COMPARISONS OF PHENOTYPIC CORRELATIONS AMONG S₁ LINES, AND THEIR TESTCROSSES, FROM FOUR IOWA STIFF STALK POPULATIONS OF MAIZE

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Received July 19, 1990

ABSTRACT - Relationships between agronomic traits of maize (Zea mays L.) parental lines and traits of hybrid progenies are important for breeders. If significant improvements in source populations are made by such procedures as recurrent selection, a breeder should know how such changes affect relationships between traits of parental lines and hybrid progenies. Correlations between agronomic traits and grain yield among random S₁ lines and S₁ line testcrosses from the original Iowa Stiff Stalk Synthetic (BSS-SC0) maize (Zea mays L.) population, two improved strains of BSSS [BS13(S)C3 and BSSS(R)C9], and the intermated cross between the two improved populations [BS13(S)C3 x BSSS(R)C9], were calculated to determine changes that occurred with recurrent selection in BSSS. Previous evaluations of these populations showed significant changes for agronomic traits and for genetic variances among S1 lines and hybrid progenies. Both S1 lines and S1-line testcrosses showed significant correlations between agronomic traits and grain vield in each population. No consistent trend in phenotypic correlations between the unimproved and improved populations were observed. Phenotypic correlations between S₁-line traits and testcross yield were too small to be of predictive value in a selection program.

KEY WORDS: Corn; Recurrent selection; Maize synthetics.

INTRODUCTION

Correlations between parental line traits of maize (*Zea mays* L.) and their testcross yield have been of interest to plant breeders for many years. Studies have been conducted to determine correlations between line performance and combining ability, but

most researchers have found this relationship to be too small for predictive value (HALLAUER and MIRAN-DA, 1988). GAMA and HALLAUER (1977) reported the correlation for grain yield between unselected lines and their single-cross hybrids developed from Iowa Stiff Stalk Synthetic (BSSS) was only 0.11. Multiple correlations of plant and ear traits of inbred lines with yield of their crosses were also small.

Previous evaluations (WALTERS et al., 1991a, b) of BSSSCO, BS13(S)C3, BSSS(R)C9, and BS13(S)C3 x BS-SS(R)C9 showed significant changes for several agronomic traits of the improved populations compared with the original. Yields of S1 populations were improved significantly and cross of the two improved populations showed significant high-parent heterosis. Average yields of testcrosses of S₁ lines from the improved populations were significantly higher than testcrosses of S1 lines from BSSSC0. Also, estimated genetic variances among S1 lines and among testcrosses showed significant changes for many traits. How such changes in performance and genetic variability affect relationships between parental lines and hybrid progenies probably is determined primarily by changes in gene frequencies and relative importance of additive and nonadditive genetic effects; however, for the breeder it is important to know if such changes affect the relationship between agronomic traits of parental inbred lines and hybrid progenies.

Objectives of this study were to compare phenotypic correlations of agronomic traits with yield among random S_1 lines, among testcrosses of the random S_1 lines, and between S_1 lines and their testcrosses from the original BSSSC0, two improved BS-SS populations [BS13(S)C3 and BSSS(R)C9], and the intermated cross of the improved BSSS populations [BS13(S)C3 x BSSS(R)C9]. The evaluation would permit an opportunity to observe changes in correlation values from unimproved to improved populations. Crosses of earlier cycles for BS13(S) and BSSS(R) had

Dep. Agronomy, Iowa State Univ., Ames, IA 50011. Joint contribution of the Cereal and Soybean Improvement Research Unit, USDA, Agricultural Research Service, and Journal Paper No. J-13946 of the Iowa Agric. and Home Econ. Exp. Stn. Project 2778. Part of the senior author's Ph.D. research. Received, 1990 - Revised July 10, 1990.

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shown significant heterotic expression for yield (Rus-SELL and EBERHART, 1975; SMITH, 1983; STANGLAND *et al.*, 1983), but detailed evaluations on correlations from such crosses, compared with correlations from the parents and the C0, have not been reported.

MATERIALS AND METHODS

The reference population used in this study was the original Iowa Stiff Stalk Synthetic, BSSSC0 (C0). Three other populations studied were BS13(S)C3 (C3), BSSS(R)C9 (C9), and BS13(S)C3 x BSSS(R)C9 (C3 x C9). C9 was developed from BSSSC0 by using nine cycles of reciprocal recurrent selection (RRS) with BSCB1(R) (PENNY and EBERHART, 1971). C3 was developed from BSSSC0 after seven cycles of half-sib recurrent selection with tester Iowa 13 [(L317 x BL349) x (BL345 x MC401)], followed by three cycles of S₂ progeny recurrent selection (EBERHART *et al.*, 1973). C3 and C9 were random-mated per se and then crossed to create C3 x C9 (F₁). The C3 x C9 cross was then intermated once to create the C3 x C9 (Syn.-2) population.

S1 lines used in Experiment I were produced in 1985 from C0, C3, C9, and Syn.-2 of C3 x C9 and increased by sib-mating each line in 1986. All S1 lines were random, with the only constraint being that there was enough seed for line increases and for testcross seed production. One hundred S1 lines from each source were planted on an ear-to-row basis in a breeding nursery and approximately five sib-matings (10 plants sampled) were made. A total of 200 unselected S1 lines (50 from each source) was used as entries in Experiment I in a randomized incomplete block design with replications in sets as described by HALLAUER and MIRANDA (1988). There were two replications within each of five sets; each set consisted of 10 lines from C0, C3, C9, and C3 x C9 for a total of 40 lines per set. Experiment I was duplicated in (Experiments Ia and Ib) 1987 and 1988. Experiment Ia contained single-row, hand-harvested plots, and Experiment Ib contained two-row, machine-harvested plots. Ear data were collected on the hand-harvested, single-row plots.

Experiment II included the same entries as Experiment I in testcrosses with B73 and Mo17. Inbred line B73 was derived from BSSS(HT)C5 maize synthetic variety (RUSSEL, 1972) and is a Reid Yellow Dent-type line. The populationns used in this study are related to B73, with the closest relationship being with BS13(S)C3, which descended from BSSS(HT) via recurrent selection. Inbred line Mo17 was selected via pedigree selection from the cross CI187-2 x C103 (ZUBER, 1973) and is a Lancaster Sure Crop-type line.

In 1986, 100 S₁ lines from each of the four sources were planted in separate isolation blocks for making testcross seed with B73 and Mo17. The S₁ lines were detasseled, and, at harvest, approximately 15 ears from each line were bulked to make testcross seed. Fifty lines from each of the eight source-by-tester combinations were used as entries in Experiment II. These 400 testcrosses were included in a randomized incomplete-block design with replications in sets. There were two replications within each of 10 sets; each set consisted of five lines from C0 x B73, C3 x B73, C9 x B73, (C3 x C9) x B73, C0 x Mo17, C3 x Mo17, C9 x Mo17, and (C3 x C9) x Mo17 for a total of 40 testcross entries per set. As with Experiment I, Experiment II also was duplicated to obtain data for ear traits.

Single-row (hand-harvested) plots were 0.76 m wide by 5.09 m long, planted with 32 seeds, and later hand-thinned at the fourto six-leaf stage to 21 plants plot⁻¹. Plant density was approximately 54,140 plants ha⁻¹. Field husbandry practices were used that promoted good plant growth and best yields for the climatic conditions that prevailed.

Before harvest, the following plant traits were measured on single-row plots: days to anthesis (number of days after June 30 until 50% of the plants in a plot had shed pollen), days to silk emergence (number of days after June 30 until 50% of the plants in a plot showed silk emergence), pollen-silk interval (difference between days to anthesis and days to silk), plant height (measured from the soil surface to the flag leaf node on five similarly spaced plants plot-1); ear height (measured from the soil surface to the primary-ear node of five similarly spaced plants plot-1), and staygreen. A rating of 1 to 9 was used for stay-green, 1 = < 10% dead leaf tissue and 9 = > 90% dead tissue. This measurement was taken the first week of September 1987, approximately 50 days after the mid-silk date. On hand-harvested plots, ears from 10 competitive plants plot-1 were harvested. The number of primary and secondary ears and the number of barren plants were recorded for each plot. Harvested ears were dried to a uniform moisture, and data were obtained for the following yield components: average number of kernel rows (for primary ears) plot-1, average ear length (primary and secondary) plot-1, average ear diameter for all primary ears, average kernel depth for the primary ears, total grain yield per plot expressed in tonnes hectare-1, and weight of 300 kernels plot-1. Hand-harvested experiments were conducted in six environments (Ames, IA; Ankeny, IA; and another research center located near Ames in 1987 and 1988). Hand-harvested grain yield will be abbreviated as HYIELD.

Two-row plots, 1.52 m wide by 5.09 m long, were overplanted by machine, thinned to 59,300 plants ha⁻¹, and were harvested by combine (MYIELD). Five traits were measured on these plots, but only grain yield (t ha⁻¹) adjusted to 15.5% moisture will be included. Machine-harvested experiments were conducted in six environments (Ames, Ankeny, and Martinsburg, IA, in 1987 and 1988).

Statistical analyses were performed according to the randomized incomplete block design with replications in sets (HALLAUER and MIRANDA, 1988) for data combined over six environments. An analysis of variance was calculated on plot values for each trait. A mixed model was used where environments and S1 progenies within each population were considered as random effects in Experiment I. Environments and testcross lines within each source were considered random and sources and testers were considered fixed effects in Experiment II. Phenotypic (Pearson product-moment) correlation coefficients were calculated for traits of S1 lines with S₁ line HYIELD, for traits of testcrosses with testcross HYIELD. and between S₁ line agronomic traits and testcross MYIELD. An analysis of covariance was not used to calculate phenotypic correlations between S₁ lines and testcrosses. These correlations were based on trait means for S₁ lines (from various numbers of environments) and testcross grain yield over six environments after adjustment for set effects (SCHUTZ and COCKERHAM, 1962). Multiple correlations were calculated between testcross yield and S₁ line traits. These plot data were adjusted for set effects, and a regression was calculated for S₁ line traits on testcross yield.

RESULTS AND DISCUSSION

Differences among S_1 lines and the interactions of S_1 lines \dot{x} environment were highly significant (P \leq 0.01) for all traits in Experiment I. In Experiment II, differences among testcrosses were highly significant

Trait	HYIELD						
	CO	С3	C9	C3 x C9	Overall		
Days to anthesis	-0.22	0.15	0.00	-0.16	-0.15*		
Days to silk emergence	-0.35*	-0.01	-0.01	-0.31*	-0.37**		
Pollen-silk interval	-0.21	-0.35*	-0.01	-0.34*	-0.42**		
Plant height	0.31*	0.45**	0.25	0.36*	0.22**		
Ear height	0.31*	0.62**	0.28	0.30*	0.19**		
Stay-green	0.18	-0.37**	0.29*	-0.16	-0.30**		
Ear length	0.75**	0.73**	0.52**	0.47**	0.75**		
Ear diameter	0.32*	0.19	0.27	0.47**	0.35**		
Kernel depth	0.48**	0.11	0.33*	0.47**	0.21**		
Kernel row number	-0.20	-0.02	-0.19	0.15	-0.10		
Ears per plant	0.70**	0.59**	0.44**	0.11	0.66**		
Weight per 300 kernels	-0.01	0.44**	0.39**	0.47**	0.27**		

TABLE 1 - Phenotypic correlation of 12 agronomic traits with hand-harvested yields among S_1 lines (by population and overall) from data combined over five environments.^a

*, ** Significant correlation at the 0.05 and 0.01 probability levels, respectively.

^a Days to anthesis, silk emergence, and pollen-silk interval were combined over four environments; stay-green and kernel row number were combined over three environments.

TABLE 2 - Phenotypic correlation of 12 agronomic traits with band-barvested yields among B73 testcrosses (Mo17 testcrosses in parenthe-
sis), by population and overall, combined over six environments. ^a

	HYIELD					
	C0	C3	С9	C3 x C9	Overall	
Days to anthesis	-0.12	-0.23	0.10	0.11	-0.45**	
	(-0.10)	(+0.30*)	(0.12)	(0.04)	(-0.04)	
Days to silk emergence	-0.22	-0.17	-0.15	0.07	-0.57**	
	(-0.18)	(0.06)	(0.03)	(-0.19)	(0.28**)	
Pollen-silk interval	-0.25	0.06	-0.48**	-0.33**	-0.43**	
	(-0.19)	(0.35*)	(-0.16)	(-0.38*)	(-0.37**)	
Plant height	0.29	0.42**	0.41**	0.52**	0.57**	
	(0.52**)	(0.57**)	(0.38*)	(0.51**)	(0.42**)	
Ear height	0.11	0.31*	0.44**	0.44**	0.26**	
	(0.24)	(0.50**)	(0.31*)	(0.34*)	(0.25**)	
Stay-green	-0.33*	-0.31*	-0.26	-0.22	-0.40**	
10	(-0.49**)	(-0.51**)	(-0.49**)	(-0.37*)	(-0.46**)	
Ear length	0.62**	0.08	0.59**	0.65**	0.62**	
	(0.36*)	(0.08)	(0.41**)	(0.50**)	(0.57**)	
Ear diameter	0.20	0.41**	0.62**	0.45**	0.50**	
	(0.31*)	(0.59**)	(0.44**)	(0.15)	(0.39**)	
Kernel depth	0.24	0.28	0.47**	0.51**	0.82**	
	(0.46**)	(0.13)	(0.59**)	(0.01)	(0.31**)	
Kernel row number	-0.16	-0.14	-0.01	0.27	0.23**	
	(-0.12)	(0.10)	(0.05)	(-0.11)	(-0.14*)	
Ears per plant	0.58**	0.14	0.44**	0.60**	0.51**	
	(0.27)	(0.27)	(0.24)	(0.19)	(0.38**)	
Weight per 300 kernels	0.41**	0.36*	0.48**	0.29	0.24**	
	(0.63*)	(0.67**)	(0.45**)	(0.43**)	(0.61**)	

*, ** Significant correlation at the 0.05 and 0.01 probability levels, respectively.

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^a Days to anthesis, silk emergence, and pollen-silk interval were combined over four environments; stay-green and kernel row number were combined over three environments.

for all traits, and testcrosses x environments were highly significant for most traits. In both experiments, the F values for the main effects were much greater than for the interactions in most instances.

Phenotypic correlations for plant and ear traits vs. HYIELD for hand-harvested S1 lines are presented in Table 1. Over all populations, significant correlations were observed for all traits vs. HYIELD except for kernel row number. Similar significant correlations have been observed in previous studies (HALLAUER and MIRANDA, 1988). Ear length (0.75**) and ears per plant (0.66**) showed the highest correlations of single traits with S₁ yield across all populations. The highly significant negative correlation between pollensilk interval and yield ($r = -0.42^{**}$) shows the importance of close synchronization for anthesis and silk emergence. Changes are evident in the magnitude and significance of correlations from C0 to the improved populations and their cross (C3 x C9). Ear length vs. HYIELD and ears per plant vs. HYIELD showed decreasing correlation coefficients from C0 to the improved populations, although the opposite trend was observed for weight of 300 kernels vs. HYIELD. The decreasing correlation trend from BSS-SC0 to the improved populations was not always observed because the improved populations did not always show decreases in genetic variance from BSS-SCO for the traits measured (WALTERS et al., 1991b).

Phenotypic correlations of agronomic plant and ear traits of B73 and Mo17 testcrosses with B73 and Mo17 testcross HYIELD are shown in Table 2 (Mo17 r-values in parentheses). Similar correlations were observed over all B73 and Mo17 testcrosses for all pairs of traits except days to anthesis vs. HYIELD and kernel row number vs. HYIELD, for which opposite trends occurred. For both sets of testcrosses across all populations, ear length showed good predictive value for yield (r = 0.62**); kernel depth had good predictive value for yield of the B73 testcrosses (0.82**) and weight per 300 kernels for yield of the Mo17 testcrosses ($r = 0.61^{**}$). For individual population sources, however, there were nonsignificant correlations of ear length with yield for C3 and of kernel depth with yield for C3 and C9. The importance of a short pollen-silk interval and good stay-green also is evident. Comparisons among sources of lines were made to determine if there were any trends for changes in magnitude of correlations. Ear height vs. HYIELD and pollen-silk interval vs. HYIELD showed similar increases in correlations from C0 to the improved populations for B73 and Mo17 testcrosses. Stay-green vs. HYIELD showed decreasing correlations from C0 to the improved B73 testcrosses, whereas Mo17 testcrosses showed little change in correlations. Kernel row number vs. HYIELD showed no correlation for either set of testcrosses, although over all testcrosses B73 had a highly significant, but small, positive correlation (0.23**), and Mo17 had a small, negative correlation (-0.14*) over all populations. Correlations of ear length vs. HYIELD were similar for both sets of testcrosses. Generally, there was no consistent trend between C0 testcrosses and the improved B73 or Mo17 testcrosses. Some pairs of traits showed increases in correlations while others showed decreases or no change among the four population testcrosses.

Plant breeders are interested in correlations of parental line traits with testcross yield. For the subdivision by population, there were only three significant correlations between plant and ear traits for handharvested S₁ lines and testcross MYIELD, which is only one more than expected for random variation (data not shown). Because there were so few significant correlations, comparisons among populations and between B73 and Mo17 have no value. Over all entries. B73 and Mo17 showed similar correlations for each trait. The correlations across all populations (data not shown) ranged from 0.00 for S₁ line staygreen vs. B73 MYIELD to 0.35** for S1 line HYIELD vs. B73 MYIELD. Most correlations were too small to be of predictive value in a breeding program, which is in agreement with previous studies in maize (HAL-LAUER and MIRANDA, 1988).

Generally, the improved populations showed smaller genetic variances than did the unselected population (WALTERS, 1989); therefore, compared with the unselected population, the improved populations would be expected to have smaller and fewer significant correlations among traits. A base population that has undergone many random-matings would be near linkage equilibrium, whereas advanced populations that have undergone only a few random-matings would remain in some level of linkage disequilibrium. Thus, the correlations among traits in the base population would be caused by pleiotropic effects and would be less affected by linkage compared with populations in linkage disequilibrium. There seem to be two opposing forces; the small genetic variance of the improved population contributes to decreased significant correlations among traits, and linkage disequilibrium in the improved populations keeps favorable alleles linked and thus contributes to increased significant correlations among traits. Changes in correlation from the unimproved to the impro-

Table and the lat	Multiple correlation coefficients					
Traits correlated ^a	CO	C3	С9	C3 x C9	Overall	
R14 vs. 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13	0.50	0.48	0.47	0.46	0.51**	
R15 vs. 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13	0.60	0.62	0.51	0.48	0.42**	
R14 vs. 7, 8, 9, 10, 11, 12, 13	0.29	0.36	0.19	0.42	0.47**	
R15 vs. 7, 8, 9, 10, 11, 12, 13	0.38	0.56*	0.34	0.46	0.37**	

TABLE 3 - Multiple correlation coefficients (R) between traits of band-barvested S₁ lines and testcross MYIELD by population and overall.

*. ** Significant correlation at the 0.05 and 0.01 probability levels, respectively.

^a Key to traits: 14 = B73 testcross MYIELD, 15 = M017 testcross MYIELD, 1 - days to anthesis, 2 = days to silk emergence, 3 = pollen-silk interval. 4 = plant height, 5 = ear height, 6 = stay-green, 7 = ear length, 8 = ear diameter, 9 = kernel depth, 10 = kernel row number, 11 = ears per plant, 12 = weight of 300 kernels, and $13 = S_1$ line HYIELD.

ved populations have shown no consistent trends for either number or magnitude of correlation values.

Multiple correlation values (R) between 13 S₁ line traits and testcross MYIELD in each of the four populations and averaged over all populations are presented in Table 3. Multiple correlations that use several inbred line traits with hybrid yield probably are more useful than individual traits with hybrid yield phenotypic correlations because breeders select for the total ideotype of the inbred line rather than for individual traits. Significant R-values were observed for all four multiple correlations over all entries. Only BS13(S)C3 x Mo17 showed a significant R-value with C3 line ear and grain traits. The overall R-values were greater for the B73 testcrosses than for the Mo17 testcrosses. The Mo17 R-values, by population, were generally larger than those involving B73 testcrosses, but most were not significant.

HAYES and JOHNSON (1939) reported an R-value of 0.67 between yields of hybrids and 12 inbred traits. RUSSELL and MACHADO (1978) reported significant R-values of 0.64 and 0.66 for hybrid yields with all inbred traits. GAMA and HALLAUER (1977), however, obtained R-values of only 0.23 and 0.21 for hybrid yields vs. six inbred traits for unselected BSSS lines. Generally, the results from this study agree with the results by HAYES and JOHNSON (1939) and RUSSELL and MACHADO (1978).

Over more than 50 years of maize breeding, there have been a number of studies to determine the relationships for parental inbred line agronomic plant and ear traits with hybrid yield. These studies have included lines from various genetic sources and grown under different environmental conditions, some including treatments such as plant densities and nitrogen levels. Generally, correlations for individual traits of inbreds with yield of hybrids have been too small to have predictive value. Usually, when multiple correlations have been ontained, the magnitudes of the values have been considerably greater and have had predictive value. Phenotypic correlations obtained in BSSS materials frequently have been lower than for other source materials, which may be a reflection of the importance of dominance variance in BSSS (HALLAUER and MIRANDA, 1988). The evidence is clear that maize breeders develop parental inbred lines with desirable agronomic plant and ear traits per se, but the real value of any line must be determined by extensive evaluation in hybrid combinations.

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