11a) \times IL677a$	
IL772b	$(IL676a \times P245) \times IL11a) \times IL677a$	
IL776a	$(IL14 \times IL11) \times Argentine) \times IL677a$	
IL797a	$(IL304a \times IL677a) \times [(IL751a \times IL752a) \times Pa405]$	
Resistant in 1 yr	, , , , , , , , , , , , , , , , , , , ,	
IL515a	$(IL103h \times IL86e) \times IL103b$	
IL685d	Self from Puerto Rican sweet	
IL731a	(Golden Sensation \times IL637a) \times Comp ^z) \times IL677a	
IL767a	$IL197a \times (IL197a \times IL677a)$	
IL769a	$(T32 \times IL677a) \times IL451b) \times IL677a$	
IL777a	$1L27a \times IL677a$	
IL796a	$(IL677a \times IL702a) \times [(IL751a \times IL752a) \times Pa405]$	
IL798a	(Gold Cup \times Pa405) \times IL677a	

² Comp = IL11a, IL27a, IL112x, IL465a, IL552a, and Y82.

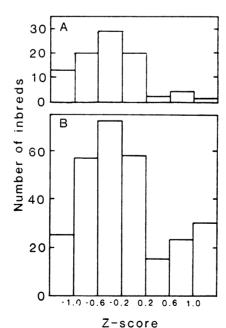


Fig. 3. Frequency distributions of (A) inbreds with IL677a in their pedigree and (B) all inbreds evaluated based on z-scores of reactions to northern leaf blight. The chisquare value for the comparison of these two distributions was 13.6.

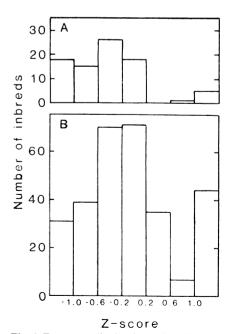


Fig. 4. Frequency distributions of (A) inbreds with IL677a in their pedigree and (B) all inbreds evaluated based on z-scores of reactions to Stewart's wilt. The chi-square value for the comparison of these two distributions was 23.2.

IL677a also appears to convey highly heritable, partial resistance to common rust caused by Puccinia sorghi Schwein. (12). Three inbreds, IL766a, IL767a, and IL772a, classified resistant to NLB and Stewart's wilt in this trial, had been identified previously as sources of partial resistance to common rust (12). In crosses of IL677a with IL442b and AA8, Kim and Brewbaker (9) observed that the partial resistance to P. sorghi in IL677a was controlled by a single recessive gene, designated rp-677a. Many of the se hybrids related to IL677a also have relatively high levels of partial resistance to common rust (14-16).

Elite inbreds used in some breeding programs, such as FA56a, I453, I2256a, I5125, and P39, were rated susceptible to NLB. This indicates the need for sources of partial resistance from sweet corn that can be used to improve resistance to NLB and Stewart's wilt while maintaining quality and agronomic characteristics.

Positive correlations between severity of NLB and ratings of Stewart's wilt have been reported previously (11,16). In this study, those correlations were not as strong possibly because the inbreds selected for evaluation in 1989 and 1990 primarily were those displaying some resistance in the previous year. Thus, the range of response to each disease decreased in each year. Even though some inbreds were resistant to NLB and Stewart's wilt, only a few inbreds had a high level of resistance to both diseases. Therefore, separate factors may condition resistance to each disease. Thus, it is important in a breeding program to

select for resistance to both NLB and Stewart's wilt.

ACKNOWLEDGMENTS

We thank John Gantz for technical assistance and Don Elliott and Jim Poppe for information about pedigrees of Illinois sweet corn inbreds.

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