Relationship Between Leaf Freckles and Wilt Severity and Yield Losses in Closely Related Maize Hybrids

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ABSTRACT

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The relationship between severity of leaf freckles and wilt, caused by *Clavibacter michiganense* subsp. *nebraskense*, and the percentage of grain yield loss was examined in a set of 42 closely related maize hybrids. Forty-two sister inbred lines, derived from a modified backcrossing program that used the inbred A632 as the recurrent parent, were crossed to A619. The resulting hybrids were evaluated over 2 yr in a split-plot field experiment with hybrids as whole plots and inoculated vs. uninoculated treatments as split plots. The hybrids varied widely in reaction to leaf freckles and wilt and in yield loss sustained from the disease. The percentages of yield loss were significantly correlated with disease severities in both years and in the combined analysis. Several hybrids had high disease severity but sustained insignificant yield loss compared with susceptible hybrids, indicating possible leaf freckles and wilt tolerance. However, when a more rigorous test of tolerance that used studentized residuals from the loss-severity regression was applied to the data, tolerance appeared to be an unstable character. Resistance to leaf freckles and wilt was not related to poor grain yield in the absence of disease.

Additional keywords: corn, Goss's wilt, *Zea mays*.

Leaf freckles and wilt, also known as Goss's wilt, is caused by the bacterium *Clavibacter michiganense* subsp. *nebraskense* (= *Corynebacterium michiganense* subsp. *nebraskense*) and is a relatively new and potentially destructive disease of maize (*Zea mays* L.) in the United States (15,16,20). First recognized in Nebraska in the late 1960s, leaf freckles and wilt has since been found in Colorado, Kansas, Iowa, South Dakota, and Illinois (20). Leaf freckles and wilt has caused grain yield losses of up to 44% in a susceptible hybrid in a controlled test (6). Although yield losses attributable to the disease were significantly correlated with disease severity ratings, not all hybrids with high foliar disease ratings sustained significant losses, and some hybrids with low disease ratings had significant losses. Susceptible sweet maize hybrids sustained primary ear weight losses in excess of 17% in 2 yr of a 3-yr yield loss assessment study (12). In a separate study, leaf freckles and wilt reduced the total ear weight of a susceptible sweet maize hybrid by 99% when inoculated at the three- to five-leaf stage (19).

Resistance is the primary means of controlling leaf freckles and wilt. Maize inbred lines and hybrids vary in reaction from resistant to highly susceptible, although no maize genotype is considered immune (3,15–17,20). Reaction of maize to artificial inoculation with *C. m. nebraskense* depends on plant age at inoculation and inoculum concentration (5,19). Diallel analyses of the inheritance of disease resistance in maize inbred lines indicate that more than one gene is probably involved and that reactions of F_1 hybrids tend to be either intermediate between parental reactions or approach that of the more susceptible parent (7,10). Generation mean analyses of segregating populations indicate that resistance to leaf freckles and wilt is highly heritable, mostly additive gene action is involved, and estimates of gene numbers involved vary from two to five, depending on the F_2 population studied (9,10).

The objectives of our study were to determine the relationship between leaf freckles and wilt severity and yield losses in a set of closely related F_1 hybrids with varying levels of disease resistance, determine the effectiveness of resistance in reducing losses, and determine if leaf freckles and wilt resistance and combining ability for grain yield can be successfully combined.

MATERIALS AND METHODS

Forty-two A632-type maize inbred lines were developed from germ plasm from a modified backcross breeding program initially designed to incorporate resistance to Stewart's bacterial wilt (caused by *Erwinia stewartii*) into an A632 inbred line background (initial seed obtained courtesy of W. L. Pedersen, University of Illinois). Because resistance to leaf freckles and wilt and Stewart's bacterial wilt is highly correlated (11,12), it was expected that this germ plasm also had some resistance to leaf freckles and wilt. Because the initial germ plasm was a bulk of selected ears from different backcross programs using different nonrecurrent (donor) parents, the exact source(s) of disease resistance in the lines is uncertain. Donor parents included Mo5Rf, RWf9Ht, ROh07Ht, Pa70, Pa83, Pa419P, Pa887P, and R109BR^{+}sel. Because the number of backcrosses to the A632 recurrent parent varied among the material contained in this initial bulk, the exact degree of relatedness of any particular line to A632 is unknown; however, all of the lines had at least 93% of the alleles of (i.e., were backcrossed at least three times) and phenotypically resembled A632. Some selection for leaf freckles and wilt resistance and the A632 phenotype was practiced in the last backcross generation. These lines were crossed to the susceptible inbred line A619 to produce F_1 hybrid seed for evaluation. The resultant 42 hybrids and the susceptible check hybrid A632 × A619 were planted in a split-plot arrangement of hybrids (whole plots) and leaf freckles and wilt inoculated vs. uninoculated treatments (split plots) in a randomized complete block design with three replications in 1985 (20 May) and 1986 (17 May) on the Plant Science research farms near Brookings, SD. Experimental units (split plots) consisted of single rows 6.1 m long and 0.9 m apart with 40 seeds planted per row. Plots were later thinned to a stand of 49,000 plants per hectare (27 plants per row).

A pinprick inoculation technique (2,4) was used to inoculate plants in inoculated rows twice at the four- to six- and eight- to 10-leaf stages with a bacterial suspension of approximately 10^8 colony-forming units (cfu) per milliliter. Inoculum was prepared by scraping colonies of *C. m. nebraskense* grown for 72 hr on nutrient broth-yeast extract (NBY) agar plates at 30 C, suspending them in 0.1 M NaCl buffer, and adjusting the resulting cell suspension to the final concentration with the aid of a calibrated Spectronic 20 spectrophotometer. A mixture of four isolates (Yankton, BonHomme, LFW11, and LFW12) was used in both inoculations.

Disease severity was estimated by rating 10 random plants in each plot at the midtassel growth stage. A 1–9 severity scale was used where 1 = no symptoms, 2 = slight wilting around pinprick wounds, 3 = extensive wilting and necrosis around the inoculation sites, 4 = spread of wilting from the inoculation site along leaf veins, 5 = wilt and blighting from inoculation sites to leaf tips, 6 = severe wilting and blighting of entire inoculated leaves, 7 = spread of symptoms to uninoculated leaves, 8 = plant visibly stunted, and 9 = entire plant wilted or dead. Although plots were observed throughout the growing seasons, no spread of leaf freckles and wilt to uninoculated plots was observed.

Plots were hand-harvested after physiological maturity, ears were weighed, and the percentage of grain moisture was determined. Grain yields were converted to megagram per hectare at 15.5% grain moisture basis.

The resulting yield and disease severity data were analyzed by analysis of variance. Disease ratings were analyzed as a randomized complete block with the use of data only from inoculated plots because no disease was observed in uninoculated plots. Yield data were analyzed as a split-plot arrangement in a randomized complete block design within years. Because there was a small but significant hybrid × year interaction in leaf freckles and wilt ratings, the hybrid × year error term in the analysis of variance (ANOVA) was used in testing for differences among hybrids across years. There was no significant hybrid × year interaction effect on grain yields, and the appropriate error terms were used to calculate LSD statistics to compare yields of inoculated vs. uninoculated plots of the same hybrids, to compare differences in yield losses (inoculated vs. uninoculated) between hybrids, and to compare yield differences between hybrids in uninoculated plots. Regression analysis was also performed to determine the relationship between the percentage of yield loss and disease ratings. Studentized residuals (with the current observation deleted from the calculation of the standard error; sometimes referred to as jackknifed residuals) from the regressions were examined to find any hybrids that did not fit the yield loss-disease severity regression model (1). These analyses were conducted on individual year data to determine if any observed significant deviations from the models were consistent between years. We were especially interested in those hybrids that sustained lower yield losses than would be predicted from their leaf freckles and wilt severity, i.e., appeared disease tolerant. Regressions between disease severities and yields of uninoculated plots and among studentized residuals from the yield loss-disease severity regressions and yields of uninoculated plots were also conducted.

RESULTS

Leaf freckles and wilt was successfully established in inoculated plots in both years with a mean rating of 4.82 and 4.39 in 1985 and 1986, respectively. Despite the genetic uniformity of the hybrids, considerable plant-to-plant variation in disease reaction was observed within each plot; hence, we decided to rate 10 plants individually in each plot rather than to attempt visual estimation of overall disease severity within each plot. Highly significant differences in hybrid disease severity ratings were observed in both years and in the combined data (Table 1). Despite a significant hybrid × year interaction in the combined ANOVA for disease ratings, the correlation among ratings for both years was highly significant ($r = 0.67$, $P < 0.01$). None of the experimental hybrids were significantly more susceptible than the A632 × A619 check hybrid, but 12 had significantly lower mean ratings of leaf freckles and wilt across years.

In the combined ANOVA over years, hybrid and hybrid × inoculation treatment effects on yield were significant ($P < 0.05$). The percentages of grain yield loss attributable to leaf freckles and wilt ranged from zero (actual estimates were negative) to 43.5%. Mean percent yield losses of 17 and 19% were measured in 1985 and 1986, respectively. No experimental hybrid suffered a significantly greater yield loss than the A632 × A619 check (Table 1). Correlations between disease ratings and the percentage of yield loss were significant ($P < 0.01$) in both years ($r = 0.65$ and 0.63 for 1985 and 1986, respectively) and in the combined analysis ($r = 0.65$). The correlation among hybrids in the percentage of yield loss among years was highly significant ($r = 0.68$, $P < 0.01$).

In 1985, two hybrids, 84369 and 84381, sustained yield losses that were significantly less than what would be predicted based on their disease ratings; that is, data from these hybrids resulted in studentized residuals from the regression of the percentage of yield loss on leaf freckles and wilt ratings that were less than −2, indicating that these hybrids did not fit the yield loss-severity relationship well (1). In 1986, only one hybrid, 84517, did not fit the yield loss-severity relationship. In the combined analysis, two hybrids, 84381 and 84517, had lower mean percent yield losses than could be explained by the regression of the percentage of yield loss on disease severity (Fig. 1). The correlation between studentized residuals from the yield loss-disease severity regressions and hybrid yields from uninoculated plots was nonsignificant in 1985 ($r = 0.23$, $P > 0.05$) but was highly significant in 1986 ($r = 0.45$, $P < 0.01$) and in the combined analysis ($r = 0.41$, $P < 0.01$). The regression between disease ratings and mean yields from uninoculated plots was not significant in 1985, 1986, or in the combined analysis ($r = 0.23$, 0.25, and 0.04, respectively).

DISCUSSION

Our estimates of grain yield losses attributable to leaf freckles and wilt are similar to those reported by Claflin et al (6). In their study, a maximum loss of 44% (1 yr of data) is similar to our maximum loss estimate of 43.5%. Unlike their study, however, our study attempted to measure losses in a closely related set of experimental hybrids differing in levels of resistance. While the A632-type inbred lines used in this study could not be considered "near isogenic" versions of A632, they closely resembled the recurrent parent in appearance and maturity. Likewise, the F_1 hybrids of these lines with A619 were nearly identical to the A632 × A619 check hybrid. Therefore, we feel confident that these hybrids allowed us to measure the effectiveness of resistance to leaf freckles and wilt in reducing yield losses as well as the relationship of resistance and yield potential in the absence of the disease, without the confounding effects of diverse genetic backgrounds, plant maturities, and plant morphologies (8,12).

The percentages of yield loss were significantly correlated to disease severity ratings, indicating that selection for low severity ratings should be effective in reducing losses to the disease. Based on the regression relationship between disease severity and the percentage of yield loss, a leaf freckles and wilt rating of two or less would be necessary to prevent substantial losses (Fig. 1). This indicates that the bacterium must spread from the inoculation site before any substantial losses will occur. It is likely that under moderate levels of natural infection, even modest levels of resistance may be adequate. Approximately 40% of the variation in the percentage of yield loss could be attributed to disease severity ratings, which indicates a substantial amount of the variability in yield loss for which we could not account.

Several hybrids sustained significantly lower yield losses when compared with hybrids with similar or nonsignificantly different disease ratings. If a cultivar sustaining a statistically significant lower yield loss than another cultivar having no significant difference in severity is accepted as a proper definition and test of disease tolerance (14,18), then several hybrids appeared tolerant relative to others in both years and in the combined analysis across years (Table 1). We feel, however, this approach to detecting disease tolerance is incorrect. Although significant differences in yield losses can be detected with a known level of confidence (probability of making a type I error), the probability that two mean leaf freckles and wilt severities are identical even though no significant difference between them was detected (the probability of a type II error) is not estimable when population parameters are unknown. Therefore, we chose an alternative approach to detect those hybrids that did not fit the yield loss-severity relationship because they sustained lower losses than would be expected, i.e., they appeared tolerant.

Any hybrid that had a studentized residual less than −2 from the loss-severity regression was considered tolerant (1). Based on this more rigorous test of tolerance, only two hybrids in 1985 and one in 1986 could be classified as tolerant. Because different hybrids were judged tolerant in each year, it appears that tolerance is sensitive to environmental fluctuations. Similar results have been reported by Roberts et al (13) working with the wheat-*Puccinia recondita* pathosystem, who found that the degree of tolerance of some cultivars depended on plant growth stage at the time of inoculation and was perhaps not a stable trait. For example, hybrid 84369 in our trials sustained only about a 4% loss despite a high disease rating in 1985 but suffered an approximate 20% loss in 1986 with a similar rating (Table 1). Hybrid 84381 appeared tolerant in 1985 with a high disease rating and no significant yield loss but in 1986 had a much lower rating and again no significant loss (Table 1). Part of the difficulties in our detection of tolerance could be attributed to a significant hybrid × year interaction effect on leaf freckles and wilt ratings. Also, our ratings are based on outward symptoms and may not fully reflect the levels of stress on infected plants. Because leaf freckles and wilt is a vascular disease, it is conceivable that infected plants may undergo internal moisture stress without exhibiting external symptoms. An additional problem is the high standard error for differences in yield losses between hybrids, making the detection of significant differences difficult.

Gaunt (8) has suggested several guidelines for identification

TABLE 1. Reactions of 42 closely related maize hybrids and the check hybrid A632 × A619 to leaf freckles and wilt caused by *Clavibacter michiganense* subsp. *nebraskense* and yield losses in a 2-yr field experiment at Brookings, SD

	1985				1986				Combined			
Hybrid	Disease rating (1–9)	Uninoculated yield (Mg/ha)	Yield loss[a] (Mg/ha)	Yield loss (%)	Disease rating (1–9)	Uninoculated yield (Mg/ha)	Yield loss (Mg/ha)	Yield loss (%)	Disease rating (1–9)	Uninoculated yield (Mg/ha)	Yield loss (Mg/ha)	Yield loss (%)
A632 × A619	5.63	8.84	1.78*	22.2	5.33	7.00	2.42**	34.6	5.48	7.52	2.10**	28.4
84315	4.40	8.93	1.58	16.8	4.70	7.31	1.62	22.2	4.55	8.12	1.56**	19.5
84321	5.87	7.99	2.96**	37.1	5.43	7.87	3.43**	43.5	5.65	7.93	3.20**	40.3
84327	3.25	8.47	1.67	19.7	4.27	7.15	1.44	20.2	3.76	7.81	1.56**	20.0
84337	5.10	6.76	0.91	13.5	4.80	5.24	0.36	6.8	4.95	6.00	0.64	10.2
84338	5.47	7.48	2.16**	28.9	5.20	6.51	1.99**	30.6	5.34	7.00	2.08**	29.8
84343	4.63	7.14	1.30	18.1	5.27	7.07	1.18	16.7	4.95	7.11	1.24*	17.4
84346	6.40	7.70	2.20**	28.6	4.63	7.15	2.00**	28.0	5.52	7.43	2.10**	28.3
84355	5.87	7.88	1.88**	23.9	4.63	7.96	2.80**	35.1	5.25	7.92	2.34**	29.5
84357	5.13	7.33	1.20	16.3	5.43	7.37	2.31**	31.3	5.28	7.35	1.76**	23.8
84361	5.40	7.56	1.46	19.3	6.33	7.06	2.90**	41.1	5.87	7.31	2.18**	30.2
84368	6.50	6.47	2.04**	31.6	5.60	7.22	2.75**	38.2	6.05	6.85	2.40**	34.9
84369	5.17	6.75	0.26	3.9	5.57	6.39	1.28	20.1	5.37	6.57	0.77	12.0
84370	5.63	7.24	2.46**	34.0	4.20	5.79	2.05**	35.6	4.92	6.52	2.26**	34.8
84374	5.40	6.96	0.58	8.3	4.97	6.91	0.76	11.0	5.19	6.94	0.67	9.7
84376	5.30	8.43	2.06**	33.9	4.43	6.95	2.38**	34.3	4.87	7.69	2.62**	34.1
84379	5.63	7.73	2.51**	32.5	5.53	7.40	3.07**	41.5	5.58	7.57	2.79**	37.0
84381	5.87	7.96	0.44	5.5	4.10	6.54	−0.21	−3.3	4.59	7.25	0.12	1.1
84385	5.13	7.20	1.69*	23.5	3.90	6.42	0.13	1.9	4.52	6.81	0.91	12.7
84397	6.00	6.30	2.30**	36.5	6.10	5.95	1.49	25.0	6.05	6.13	1.90**	30.8
84398	5.70	9.33	3.04**	32.6	5.03	6.64	1.57	23.6	5.37	7.99	2.31**	28.1
84410	4.77	7.03	0.67	9.6	4.73	6.62	0.65	9.8	4.75	6.83	0.66	9.7
84411	3.97	7.38	0.75	10.2	2.43	6.28	−0.14	−2.2	3.20	6.83	0.31	4.0
84412	2.47	8.00	0.28	3.2	3.20	7.18	0.73	10.2	2.84	7.99	0.51	6.7
84417	3.27	8.44	0.08	1.0	3.07	6.39	−0.14	−2.2	3.17	7.42	−0.03	−0.6
84418	4.03	7.68	1.37	17.9	4.77	7.13	2.09**	29.2	4.40	7.41	1.73**	23.6
84422	3.27	8.53	1.55	18.1	4.20	7.67	1.70*	22.2	3.74	8.10	1.63**	20.2
84428	5.00	7.22	2.06**	28.6	4.00	5.99	1.81*	30.2	4.50	6.61	1.94**	29.4
84429	5.50	6.01	1.19	19.9	2.77	4.37	−0.22	−5.0	4.14	5.19	0.49	7.5
84439	4.93	7.59	1.20	15.8	3.10	6.57	0.56	8.6	4.02	7.08	0.88	12.2
84440	2.30	7.03	0.82	11.6	1.97	6.23	0.45	7.2	2.14	6.63	0.64	9.4
84453	3.10	7.82	1.17	15.0	3.10	7.47	1.55	20.7	3.10	7.65	1.36**	17.9
84454	3.53	8.52	0.74	8.7	3.30	6.32	−0.06	−1.0	3.42	7.42	0.34	3.9
84463	5.20	6.02	1.16	19.2	4.77	5.62	0.09	1.5	4.99	5.82	0.63	10.4
84469	1.50	7.05	−0.10	−1.4	2.20	7.02	−0.01	−0.2	1.85	7.04	−0.06	−0.8
84487	5.07	7.94	1.56	19.7	3.47	6.51	0.71	10.9	4.27	7.23	1.14**	15.3
84494	4.90	7.50	2.42**	31.9	4.07	7.20	0.59	8.2	4.49	7.39	1.51**	20.1
84495	5.50	7.55	1.73*	22.9	6.07	6.20	1.46	23.5	5.76	6.88	1.60**	23.2
84517	5.17	6.49	0.70	10.8	5.20	6.20	−0.14	−2.3	5.19	6.35	0.28	4.3
94520	6.10	0.24	1.51	18.3	4.53	7.86	1.42	18.0	5.32	8.05	1.47**	18.2
84529	4.50	7.69	1.40	18.2	2.33	6.46	0.39	6.0	3.42	7.08	0.90	12.1
84536	4.67	8.07	1.10	13.6	4.43	6.63	0.49	7.3	4.55	7.35	0.80	10.5
84544	5.23	8.11	2.49**	30.7	5.67	7.83	2.05**	26.2	5.45	7.97	2.27**	28.5
LSD (0.05) (between hybrids)	1.47	1.71	2.22		1.40	1.58	2.33		1.32	1.14	1.53	

[a]* = yield loss significantly different from zero at $P = 0.05$, ** = yield loss significantly different from zero at $P = 0.01$.

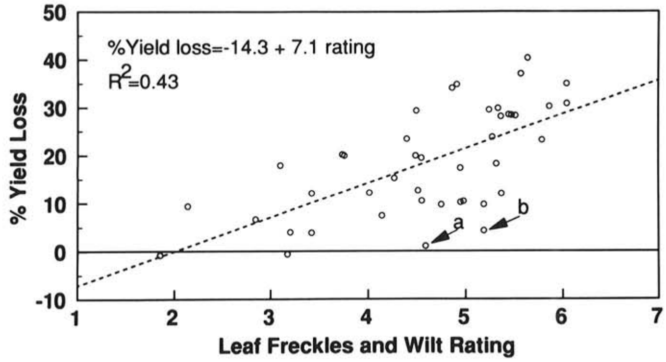

Fig. 1. Relationship between mean leaf freckles and wilt severity rating and the percentage of yield loss in 42 closely related maize hybrids and the susceptible check hybrid A632 × A619. Data points representing hybrids 84381 and 84517, two hybrids judged disease tolerant, are represented above by **a** and **b**, respectively.

of disease tolerance. By using a closely related, phenotypically similar set of maize hybrids, we are confident that interplot competition among plants was not a significant factor in these experiments. We also examined the relationship between leaf freckles and wilt tolerance and yield potential by regressing studentized residuals from the regression of percentage of yield loss on disease severity upon hybrid yields from uninoculated plots. The lower (more negative) the studentized residual, the more it indicates that yield loss is lower than predicted from disease severity; i.e., the more tolerant the hybrid. Based on this analysis, there is some indication that tolerance may be associated with low productive capacity or yield potential as postulated by Gaunt (8), because the regression was significant in 1986 and in the combined data. Because of the relatively small number of hybrids in these experiments, especially those considered tolerant, and the low magnitude of the correlation coefficients, any generalizations about the relationship of tolerance and yield potential are tentative at best. Gaunt also suggested that disease should be measured frequently during the whole epidemic (8). While this may be an important consideration in working with polycyclic, foliar diseases, we have found that leaf freckles and wilt severity is best measured at the tasseling stage of plant development. Later evaluations of disease severity can be difficult because of the presence of other foliar diseases, leaf senescence, and the disappearance of plants killed earlier in the season. Although it is probably not practical for evaluating large numbers of genotypes in a field situation, the measurement of host plant factors, such as total photosynthesis and internal moisture stress levels as suggested by Gaunt (8), might be a better approach to measuring the effects of leaf freckles and wilt on maize plants.

Possible mechanisms of tolerance to leaf freckles and wilt also need to be explored. It is possible that tolerant genotypes could have the ability to better compensate for a depleted plant stand, when young plants are killed by the disease, than do intolerant genotypes. Also, tolerant genotypes may produce more tillers capable of producing grain than do intolerant ones. We commonly observed that tillers often continued to grow after the main stem had been killed by leaf freckles and wilt.

We are encouraged that among the A632-type lines evaluated in hybrid combination, there was no relationship between yield potential in the absence of disease and leaf freckles and wilt severity ratings, indicating that it is possible to combine resistance and combining ability for grain yield in the same inbred line. It is also encouraging that we could do this through the modified backcross program of alternating generations of selfing or sibbing of more resistant plants with backcrossing to the susceptible A632 recurrent parent. This is further evidence that leaf freckles and wilt resistance is controlled by relatively few genes. We do recommend, however, that disease evaluation and selection be done on a progeny mean rather than an individual plant basis because of the large plant-to-plant variation in disease reaction we observed. Although it is conceivable that some of this plant-to-plant variation could have been caused by segregation in these advanced generation lines, similar variability was also observed in the homogeneous check hybrid. We also recommend that leaf freckles and wilt reactions and, preferably, yield loss reactions of hybrids, be evaluated over several environments or years because of the significant hybrid × year interaction for disease ratings.

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