Reaction of Two Maize Synthetics to Anthracnose Stalk Rot and Northern Corn Leaf Blight Following Recurrent Selection for Resistance to Diplodia Stalk Rot and European Corn Borer

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ABSTRACT

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Two maize (*Zea mays*) synthetics, BSAA and BSBB, were recurrently selected for resistance to Diplodia (*Diplodia maydis*) stalk rot (DSR) and leaf feeding caused by the first-generation European corn borer (*Ostrinia nubilalis*) (ECB), based on the reaction of S_1 lines to artificial inoculations of *D. maydis* and artificial infestations of the ECB. This study was conducted to determine if plant factors contributing to DSR and ECB resistance also conferred resistance to anthracnose stalk rot (ASR) caused by *Colletotrichum graminicola* and northern corn leaf blight (NLB) caused by *Exserohilum turcicum*. Highly significant linear improvements in ASR resistance were observed over cycles (C0 to C4) of selection in both synthetics. These improvements mirrored the gains reported previously for DSR resistance in BSAA and BSBB and suggested that a genetic correlation exists between DSR resistance and ASR resistance in these populations. NLB severity ratings were recorded on six dates throughout the growing season. A natural logarithm transformation was used to describe the disease progress curve for each of the C0 to C4 populations of each synthetic. Linear regression of lnNLB ratings on lnDATE (days after inoculation) accounted for more than 97% of the variation among entries when averaged over replications. Our results showed no concomitant improvement in NLB resistance over cycles of selection for ECB resistance, contradicting previous reports that 2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3-one (DIMBOA), a known biochemical factor in leaf-feeding resistance, confers resistance to NLB.

Recurrent selection has proved a useful means for maize breeders to improve disease and insect resistance in maize populations. Recurrent selection procedures concentrate favorable genes for the trait or traits under selection. Populations improved by recurrent selection should have enhanced value as sources of inbred lines for hybrid maize breeding programs.

Recurrent selection has been conducted in two maize synthetics, BSAA and BSBB, for resistance to Diplodia (*Diplodia maydis* (Berk.) Sacc.) stalk rot (DSR) and first-generation European corn borer (*Ostrinia nubilalis* Hübner) (ECB) leaf feeding. Selection was based on the evaluation of S_1 lines. The most advanced cycle population (C4) of BSAA was significantly improved for DSR resistance but not for ECB resistance; the C4 population of BSBB was significantly improved for both ECB and DSR resistance (15).

Genetic resistances to DSR and ECB are quantitative; that is, they are conditioned by many genes, each with relatively minor effect. A genetic correlation between two pest-resistance traits exists if some genes influence both traits (pleiotropy) or if genes for each trait are inherited together on the same linkage group. Genetic correlations may be advantageous to the plant breeder and may enhance the usefulness of the germ plasm.

Anthracnose stalk rot (ASR), caused by *Colletotrichum graminicola* (Ces.) G. W. Wils., is a maize disease of increasing importance. A severe infection of ASR is characterized by black streaks on the outer surface on the stalk and discoloration of the pith that often extends through several internodes, starting from the crown (21). *C. graminicola* is an aggressive pathogen, which, unlike most stalk-rotting organisms, is able to colonize living tissue (2). Resistance to ASR also is quantitative in nature; Carson and Hooker (1) identified at least five dominant genes for resistance by using reciprocal translocation testcross analysis in the inbred line A556. Other researchers have concluded that resistance to ASR would not be obtained via selection for resistance to DSR or stalk rot caused by *Gibberella*. White (22) evaluated 99 inbred lines for DSR and ASR reaction. The correlation between ratings for the two stalk rots was 0.32 for early lines and 0.26 for late lines. In another study among 23 inbreds and 25 single crosses, correlations between DSR or Gibberella stalk rot and ASR ratings ranged from 0.36 to 0.63 (6). Although the correlations were highly significant, they were deemed low enough to warrant separate breeding programs.

Northern corn leaf blight (NLB), caused by the organism *Exserohilum turcicum* (Pass.) Leonard & Suggs, remains an important maize pest. Monogenic resistance, as well as multigenic resistance, have been used in the control of NLB. Also, 2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3-one (DIMBOA) has been implicated as a chemical factor involved in NLB resistance (11–13). The relationship between DIMBOA and ECB leaf-feeding resistance is well established. DIMBOA concentrations in maize whorl tissue were highly correlated with field resistance ratings (8,20); DIMBOA also has been shown to cause ECB larval mortality in artificial diets (9,16). Molot and Anglade (14) compared the first-generation ECB damage ratings, the NLB severity ratings, and the log10 concentration 6-methoxy-benzoxalinone (MBOA, the stable breakdown product of DIMBOA) of 12 maize inbreds. The correlation coefficients for ECB and NLB ratings with MBOA levels were −0.77 and −0.95, respectively, and 0.76 between ECB and NLB resistance. Other reported significant correlations between NLB severity and DIMBOA concentration were −0.61 among 13 inbreds (11) and −0.64 among 16 inbreds (12).

The association between NLB resistance and ECB resistance has been demonstrated only in small, fixed sets of genotypes. A much more extensive study of the relationship among 7,537 genotypes over a period of 12 yr by Guthrie et al (5) has shown the correlation between NLB resistance and ECB resistance to be 0.003. Their study found that only 1.5% of the genotypes tested were highly resistant to both NLB and leaf feeding by the ECB. Klenke et al (7) described the effect of four cycles of S_1 line recurrent selection for first- and second-generation ECB resistance

on NLB reaction. A significant improvement in first-generation ECB resistance was not associated with gains in NLB resistance; the trend was toward decreasing resistance to NLB over cycles.

The purpose of this study was to investigate the effect of four cycles of S_1 recurrent selection for ECB and DSR resistance on the resistance to two other maize diseases, anthracnose stalk rot and northern corn leaf blight.

MATERIALS AND METHODS

BSAA and BSBB are genetically diverse maize synthetics of early AES800 maturity. The 58 and 44 inbred lines that were recombined to form the original BSAA and BSBB populations, respectively, were selected to represent a sampling of the best material available from public corn-belt breeding programs (18).

The four cycles of recurrent selection in BSAA and BSBB were based on visual evaluation of S_1 lines for resistance to first-generation ECB (leaf feeding) and to DSR (pith spread). Evaluations for each trait were made in separate experiments in the same year; identical procedures were followed for each synthetic. Twenty selected S_1 lines were recombined in each cycle of selection (with the exception of cycle 2 when 16 and 18 lines were recombined for BSAA and BSBB, respectively). The selection intensity ranged from 10 to 15%. The development of BSAA(SRCB)C4 and BSBB(SRCB)C4 has been reported (17).

Reaction to anthracnose stalk rot was evaluated in 1984 and 1985 at the Agronomy and Agricultural Engineering Research Center near Ames, IA. The experimental design was a randomized complete block with five replications per environment. Single-row plots were planted by hand in 1984 and by machine in 1985. The hand-planted plots measured 0.76 × 4.39 m. Seeds were planted two per hill in 13 hills spaced 33.8 cm and later thinned to one plant per hill for a final density of 51,666 plants ha^{-1}. The machine-planted plots, 0.76 × 4.90 m, were overplanted and later thinned to the same plant density and within-row spacing as the hand-planted plots.

The following 28 entries were included in the anthracnose evaluation experiment: the original and improved cycle populations of BSAA and BSBB per se (BSAAC0, BSAA[SRCB]C1, BSAA[SRCB]C2, BSAA[SRCB]C3, BSAA[SRCB]C4, BSBBC0, BSBB[SRCB]C1, BSBB[SRCB]C2, BSBB[SRCB]C3, and BSBB[SRCB]C4), cycle crosses between the synthetics (BSAACn × BSBBCn), and the original and improved cycle populations of BSAA and BSBB crossed to the single-cross tester Os420 × 187-2. Three single-cross checks were included: B14A × C103 (DSR resistant), B14A × Oh41 (intermediate resistance to DSR), and Os420 × 187-2 (highly susceptible to DSR).

Approximately 2 wk after anthesis, eight plants in each plot were inoculated with a water suspension of *C. graminicola* spores. One milliliter (1.5×10^4 spores ml^{-1}) was injected into the first fully elongated internode above the ground by using a 50-ml repetitive hog vaccinator. *C. graminicola* spores, provided by D. C. Foley, Iowa State University, Ames, were produced on oatmeal agar by a recent isolate from diseased stalks. Approximately 6 wk after inoculation, five competitive plants per plot were split longitudinally and given two ratings: the number of internodes with 75% or more discoloration, and the total number of internodes with discoloration (10).

All data were expressed on the basis of plot means for statistical analysis. Analyses of variance were computed for each environment before computing the combined analyses of variance in which years were considered random effects. The sums of squares for entries (considered a fixed effect with 27 degees of freedom [df]) in the combined analysis were partitioned into variation due to populations (24 df), checks (2 df), and populations versus checks (1 df). Variation within populations was further partitioned into five groups (4 df each): BSAA per se, BSBB per se, BSAA × BSBB, BSAA testcrosses, and BSBB testcrosses; variation also was partitioned among groups (4 df). A one-degree-of-freedom contrast between the midparent of the BSAA and BSBB and the crosses, BSAA × BSBB, was made as a test of heterosis. The sums of squares for each group were partitioned into sequential sums of squares due to linear, quadratic, and cubic regressions, and residual. *F*-tests were made by using the appropriate mean squares based on their expected variance components. Linear, quadratic, and cubic regression coefficients were calculated from cycle means within each group by using orthogonal polynomials (19), and their standard errors were calculated as described by Draper and Smith (3). *T*-tests were performed to test the hypothesis that the regression coefficient is equal to zero.

Reaction to northern corn leaf blight was evaluated in 1984 and 1985 at a location near Ames. The 1985 experiment was abandoned because of lack of sufficient moisture for adequate blight development. The experimental design was a randomized complete block with 10 replications. The 10 entries, which consisted of the C0 through C4 populations of BSAA and BSBB, were hand planted into single-row plots measuring 0.76 × 2.29 m. Six seeds were planted into each of five hills spaced 76.2 cm and later thinned to three plants per hill. The center three hills were planted to one of the 10 entries; the two end hills were planted to a highly susceptible hybrid and served as spreader hills.

Plants in each plot were inoculated twice, on June 25 and June 30, when the plants were approximately 60 cm high. The inoculum consisted of a conidial suspension of *E. turcicum* obtained from infected leaf tissue produced in the greenhouse that had been allowed to sporulate under moist conditions in the laboratory. An approximate volume of 10 ml of inoculum/plant, with an average concentration of 2×10^3 spores ml^{-1} water, was applied in the whorl of each plant with a hand sprayer. Six ratings were taken at 9- or 10-day intervals beginning 16 days after the first inoculation and ending when natural senescence began to interfere with the ratings. NLB reaction was recorded as the percentage of infected leaf area in each of the three center hills. Plot means were transformed to the natural logarithm of NLB ratings (lnNLB) and the natural logarithm of days after the first inoculation (lnDATE). The disease progress curve for each entry within a replication was fit to a straight line in this manner. The linear model accounted for more than 95% of the variation among NLB severity ratings in nearly all instances ($r^2 > 0.97$ on the average). An analysis of variance (49 df) for slope values was performed separately for BSAA and BSBB entries, and the standard errors of the difference between two entry means were calculated. Additional analyses of variance for NLB were computed within each rating date to detect trends over cycles of selection. The sums of squares for each synthetic were partitioned into sequential sums of squares due to linear and quadratic regression, and residual. *F*-tests were made using the appropriate mean squares based on their expected variance components.

RESULTS AND DISCUSSION

Response to anthracnose stalk rot. The overall means for ASR ratings were 3.6 and 4.1 for the number of internodes 75% or more discolored and the total number of discolored internodes, respectively. The correlation between values of the two rating methods was 0.99; therefore, only the number of internodes 75% or more discolored will be discussed. In contrast, Lim and White (10) reported a correlation of 0.52 between the same two measures of ASR resistance for a diallel set of 45 single crosses.

Highly significant differences among entries (27 df) were observed in the combined analysis of variance (not shown) for ASR ratings. The largest portion of the variation observed among the random-mated populations and their crosses was due to linear responses in the BSAA and BSBB cycles per se, which were highly significant ($P < 0.01$). Linear sources of variation were not significant for the population crosses and testcrosses. Highly significant differences among population groups (4 df) and among checks (2 df) also were observed.

Entry means and regression coefficients for ASR ratings are shown in Table 1. Because the nonlinear sources of variation in the combined analysis were nonsignificant in all instances, only the intercepts (averages) and linear regression coefficients are included in Table 1. The genotype × environment interaction (27 df) (combined analysis of variance not shown) was highly significant

and therefore was used as the error term in the F-test of entry means and to calculate a standard error for the regression coefficients. The only significant components of the genotype × environment interaction were the BSBB linear × environment, BSBB quadratic × environment, and the BSAA × BSBB linear × environment. The linear regression coefficients for the BSBB cycles and the population cross cycles were both low in 1984 (−0.25 and −0.07, respectively) and high in 1985 (−0.67 and −0.48, respectively), accounting for the linear × environment interactions. The BSBB cycles had a curvilinear trend in 1985, accounting for the BSBB quadratic × environment interaction.

Highly significant linear decreases in ASR susceptibility of 0.51 and 0.46 internodes per cycle were observed in BSAA and BSBB populations per se (Table 1). Similar linear reductions in DSR susceptibility of 0.38 and 0.36 units per cycle (1 = resistant, 6 = susceptible) for BSAA and BSBB, respectively, were reported by Nyhus et al (15). Therefore, selection for DSR resistance was also effective for ASR resistance in the populations per se and may be indicative of a genetic correlation between the two traits. Nonsignificant linear reductions were observed for the population crosses and testcrosses. The tester, Os420 × 187-2, had a rating of 4.5, slightly more susceptible than the C0 populations of BSAA and BSBB. Previous reports indicate that the gene action of ASR resistance is primarily additive, with resistance being partially dominant to susceptibility (1,10). Our data are not consistent with respect to the direction of dominance. Two of the four population crosses (the C2 and C4 crosses) were more susceptible than the high-parent values; all five of the BSAA testcrosses and three of the five BSBB testcrosses were more susceptible than their midparent values. Because of the inconsistency in the population crosses, the contrast for heterosis between BSAA and BSBB in the combined analysis of variance (not shown) was nonsignificant. On the basis of additive gene action alone, the linear regression coefficient of the population crosses would have an expected value similar to those of the populations per se; the linear regression coefficients of the testcrosses have expected values approximately half those of the populations per se because the frequency of favorable alleles in the tester is constant. The actual magnitudes of the linear regression coefficients are lower than expected, which cannot be explained simply on the basis of partial dominance for resistance. Conclusions about the gene action of ASR resistance are best drawn from the results of experiments designed specifically for that purpose; however, our results suggest that inbred lines derived from BSAA and BSBB may not contribute a high level of ASR resistance in a single-cross hybrid.

Despite the variable reactions to ASR among the different genetic backgrounds used in this study, the phenotypic correlation coefficient (check hybrids not included) between mean ASR ratings and mean DSR ratings, as reported by Nyhus et al (15), was 0.86 ($P < 0.01$), indicating a close relationship between the mechanisms of resistance to the two diseases in BSAA and BSBB. These results, however, cannot be considered representative of all maize populations or even a large sample of lines within BSAA or BSBB. The correlation between ASR and DSR could be lower among an unselected set of selfed lines derived from these synthetics and would be similar to the correlations reported by White (22) and Booker (6).

During the selection program, a six-class rating scale was used, for which classes 1–5 described the spread of pith discoloration from the point of the inoculation with *D. maydis*. The sixth class was given to any prematurely dead plant, regardless of the cause. It is conceivable that S_0 plants or S_1 lines (evaluations were made in both generations) resistant to DSR could have been discarded because of a high degree of susceptibility to any one of the stalk-rotting organisms that may be a part of the stalk-rot complex. However, because ASR was not prevalent in central Iowa during selection, it is likely that a genetic correlation between DSR resistance and ASR resistance accounted for the improvement in ASR resistance observed in BSAA and BSBB.

Response to northern corn leaf blight. The analyses of variance (not shown) indicated significant differences ($P < 0.05$) among entry means for slope values of the disease progress curve in BSBB, but not BSAA. Entry means of lnNLB for the original and improved cycles of BSAA and BSBB at six rating dates are shown in Table 2, along with the slope of the disease progress curve for each population, its ECB leaf-feeding rating, and the significance level of the regression mean squares over cycles. Table 2 reveals that no significant changes in NLB reaction occurred over cycles in BSAA, either within a rating date or over dates as indicated by the nonsignificant differences among slopes of the disease progress curve. This is not surprising since leaf-feeding resistance was not significantly altered in BSAA. In BSBB, for which significant improvement in ECB resistance was observed over cycles (particularly as a result of the first cycles of selection), a significant decrease in NLB resistance was observed. Generally, a lower slope of the disease progress curve would be desirable and would indicate greater resistance to a leaf-blight pathogen. However, Table 2 also shows that, at 25 and 35 days after inoculation, the improved cycle populations had greater levels of NLB severity than the original populations. In both instances, the linear trend was highly significant. Within the remaining four rating dates, the trend across cycles is much less clear. The data clearly do not support the hypothesis that the same biochemical factor(s) contributes resistance to both ECB leaf feeding and NLB. The data even suggest a slight negative association in BSAA and BSBB and are consistent with the results of Klenke et al (7), who conducted a similar study with the synthetic 'BS9.' Klenke et al obtained data from three environments using similar experimental procedures and reported nonsignificant genotype × environment interaction. This information gives us greater confidence in our data than we might otherwise have, because in our study only one environment was used in the analysis.

Our results also support those of Guthrie et al (5), who concluded that researchers cannot select for resistance to ECB and expect to have resistance to NLB, or vice versa. A firm conclusion based on the concentration of DIMBOA in BSAA and BSBB plant tissue cannot be made because chemical analyses of these populations were not conducted; it may be expected, however, that DIMBOA concentration increased in proportion to the progress for leaf-feeding resistance as was observed in the synthetics BS1 (20) and BS9 (4). It is, therefore, unlikely that DIMBOA concentrations, increased by selection for leaf-feeding resistance, will effect nonspecific resistance to a variety of leaf diseases. In contrast, host-pathogen relationships within the stalk-rot complex are likely to have much in common; mechanisms for resistance to stalk-rotting pathogens may be nonspecific enough to account for the correlated improvement in ASR resistance observed in our study.

TABLE 1. Mean anthracnose stalk rot (ASR) ratings of five selection cycles of two maize synthetics, their interpopulation crosses, and their testcrosses; and the regression coefficients of ASR ratings on linear orthogonal polynomials

	Cycle means[a]					Regression coefficients[b]	
Entry group	C0	C1	C2	C3	C4	$\bar{X}$	b
BSAA	3.9	3.7	2.6	2.6	1.9	2.94	−0.51[c]
BSBB	4.2	3.9	3.1	2.6	2.5	3.27	−0.46[c]
BSAA × BSBB	4.0	3.6	3.8	2.6	3.2	3.44	−0.27
BSAA × (Os420 × 187-2)	4.3	4.5	3.7	3.6	4.2	4.07	−0.10
BSBB × (Os420 × 187-2)	4.3	3.9	3.8	3.8	3.8	3.94	−0.12
Standard error							0.14
Least significant difference						0.07	
Checks							
B14A × C103	1.7						
B14A × Oh41	5.1						
Os420 × 187-2	4.5						

[a] Evaluated in two environments (1984 and 1985); the least significant difference ($P < 0.05$) for any two anthracnose stalk rot ratings is 0.2. Values are the number of internodes 75% discolored.

[b] Orthogonal polynomials are −2, −1, 0, 1, 2. Values are the number of internodes 75% discolored.

[c] Significant at the 0.01 probability level.

TABLE 2. Comparison of northern corn leaf blight severity ratings (lnNLB) and European corn borer (ECB) leaf-feeding resistance ratings in the original and improved populations of two maize synthetics—their disease progress curves and the significance levels of the mean squares for regression (over cycles) within six rating dates

Population	lnNLB						Slope of disease progress curve[b]	ECB leaf-feeding ratings (1–9)[c]
	16 dpi[a]	25 dpi	35 dpi	44 dpi	54 dpi	64 dpi		
BSAAC0	1.31	2.03	2.60	3.05	3.26	3.66	1.67	2.92
BSAA(SRCB)C1	1.33	1.98	2.54	2.99	3.23	3.66	1.66	3.01
BSAA(SRCB)C2	1.41	2.10	2.61	3.05	3.38	3.60	1.60	2.57
BSAA(SRCB)C3	1.39	1.98	2.60	3.02	3.25	3.50	1.56	2.58
BSAA(SRCB)C4	1.43	2.09	2.66	3.04	3.31	3.59	1.57	2.63
Regression mean squares[d]								
Linear	ns[e]	ns	ns	ns	ns	ns		
Quadratic	ns	ns	ns	ns	ns	ns		
Residual	ns	ns	ns	ns	*[f]	ns		
BSBBC0	1.27	1.98	2.49	2.98	3.19	3.81	1.75	5.75
BSBB(SRCB)C1	1.32	1.98	2.54	2.97	3.09	3.54	1.56	3.03
BSBB(SRCB)C2	1.35	2.15	2.69	3.08	3.29	3.66	1.63	3.13
BSBB(SRCB)C3	1.32	2.07	2.58	2.95	3.18	3.58	1.58	2.67
BSBB(SRCB)C4	1.42	2.26	2.78	3.06	3.31	3.69	1.57	2.88
Regression mean squares[c]								
Linear	ns	**	**	ns	*	ns		
Quadratic	ns	ns	ns	ns	ns	**		
Residual	ns	ns	ns	*	*	*		

[a] dpi = days postinoculation.
[b] The natural logarithm of NLB severity (percent leaf area infected) regressed on the natural logarithm of days after inoculation in one environment (1984). The least significant difference (LSD) ($P < 0.05$) between two slopes is 0.12 for BSAA populations and 0.13 for BSBB populations.
[c] Evaluated on a visual scale (1 = highly resistant, 9 = highly susceptible) in five environments: two locations in 1984 and 1985, and one location in 1986 (17). The LSD ($P < 0.05$) between two ECB means is 0.60 for BSAA and BSBB populations.
[d] Orthogonal polynomial coefficients for regression are −2, −1, 0, 1, 2 (linear) and 2, −1, −2, −1, 2 (quadratic).
[e] Nonsignificant ($P > 0.05$).
[f] * and ** = significant at the 0.05 and 0.01 probability levels, respectively.

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