Potential Use of Alien Germplasm for Maize Improvement[1]

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ABSTRACT

Plant breeders have demonstrated the potential ability of exotic and alien germplasm to enhance particular qualitative genetic traits of maize, (*Zea mays* L.). Results from such programs include the incorporation of genes that condition resistance to pathogens or insect pests. Fewer examples exist which provide information on how alien and exotic germplasm affect quantitative traits, although studies have shown it is possible to increase heterosis or to expand the level of genetic divergence between breeding populations by using such germplasm. However, in either case, most breeders prefer current, elite inbreds with known combining ability as sources for inbred development and for improvement of hybrid performance. Alien germplasm was evaluated for its effects on quantitative traits by crossing seven substitution lines, each containing various segments of germplasm from teosinte (*Zea mexicana*), with three testers, and measuring the effects on maize hybrids. A performance trial was used for this evaluation from which data were collected for 12 traits on 23 hybrids. Significant differences in grain yield and heterosis were obtained between the means of the three testers and among the various substitution line hybrids. One tester, Havels-(20 + 2Tr7), contained an extra disomic chromosome from *Tripsacum dactyloides*. Hybrids with this tester had a combining ability value 8% higher than the isogenic control. The highest yielding hybrids were the teosinte A158-substitution lines involving the Florida and Durango teosinte types crossed with the Havels testers. The two highest yields occurred from crossing the Havels tester containing the *Tripsacum* chromosome with the A158-Florida 4,9 and the A158-Florida 9 teosinte substitution lines.

Additional index words: Genetic vulnerability, Teosinte, *Tripsacum*, Heterosis, Combining Ability, Inter-generic hybridization.

PLANT breeders are well aware of the potential variation yet to be extracted from elite and adapted lines by genetic manipulation through recombination and selection. The recognition of this fact contributes to a degree of reluctance concerning the practicality of using either exotic or alien germplasm within an applied cereal breeding program. Any potential enhancement that this germplasm could provide to contemporary corn breeding programs is carefully scrutinized by testing the material in combination with adapted corn varieties prior to distribution or continued development. The successful introgression of this germplasm would help to expand both the limited germplasm base from which modern crop cultivars have evolved (Frankel, 1974) and the narrow genetic base which continues to be the primary source of elite lines and highly adapted breeding populations.

When germplasm from a wild species or an exotic race contributes to a breeding program, usually the transfer of qualitative rather than quantitative genes is involved (Stalker, 1980). Examples of alien, progenitor, and exotic germplasm beneficially modifying agronomic traits are infrequent. Breeders usually depend upon traditional sources of elite germplasm from somewhat related strains to alter traits such as yield, stalk quality and combining ability while virtually ignoring more alien sources of germplasm. One reason for this is the low probability that exists for successfully integrating polygenic segments of alien germplasm into the complex genetic and metabolic regimes of highly selected modern varieties (Robbelen, 1979). The methodology used in most conventional corn breeding programs would tend to support these generalizations despite the growing concern that has developed in regards to the narrow genetic base of which many commercial hybrids are comprised (Zuber and Darrah, 1980).

A recent isozyme analysis has demonstrated the great loss of qualitative genetic variability, as measured by 58 alleles at 20 loci in maize, in commercial hybrids (Senadhira, 1976). An allelic index proved synthetic varieties and annual teosintes to contain the greatest number of alleles. Commercial hybrids possessed only 30 alleles present which represented a 21% decrease in variability from synthetic populations of corn. The hybrids tested were found to have the lowest values for all measurements of variability except heterozygosity.

Restrictions imposed by the bias of breeders, the demands of uniform high-production agriculture, and the size and cost of breeding programs have all contributed to the narrowing of the genetic base of current hybrids so that they reflect only a small, but elite minority of the extant germplasm (Brown, 1975). The narrow genetic base that comprises current commercial hybrids substantiates the previously mentioned decline in allelic frequency of hybrid isozymes. This decline in genetic variability has led to new considerations for the management of corn's genetic base. A recent survey demonstrates the intention to broaden the genetic base for commercial maize germplasm and to increase the utilization of exotic material in maize breeding programs (Duvick, 1981).

The objectives of this study were to determine if the grain yield of specific corn hybrids could be increased by the incorporation of nonadapted genetic material into the parental inbreds and to analyze the additional genetic variability which this germplasm could contribute to these inbred lines. In this study, the nonadapted germplasm came from three different races of teosinte (*Zea mexicana*) and from *Tripsacum dactyloides*.

MATERIALS AND METHODS

The sources of alien germplasm utilized in this study came from three different races of teosinte and from *Tripsacum dactyloides*. The teosinte germplasm was used in the form of seven different isogenic substitution lines. The

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Tripsacum germplasm came from a disomic addition tester stock, (20 *Z.mays* + 2 *T dactyloides*).

The seven substitution lines contained segments from the following races of teosinte: Guatemala (*Zea luxurians*, Doebley and Iltis), Durango, and Nobogame (*Zea mays*, spp. *mexicana*, Doebley and Iltis). These races were initially hybridized with maize by Mangelsdorf (1947), then backcrossed three times to maize while selecting for particular phenotypic traits of teosinte within a maize background. The teosinte germplasm was marked by ear phenotypes where teosinte's effect on increasing the prominence and induration of the lower glumes, reducing kernel row numbers and size of kernels (Mangelsdorf, 1947), can be observed. The original recurrent parent was the maize inbred Texas 4R-3. After several generations of selfing to ensure homozygosity, a linkage analysis was undertaken and the proper homologies were established between the experimentally introgressed chromosomal segment(s) from teosinte and their maize counterparts (Mangelsdorf, 1974; Sehgal, 1963). This linkage analysis was done by crossing the derivative stocks to a tester having recessive genes on nine of the ten chromosomes. The F_1's were backcrossed to the tester parent. The ears were then classified with respect to the recessive markers and particular teosinte-derived phenotypes (Mangelsdorf, 1947; Sehgal, 1963; Mangelsdorf, 1974).

These homozygous derivatives were later backcrossed to the inbred A158, by the same procedures described above, in order to transfer the teosinte germplasm to an inbred more adapted to Massachusetts. This second transfer of teosinte germplasm was completed by extensive backcrossing and a linkage analysis (Mangelsdorf, 1974). These isogenic substitution lines are identified by the race of teosinte present and by the number(s) of the particular maize chromosome(s) to which the teosinte segments were found to be homologous.

The three testers were selected to minimize the variation within the hybrids, while maximizing the amount of variation between groups of hybrids or testers. The testers were: A158, Havels-(20 + 0), and Havels-(20 + 2Tr7). The latter tester carries an extra disomic chromosome from *T. dactyloides* in addition to the full complement of twenty maize chromosomes. This alien chromosome has been mapped to several corn chromosomes and found to be homologous to maize chromosome four (Galinat, 1973). This inbred tester has been shown to transmit the disomic chromosome to all progeny (Rao and Galinat, 1974) and this transmittance was confirmed in the present study (Cohen et al., 1981). This disomic tester was selected to evaluate the combining ability of the *Tripsacum* germplasm with the corn inbreds and the teosinte substitution lines. The pedigree descriptions of the seven teosinte substitution lines and the three testers are listed in Table 1.

The hybrids were evaluated during 1979 and 1980 at Waltham, MA. A split-plot design was used with the three testers comprising the main plots which were arranged in a randomized complete block design. The eight A158 lines were the subplots. Within each tester, each hybrid was grown in two randomly assigned rows or subsamples. The randomization of subsample rows was used to control hybrid and position effects within the tester groups. Each row was 3.1 m long with 91 cm row spacing. Plant density was 35 864 plants/ha. A single replication was grown in 1979 to determine if differences between hybrid means occurred. The second and third replications were then grown in 1980. Good plant develoment was attained in all three replications and adequate moisture was available throughout the growing season.

Ears were harvested separately from both rows of a plot.

Table 1. Pedigrees of the A158-teosinte substitution lines and the three tester inbreds indicating their linkage homologies to maize.

Teosinte substitution lines in A158 background:

Source of teosinte germplasm	Teosinte germplasm homologous to maize chromosome number
Race: Florida	3
Race: Florida	4
Race: Florida	9
Race: Florida	4, 9
Race: Florida	3, 4, 9
Race: Nobogame	4
Race: Durango	1, 7, 9

Tester lines:

Maize background	Source of Tripsacum germplasm	T. dactyloides chromosome number	Homologous to maize chromosome number
A158 dent	None present	–	–
Havels dent	None present	–	–
Havels dent	T. dactyloides	Tr7	4

They were sorted into two groups depending on whether they were primary, (i.e., the uppermost), or prolific ears. The two groups of ears were weighed separately and combined for grain moisture determination adjusted to 15% moisture for yield calculations. Due to local growing conditions, the ears harvested occasionally showed moisture values over 40%. The Dickey-John grain moisture tester was not accurate in this moisture range so oven drying was used on these samples.

Total number of ears per row were determined during harvest along with number of tillers. Plant height (cm) was measured from the soil surface to the tip of the tassel for six plants in each row. The number of days from planting to anthesis was recorded for each row when 50% of the tassels were shedding pollen.

Ear length measurements (cm) were recorded for ten randomly selected ears from each row. Ear diameter (cm) was measured at the base of the ear and represents the average of 10 random ears from each row. Kernel row number was determined on 10 ears per hybrid. The number of kernels per row was determined on three separate rows per ear for the 10-ear sample. The mean values for these plant and ear measurements were used in the analysis.

An analysis of the microsporocytes from the eight hybrids with the Havels-(20 + 2Tr7) tester was undertaken to confirm the transmittance of the alien *Tripsacum* chromosome (Cohen, 1982). The presence of the *Tripsacum* monosomic chromosome in the hybrids results from crossing the alien addition disomic inbred with the seven A158-teosinte substitution lines and with the A158 control. The presence of this *Tripsacum* univalent was confirmed in all the F1 hybrids.

The analysis of variance for grain yield, (total, primary, and prolific), was performed on the actual subsample values as measured in kilograms. These values were later converted to kilogram per hectare. The data were analyzed using the SAS GLM Type IV sums of squares for unbalanced data with the analysis performed on subsample averages. The three testers and years were tested by the year × tester mean square except where this was not significant. In this case, error a was used. The substitution lines were tested by year × line mean square except when it was not significant. Then, error b was used to test lines. Duncan's Multiple Range Analysis (Steel and Torrie, 1960, p. 106–109) was used to test for significant differences between mean values for total yield within each main plot.

Heterosis measurements for the 23 hybrids were based

Table 2. Mean squares from the analyses of variance for 12 characteristics measured for each hybrid grown in the performance trials.

Source	df	Total grain yield†	Primary grain yield†	Prolific grain yield†	Number of ears/row	Number days to anthesis	Number tillers per row	Plant height	Percent grain moisture	Ear length	Ear diameter	Kernels rows per ear	Kernels per row
								cm		cm			
Year (Y)	1	0.18	0.39	0.02	0.5	0.7	28	974	195	1.6	0.04	0.01	1
Reps within Y	1	0.36	0.05	0.15	15.8	10.1	29	21	269	0.1	0.42	1.02	5
Tester (T)	2	1.73	1.02*	0.27	25.6	5.6	331	20 083**	40	64.7*	0.08	17.21*	105*
Y × T	2	0.02	0.06	0.02	1.7	0.6	15	68	130	1.2*	0.10	0.22	21
Error a	2	0.23	0.01	0.15	13.3	1.3	26	47	19	0.1*	0.07	0.27	4
Line (L)	7	0.32**	0.54*	0.55**	99.8**	8.5**	43**	1 342**	17*	11.7**	0.65**	7.31**	78**
T × L	14	0.08	0.12	0.03	3.4	1.7	7	90*	17	7.9**	0.03	0.97	20**
Y × L	7	0.06	0.11**	0.01	2.5	1.3	5	61	34	1.2*	0.03	0.63	6
Y × T × L	14	0.05	0.06**	0.02	3.2	1.2**	7	25	20**	2.1**	0.03	0.57	4
Error b	21	0.04	0.01	0.13	2.5	0.3	4	42	6	0.2	0.03	1.00	7

*,** Significant at the 0.05 and 0.01 levels of probability, respectively.   † Mean squares determined from kg per row (subsample) average.

upon total yield and were measured as the percent increase in yield over the higher yielding parent line. The parental inbreds were grown each season under identical conditions as the hybrids and their yield was determined. The following formula was used:

$$\text{percent heterosis} = \frac{\text{F1 yield - high parent yield}}{\text{high parent yield}} \times 100$$

Procedures modified from Simmonds (1979, p. 110–115) were used to compute combining ability values for total yield. These values were computed as deviations from the grand mean and the inferences drawn from the combining ability estimates are restricted to this experiment. The combining ability values for the teosinte substitution lines were calculated as follows:

$$\text{C.A.:L.1} = \frac{T_1.}{3} - \frac{T..}{24}$$

where Tl. is the marginal total for line 1 and T.. is the grand total. The combining ability estimates for testers were calculated as follows:

$$\text{C.A.:T1} = \frac{T._1}{8} - \frac{T..}{24}$$

where T.1 is the marginal total for a tester and T.. is the grand total. A parental analysis of variance was performed (Simmonds, 1979, p. 110–115) to determine significant differences among the combining ability values of the substitution lines and among the three testers.

RESULTS AND DISCUSSION

The mean squares for the 12 traits measured in the performance trial are presented in Table 2. The testers showed significant variation for five traits: primary yield, plant height, ear length, number of kernel rows per ear, and number of kernels per row. Testers did not differ significantly for either days to anthesis or in percent grain moisture which indicates that the *Tripsacum* germplasm did not significantly affect flowering or moisture levels at harvest. The teosinte substitution lines showed significant variation for all traits measured. Variation for total yield and prolific yield, as well as for all yield component traits was highly significant. The substitution lines also varied for maturity indicators as shown by the significant mean squares for number of days to anthesis and percent grain moisture at harvest.

As shown in Table 3, a few of the hybrids con-

Table 3. Total grain yield and percent heterosis for 23 hybrids involving seven teosinte substitution lines with three testers grown in 1979 and 1980.

Tester group	Teosinte substitution line	Total yield	High parent total yield	Percent heterosis over high parent
			kg/ha	
A158	A158—Durango 1, 7, 9	4861 a†	3121	56
	A158—Florida 9	4143 ab	3176	30
	A158—Florida 3, 4, 9	3812 b	3121	22
	A158—Florida 4	3701 b	3314	12
	A158—Florida 3	3452 b	3176	9
	A158—Nobogame 4	3452 b	3121	12
	A158—Florida 4, 9	3370 b	3259	3
	A158 (control)	3121 b	3121	0
Havels—	A158—Florida 3, 4, 9	5911 a	3591	65
(20 + 0)	A158—Florida 9	5828 a	3591	81
	A158—Durango 1, 7, 9	5662 a	3591	58
	A158—Florida 4	5275 ab	3591	47
	A158—Florida 4, 9	5082 ab	3591	42
	A158 (control)	5055 ab	3591	41
	A158—Florida 3	4834 abc	3591	35
	A158—Nobogame 4	4419 bc	3591	23
Havels—	A158—Florida 4, 9	6712 a	3729	80
(20 + 2 Tr7)	A158—Florida 9	6436 ab	3729	73
	A158—Florida 4	5800 abc	3729	55
	A158—Durango 1, 7, 9	5690 bc	3729	53
	A158—Florida 3, 4, 9	5552 bc	3729	49
	A158—Florida 3	5524 bc	3729	48
	A158 (control)	5027 cd	3729	35
	A158—Nobogame 4	4364 d	3729	17

† Means followed by the same letter within a column within each tester group are not significantly different at P = 0.05 as determined by Duncan's New Multiple Range Test.

taining teosinte germplasm showed significantly greater yield than their particular control lines, none of which contained germplasm from teosinte. These findings support those of Sehgal (1963) and Reeves (1950) which show that heterosis could occur when teosinte germplasm was in a heterozygous condition with maize germplasm. The greatest variation in yield occurred among the hybrids that involved the Havels-(20 + 2Tr7) tester. When it was crossed with A158-Florida teosinte 4,9 and with A158-Florida teosinte 9 the yields were 34 and 28 percent greater than the control, respectively. This A158-Florida teosinte 4,9 hybrid produced the highest yield in the experiment, 6712 kg/ha.

These two substitution lines crossed with the Havels-(20 + 0) tester produced lower yields than when crossed to the disomic tester, and none of the Havels-(20 + 0) hybrids differed significantly from their con-

Table 4. Estimates of combining ability and mean square values from combining ability analysis (Simmonds, 1979, p. 110–115) for total grain yield for the seven A158 teosinte substitution lines and the three testers.

Source	df	Mean square for total grain yield	Combining ability estimates in deviations from mean
A158-teosinte substitution lines	7	253*	
Florida 3			−276
Florida 4			28
Florida 9			580
Florida 4, 9			166
Florida 3, 4, 9			193
Nobogame 4			−801
Durango 1, 7, 9			525
LSD$_{0.05}$			525
Tester lines	2	2914**	
A158			−1160
Havels—(20 + 0)			359
Havels—(20 + 2 Tr7)			746
LSD$_{0.05}$			829
Error	14	85	

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

trol. Of the crosses to A158, the A158-Durango teosinte 1,7,9 produced the highest yield; it also produced the most prolific grain yield, as shown in Table 5. Its hybrid with A158 differed significantly from its control, but when crossed with the Havels-(20 + 0) or the Havels-(20 + 2Tr7) testers there were no significant differences from the respective controls.

Heterosis estimates are also shown in Table 3. The A158 tester hybrids estimate heterosis between the introgressed segments on teosinte germplasm and their maize homologs. These hybrids should differ only in their introgressed teosinte germplasm. The average heterosis estimate for this group is 18%. This relatively low value is to be expected because of the limited genomic difference between the parents and because the control line here was A158 open pollinated. The genomic divergence among the hybrids with the Havels-(20 + 0) tester is greater than that shown by the hybrids with A158. Consequently the average heterosis estimate rose to 49%. The average heterosis estimate for the hybrids with the disomic tester was 51% which did not differ significantly from the estimate for the Havels-(20 + 0) hybrids. However, the most heterotic hybrid, [Havels-(20 + 2Tr7) × A158-Florida 4,9] had a mean yield of 6712 kg/ha, which was the highest yield of the experiment, and had a heterosis estimate of 80%.

Combining abilities for total grain yield are presented in Table 4. The tester with the greatest combining ability was the Havels-(20 + 2Tr7) line. It contributed 8% more total yield than the Havels-(20 + 0) tester which contained no *Tripsacum* germplasm. Variation among the three testers was found to be highly significant while variation among the A158-teosinte substitution lines was significant at the 0.05 level as shown in Table 4. The low yields from the hybrids with A158 produced the −1160 kg/ha combining ability estimate for this tester which is indicative of the genomic similarity of the parents. The greater combining ability values for the disomic tester over those for the Havels-(20 + 0) tester would indicate a potential ability to increase combining ability

Table 5. Mean values for five traits from hybrids involving seven teosinte substitution lines and three testers.

Tester group	A158-teosinte substitution line	Primary grain yield	Prolific grain yield	Average total number of ears per row	Average number of tillers per row	Plant height
		kg/ha				cm
A158	Florida 3	3452	–	10	0	185
	Florida 4	3701	–	10	0	187
	Florida 9	4005	138	11	1	206
	Florida 4, 9	3149	221	11	1	207
	Florida 3, 4, 9	3232	580	13	0	218
	Nobogame 4	3010	442	14	5	210
	Durango 1, 7, 9	2790	2072	19	0	225
	A158 (control)	3066	55	10	0	188
Havels— (20 + 0)	Florida 3	4447	387	12	7	256
	Florida 4	5055	220	11	4	258
	Florida 9	5303	525	13	9	284
	Florida 4, 9	4695	387	14	5	274
	Florida 3, 4, 9	5414	497	15	8	293
	Nobogame 4	2955	1464	15	11	262
	Durango 1, 7, 9	4005	1657	19	10	272
	A158 (control)	5055	0	10	5	256
Havels— (20 + 2 Tr7)	Florida 3	4806	718	12	12	258
	Florida 4	5607	193	11	6	266
	Florida 9	5275	1161	14	12	277
	Florida 4, 9	5027	1685	16	12	283
	Florida 3, 4, 9	4336	1216	16	12	299
	Nobogame 4	2458	1906	19	19	269
	Durango 1, 7, 9	2790	2900	25	15	280
	A158 (control)	4972	55	11	7	262
LSD$_{0.05}$		363	1718	3	3	11
CV		5%	130%	12%	30%	3%

in certain hybrid combinations with discrete segments of germplasm from *Tripsacum*.

Two of the A158 lines had combining ability effects that ranked below the mean of the experiment (Table 4). The A158-Nobogame 4 line had poor combining ability with all three testers. This line produced ears with irregular kernel rows and of poor grain quality that limited its yield potential. The A158-Florida 3 line combined best with the Havels-(20 + 2Tr7) tester but produced no more yield than the control in this group. The highest combining ability value for the substitution lines was from the Florida 9 line because it combined well with all three testers and produced upper ears of good quality. The A158-Durango 1,7,9 line had the second highest value and combined well with the three testers but produced yields mostly from small prolific ears as compared to control hybrids.

The data for primary and prolific grain yield, average number of ears and tillers per row, and plant height for the 23 hybrids are presented in Table 5. The hybrids with the Havels-(20 + 0) tester had the greatest primary yield, an average of 4616 kg/ha, while the hybrids with the Havels-(20 + 2Tr7) tester had the greatest prolific yield with an average of 1229 kg/ha. The Florida 4 line and A158 are the exceptions for prolific yield among the hybrids with the disomic tester while the Durango 1,7,9 line produced about equal amounts of primary and prolific yield. The hybrids with the A158 tester had the least amount of prolific yield as a group with an average total ear number of 12 per row and only one tiller per row. The hybrids with the Havels-(20 + 2Tr7) tester had the highest average number of ears and tillers per row with values of 15 and 12, respectively.

Table 6. Mean values for four ear traits from hybrids involving seven teosinte substitution lines and three testers.

Tester group	A158-teosinte substitution line	Ear length	Ear diameter	Number of kernel rows per ear	Number of kernels per row
			cm		
A158	Florida 3	17.9	4.0	12	38
	Florida 4	18.9	3.9	14	36
	Florida 9	19.4	4.0	14	41
	Florida 4, 9	18.3	3.7	12	37
	Florida 3, 4, 9	20.0	3.7	12	36
	Nobogame 4	20.7	3.6	12	37
	Durango, 1, 7, 9	17.6	3.5	14	37
	A158	17.2	3.9	12	37
Havels—	Florida 3	22.5	4.0	15	42
(20 + 0)	Florida 4	24.3	4.2	16	41
	Florida 9	24.4	4.1	15	49
	Florida 4, 9	23.5	3.7	14	40
	Florida 3, 4, 9	24.2	3.7	14	44
	Nobogame 4	23.3	3.4	15	39
	Durango 1, 7, 9	21.8	3.4	14	39
	A158	23.3	3.9	14	44
Havels—	Florida 3	23.0	4.0	16	40
(20 + 2 Tr7)	Florida 4	23.5	4.1	16	43
	Florida 9	23.0	4.1	16	44
	Florida 4, 9	23.0	3.7	14	38
	Florida 3, 4, 9	24.0	3.5	14	39
	Nobogame 4	20.0	3.2	14	32
	Durango 1, 7, 9	17.0	3.1	14	30
	A158	23.0	3.8	16	41
LSD$_{0.05}$		0.8	0.3	2	5
CV		2%	4%	7%	7%

Their average height was 5 cm taller than the hybrids with the Havels-(20 + 0) tester and 71 cm taller than those with A158. Effects of the *Tripsacum* chromosome, in specific hybrid combinations, are evident for all traits presented in Table 5.

Table 6 summarizes data for the ear traits on the hybrids grown in the performance trials. The average ear lengths for the A158, Havels-(20 + 0), and Havels-(20 + 2Tr7) hybrids were 18.7, 23.4, and 22.3 cm, respectively. The average ear diameters for the three tester groups were essentially the same. The number of kernel rows per ear increased from the A158 hybrids to the hybrids with the disomic tester; four of the latter hybrids had 16 kernel rows per ear. The number of kernels per row was highest for the hybrids with the Havels-(20 + 0) tester which had an average of 42. The effects of the *Tripsacum* germplasm on ear phenotypic characters, as shown in Table 6, are less obvious than for the plant traits shown in Table 5. Ear length and the number of kernels per row were highest among the hybrids with the Havels-(20 + 0) tester.

The potential genetic variability released by selfing in hybrids made from current elite inbreds continues to be the breeder's primary source of material for corn improvement (Walsh, 1981). Breeders have used germplasm from numerous exotic races of corn to effect supplemental genetic improvement (Hallauer, 1978). This study documents the potential utility of progenitor and wild species germplasm to contribute to a maize improvement program. Teosinte has been shown to contain a relatively broad range of genetic variability as measured by isozyme analysis (Senadhira, 1976) when compared to commercial hybrids. The current study has demonstrated that limited portions of this variability have been effective in broadening the genetic variation of corn and increasing

heterosis when this germplasm is in a heterozygous state. The introgression of genetic segments from teosinte has been accomplished by selection for modifications of the female spike during the backcross generations. The progenitor germplasm was thus successfully integrated into the plant to positively affect quantitatively inherited traits. The *Tripsacum* chromosome was found to increase the combining ability of the Havel's line in which it was incorporated. This segment of alien germplasm, homologous to maize chromosome four, contributes increased yield and affects other quantitative traits as well. This ability to enhance yield and combining ability adds new dimensions to the utility of *Tripsacum* germplasm beyond that summarized by de Wet (1979).

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