MORPHOLOGY AND COMBINING ABILITY STUDIES OF MAIZE POPULATIONS RECOVERED FROM THE INTERGENERIC CROSS *ZEA* X *TRIPSACUM*[1]

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ABSTRACT - The extent, diversity and breeding potentials of gene transfers between maize and gama grass were investigated. The original cross *Zea mays* x *Tripsacum dactyloides* (2n = 72) was followed by seven backcrosses to several maize pollen sources resulting in a recovered maize bulk (2n = 20). Four populations ranging from highly tripsacoid to maizoid were derived through selection. They were studied for grain yield plus 17 plant and ear characters, either *per se* or in F_1 or backcross (BC) combinations with inbreds 0h43, Mo17, and B73. Variance, correlation, stepwise multiple regression, and diallel analyses were used to differentiate populations. Polyacrylamide electrophoresis performed on BC populations A, B (tripsacoid), and C (maizoid) suggests genetic transfer from *Tripsacum*.

Morphological studies show that the populations selected not only differ but also that they could be maintained during five generations for the intended kind and degree of tripsacoidy. Is was possible to derive a still more tripsacoid population D from population A.

Phenotypic variability is greatest among traits indicative for tripsacoidy: length of lateral branches, number of ears, and kernel thickness decrease towards more maizoid introgression, whereas ear length, kernel number/ear, pith diameter, kernel and ear volumes increase in this direction.

Correlation matrices show kernel thickness negatively correlated with eitht ear and kernel traits for maizoid population C, while corresponding correlations for tripsacoid populations A, B and D are mostly non-significant or positive. Differences between populations C and D are strikingly obvious when comparing multiple regression response models for dependent trait kernel number/ear. Diallel analyses show significant differences due to general combining ability for prolificacy and ear length in BC's of populations A and B, and C respectively, with B73. Traits for significant specific combining ability are grain yield, prolificacy and ear length. The upper 17 diallel crosses averaged 5,225 kg/ha as compared to hybrid checks's average yield of 5,417 kg/ha. Evidence points to B73 as the best inbred for maintenance of tripsacoid gene transfers during the described back-cross program.

The successful controlled introgression procedure may encourage breeders trying to enrich the primary maize gene pool with different traits for plant architecture, floral and reproduction biology, and disease, pest, and drought resistance from *Tripsacum*.

Running Title: Maize Populations introgressed from *Tripsacum*.

Index Terms: Tetraploid *T. dactyloides*, Tripsacoid, Maizoid, Genetic Transfers.

MORFOLOGIA E CAPACIDADE DE COMBINAÇÃO DE POPULAÇÕES DE MILHO RECUPERADAS DO CRUZAMENTO INTERGENÉRICO MILHO x *TRIPSACUM*

RESUMO - Estudou-se a amplitude, a diversidade e os potenciais de culturas destinadas a transferência de genes entre milho e *Tripsacum*. O cruzamento original *Zea mays* x *Tripsacum dactyloides* (2n = 72) foi seguido de sete retrocruzamentos com várias fontes de pólen de milho, resultando daí a recuperação do tamanho do pé de milho (2n = 20). Quatro populações, variando de "altamente tripsacóides" para "milhóides", foram derivadas através de seleção. Foram estudadas

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quanto à produção de grãos e quanto a 17 caracteres da planta e das espigas, quer per se, quer em F$_1$, quer em combinação de retrocruzamento (RC) com OH$_{43}$, Mo 17 e B 73 autofecundados. Empregaram-se análises de variância, de correlação e de múltipla regressão passo-a-passo; utilizaram-se análises dialélicas para diferenciar as populações. A eletroforese de poliacrimida, realizada nas populações A e B (tripsacóides) e C (milhóides) de retrocruzamento, sugere a transferência genética a partir do *Tripsacum*.

Estudos morfológicos mostram que as populações selecionadas não só se diferenciam, mas também podem ser mantidas durante cinco gerações quanto ao grau de tripsacoididade pretendido. Foi possível derivar da população A uma população D, mais tripsacóide ainda.

A variedade fenotípica é máxima entre as características indicativas de tripsacoididade, quais sejam: comprimento dos ramos laterais, número de espigas, e diminuição da espessura dos grãos com tendência para introgressão mais milhóide, enquanto o comprimento das espigas, o número de grãos/espiga, diâmetro do núcleo e o volume dos grãos e das espigas aumentam nessa direção.

As matrizes de correlação apresentam espessura do grão negativamente correlacionada com oito características das espigas e dos grãos em relação à população milhóide C, enquanto as correspondentes correlações em relação às populações tripsacóides A, B e D são muito insignificantes ou positivas. As diferenças entre as populações C e D são plenamente óbvias, em comparação com os modelos de resposta de regressão múltipla em relação à característica número de grãos/espiga. As análises dialélicas apresentam diferenças significativas, por sua capacidade de combinação quanto à prolificidade e ao comprimento das espigas, nos retrocruzamentos das populações A, B e C, respectivamente, com B 73. As características relativas à capacidade de combinação específica são: produção de grãos, prolificidade e comprimento das espigas. Os 17 cruzamentos dialélicos acima mencionados alcançaram a média de produção de 5.225 kg/ha, enquanto os híbridos-testemunhas alcançaram a média de 5.417 kg/ha. As evidências apontam para B 73 como o melhor produto de autofecundação para manutenção das transferências de genes tripsacóides durante o programa de retrocruzamento acima descrito.

O bem-sucedido procedimento de introgressão controlada pode encorajar os melhoristas a enriquecerem, a partir do *Tripsacum*, o complexo de genes portadores de características relativas à arquitetura das plantas, à biologia floral e da reprodução, e à resistência a doenças, às pragas e à seca.

Título abreviado: Populações de milho introgressadas de *Tripsacum*.

Termos para indexação: tetraplóide *Tripsacum dactyloides*, tripsacóide, milhóide, transferências genéticas.

INTRODUCTION

Introgression of *Tripsacum* germplasm into maize (*Zea mays* L.) seems not to occur spontaneously. At one time, however, maize did cross in nature with *Tripsacum* as the female parent. Hybrids between maize and *T. dactyloides* (L.) L. (2n=36) have been found in Venezuela (De Wet et al., 1981). Guatemalagrass (*T. andersonii* Gray) is an extensively used, vegetatively reproduced forage grass in humid tropical Latin America. Its genome of 64 somatic chromosomes is presumed to be a combination of 54 (3 x 18) from *T. latifolium* Hitchc. (2n=36) and 10 *Zea* chromosomes (De Wet et al., 1976). Hybrids between maize as female parent and *Tripsacum* (36,72) may be produced with or without embryo culture. These hybrids are male sterile, but female fertile, and can be backcrossed repeatedly with maize until all *Tripsacum* chromosomes are eliminated. Resulting recovered maize phenotypes are similar in some traits to those occurring in maize x teosinte (*Zea mays* ssp. *mexicana*) introgression populations.

Considering that teosinte is from the primary gene pool (GPI) and *Tripsacum* from GP2, in relation to *Zea mays* (Harlan & De Wet, 1971), one would expect to be able to transfer to commercial maize inbreds, through *Tripsacum* introgression, traits which differ genetically from those available from teosinte. *Tripsacum* is known to contain within its variability resistance to some of the major diseases of maize. Other potentially useful tripsacoid traits are gametophytic apomixis, weak perennialism, and prolificacy (De Wet, 1979b).

In maize, general and specific combining ability are of primary concern in commercial breeding programs. In intergeneric introgressed maize, yielding ability is low in highly tripsacoid populations. General combining ability would be expected to be poor if governed by additive gene action. Specific combining ability would also be expected to be poor because heterosis has been found to cause less hybrid vigor for yield in crosses among parents with too diverse genotypes (Moll et al., 1965). Crosses among related populations, however, result in no hybrid vigor, even causing varying degrees of yield depression, depending on the degree of relatedness among parents. Genetically diverse, but poorly yielding germplasm sources, can be used in long-term breeding objectives and should be included in a backcross breeding program (Hallauer & Miranda Filho, 1981).

Exotic and interspecific introgressed materials would broaden the germplasm base used by the hybrid seed industry. On the long term, maize production could become more efficient with introduction of new genes for modified plant architecture, different reproductive patterns, pest resistance, and other desirable traits (De Wet, 1979a).

Only a few studies have been reported on controled introgression of wild germplasm into cultivated forms. In the case of oats, *Avena sterilis* was used as a source of variability (Frey, 1976). Transgressive segregates were obtained for greater vegetative vigor and, in lower proportion, grain yield (Cox & Frey, 1984; Murphy & Frey, 1984). Guok et al. (1986) evaluated three cycles of recurrent selection within a population derived from the cross *Arachis hypogaea* L. ($2n=40$) x *A. cardenasii* Krap et Greg. nom. nud. ($2n=20$). Fruit yield and seed weight increased significantly due to selection during the first two cycles. Experimental introgression of alien germplasm into maize gave better combining ability in hybrids (20Zm + 1 Td) with a tester containing two *T. dactyloides* no. 7 chromosomes in addition to the maize genome (20Zm + 2Td), when compared to a nearly isogenic control tester (Cohen & Galinat, 1984).

The present work was designed to study controlled introgression of *Tripsacum* into maize.

Because the early generations are sterile, it was necessary to obtain tripsacoid lines with all *Tripsacum* chromosomes eliminated and reasonably good fertility restored. Different tripsacoid populations were synthesized and maintained through five cycles of selection for their different phenotypes. The recovered maize populations, ranging from very tripsacoid to maizoid phenotypes, were studied morphologically as well as in their interactions and yielding capacity within a backcross testing context, involving 3 standard U.S. Corn Belt maize inbreds as recurrent parents.

MATERIALS AND METHODS

Harlan & De Wet (1977) described a cytogenetic system obtained from one 56-chromosome BC_3 plant, which yielded highly tripsacoid, 20-chromosome recovered maize lines. The original cross was between a maize stock heterozygous for 1-6c translocation (♀) x *Tripsacum dactyloides* ($2n=72$) collected from Horseshoe Lake, Illinois. Through an elimination and replacement phenomenon of maize chromosomes during early backcrosses with maize, a BC_3 plant was obtained because of an unreduced functional female gamete in BC$_1$ (with 36 Td + 20 Zm) (Harlan & De Wet, 1977). The presence of trivalent and quadrivalent chromosomes in cells of this plant suggested the "contamination" of the *Tripsacum* genome by maize DNA. After BC$_3$ generation, *Tripsacum* chromosomes were very slowly eliminated, through BC$_7$ or BC$_8$. A linkage study suggested that chromosomes 2, 4, 7 and 9 of the recovered maize genome had been "contaminated" with *Tripsacum* DNA, accounting for the tripsacoid morphology of progeny lines (Stalker et. al., 1977a).

The present study was started in 1976 with a large number of lines, obtained from the above mentioned BC$_7$, used as a bulk source. Pedigree records show that maize pollen sources, which have been used during BC generations, were those found to easily obtain and identify crosses with *Tripsacum*: Strawberry Popcorn, different Purple Plant genotypes and a Tunicate stock were used. Plants of three contrasting phenotypes were selected from the bulk without regard to pedigree. Approximately 100 plants of each phenotype were bulked to develop populations A, B and C. Population D was derived later as a subset of A.

Population A: highly tripsacoid, tall, late plants, with robust stalks, bearing highly tripsacoid branches and ears (Fig. 1). Population B: Tripsacoid, shorter plants, with many tillers, that are thin and grassy, midseason in maturity with highly tripsacoid ears. Population C: maizoid, short plants, with midseason maturity, 3 to 5 tillers, highly prolific with 3 to 15 maizoid ears/plant. Population D was developed later, after backcross tests were completed on A, B and C. Population D was derived by selecting extremely tripsacoid phenotypes from population A and maintained on a plant--per-row basis. Ear-to-row was impossible because no ear produced enough seed to plant a row.

Within populations the described phenotypes were selected, during five cycles. Twenty seeds from about 100 plants/cycle were used to establish generation by open pollination. Measurements were taken during the first four cycles (1978-1981) on length of longest ear-bearing branch (LLEB), length of normal ears (LE), number of ears (NE) per LLEB and several other traits. Only the first three traits, however, were considered the most characteristic for describing the populations. The longest lateral ear-bearing branch of each plant was measured from its base up to the ear or tassel tip.

Populations A, B and C were crossed and backcrossed twice to inbreds 0h43, Mo17, and B73. Nine BC$_1$'s and nine BC$_2$'s were separately intercrossed in diallel crossing plots in the 1980 Florida winter nursery. The three inbreds were also crossed to produced the three possible single hybrids, utilized as controls in the diallel yield experiment grown in 1981 near Urbana. The 75 entries were evaluated in a randomized complete block design with three replications. Data were recorded on 35 plants. Plot size was 8.134m^2, consisting of a single 10.67m x 0,76m (35' x 30'') row. Analyses of covariance and variance and the diallel analysis were performed for grain yield, number of ears harvested per plot, and length of ears.

A total of 67 individuals from A, B and C backcross populations were tested for relative mobilities of esterase and malate dehydrogenase bands in 7,5% polyacrylamide gels (Harlan et al., 1980).

In 1985, seed from six open-pollinated ears, drawn randomly from 1983 harvested populations A, B, C and D, respectively, were grown ear-to-row. Each row was 15.24m long with 0.762m between rows and included 60 plants/row. About 20 random open-pollinated (upper) ears/row were sampled at harvest. Ear and kernel traits were measured on 80 ears/population. Traits are identified as follows: ELE = ear length, EDI = maximum ear diameter, KRN = kernel row number, MKN = maximum kernel number per row, HTT = hard tissue thickness of cob, PDI = soft pith diameter, KLE = kernel length, KWI = kernel width, KTH = kernel thickness, ETV = ear total volume estimate ($1/3\pi\ r^2h$), TKN = total kernel number estimate (KRN x MKN), PHR = pith/hard tissue ratio, KVE = kernel volume estimate (KLE x KWI/2 x KTH).

Traits were chosen to include those most useful to differentiate varying degrees of tripsacoidy among populations (Stalker et al., 1977b). Variables were tested for normal distribution. Nested analyses of variance for the randomized complete block design (Steel & Torrie, 1980) and stepwise multiple linear regression (Draper & Smith, 1981) analyses were performed.

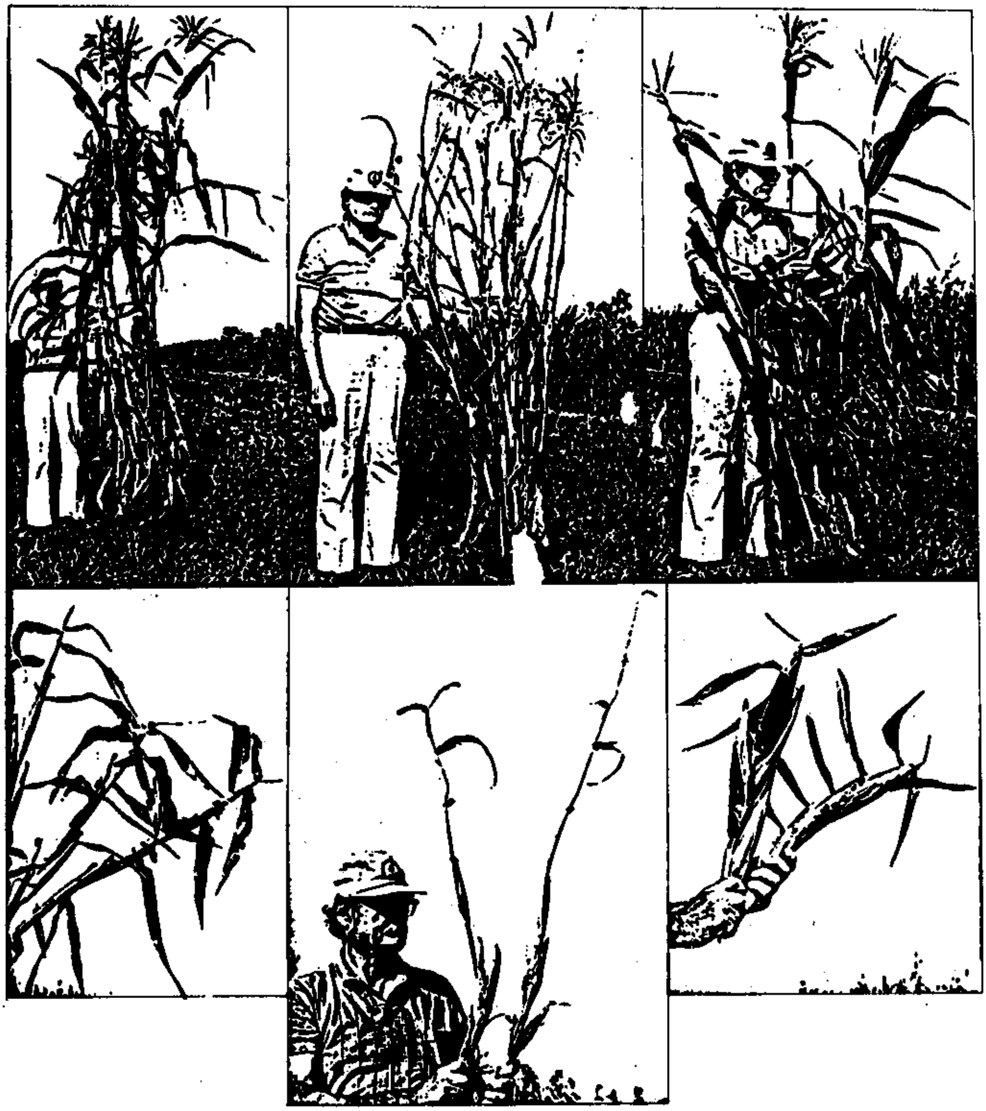

FIG. 1. J. R. Harlan shows plant phenotypes for which populations A, B and C (from left to right) were selected, with the respective typical lateral branches below. The B plant was defoliated to show the branching.

RESULTS AND DISCUSSION

Data obtained on pre- and post-harvest morphology and grain yield of populations are used to illustrate the effects of loading maize chromosomes with genetic transfers from *Tripsacum dactyloides*. The ear of maize is a highly specialized inflorescence derived from a branch system. In more advanced races, the number of ears per branch (shank) is effectively reduced to one. One of the most conspicuous features of tripsacoidy is a reversion to a more primitive condition with elongated shanks and two to several functional ears per shank or lateral branch complete with a terminal tassel (Fig. 1).

Four-year averages of pre-harvest measurements for populations, inbreds, and the F$_1$'s are shown in Table 1. Differences due to interaction were nonsignificant and indicate that populations, inbreds, and years (environments) tend to have parallel effects on character expression.

The length of the longest ear-bearing branch (LLBR, Table 1) for population C differs significantly ($P \leq 0.05$) from that of populations A and B. Although population C has longer LLBR than the inbreds, it does not differ significantly from Mo17. Mo17 has the longest ear (LE), but does not differ from the F$_1$'s, B73 and 0h43. The most tripsacoid populations (A and B) have the shortest ears, although not significantly different from population C, B73, and some of the F$_1$'s. The number of ears per longest shank is

TABLE 1. Averages (1978, 79, 80 and 81) of traits indicative of tripsacoidy in tripsacoid recovered maize populations A, B, C, maize inbreds, and F$_1$'s. BC$_1$ measurements are one year (1980) averages. Traits are length of longest lateral branch (LLBR), length of normal ear (LE), and number of ears per longest lateral branch (NE/LLBR). Phenotypic C.V.'s in parentheses (%).

Populations, Inbreds, and F$_1$'s	1978, 1979, 1980, 1981 Averages (cm)					
	LLBR (cm)		LE (cm)		NE/LLBR	
A	70.3	(51)	10.8	(37)	5.4	(71)
B	60.3	(50)	11.4	(33)	3.6	(72)
C	39.8	(30)	14.6	(34)	2.4	(46)
Oh43	28.4	(12)	18.4	(11)	1.0	(00)
Mo17	36.4	(16)	20.5	(11)	1.0	(04)
B73	29.2	(13)	15.8	(09)	1.0	(00)
Oh43 x A	48.5	(24)	18.2	(28)	1.9	(60)
Mo17 x A	55.0	(20)	18.1	(31)	2.2	(47)
B73 x A	53.5	(28)	17.3	(25)	2.0	(61)
Oh43 x B	46.3	(26)	19.2	(21)	1.4	(50)
Mo17 x B	47.3	(19)	18.5	(25)	1.7	(55)
B73 x B	46.5	(26)	16.0	(29)	1.6	(53)
Oh43 x C	45.7	(22)	20.0	(23)	1.6	(45)
Mo17 x C	43.9	(18)	19.6	(24)	1.6	(48)
B73 x C	46.9	(22)	17.2	(29)	1.9	(53)
HSD (Tukey p=0.95)	23.79		7.136		1.621	
Reid Yellow Dent (1)	44.7		24.45		1.1	
BC$_1$'s	1980 Averages					
Oh43 (Oh43 x A)	34.7		18.9		1.3	
Mo17 (Mo17 x A)	41.9		19.6		1.3	
B73 (B73 x A)	34.5		17.1		1.2	
Oh43 (Oh43 x B)	32.9		19.9		1.2	
Mo17 (Mo17 x B)	39.8		19.4		1.4	
B73 (B73 x B)	34.6		16.9		1.4	
Oh43 (Oh43 x C)	35.7		22.3		1.1	
Mo17 (Mo17 x C)	37.3		21.9		1.2	
B73 (B73 x C)	33.4		18.1		1.3	

(1) Traditional open-pollinated U.S. Corn Belt variety

highest for population A, and decreasing through populations B and C. For this trait, populations B and C do not differ significantly and are similar to only two F_1's (Mo17 x A and B73 x A).

The length of the normal ear (LE) is an important grain production factor, whereas a long lateral branch or shank with several ears on it is not desirable for high grain production. Conveniently, length of normal ear (LE) is negatively correlated with length of longest ear-bearing branch (LLBR, r=-0.45) and number of ears/longest branch (NE/LLBR, r = -0.72), whereas LLBR and NE/LLBR are positively correlated (r = 0.78). Data from BC_1 plants for those traits indicate lower values than those recorded form "Reid Yellow Dent", except for NE/LLBR. Phenotypic coefficients of variability (in parenthesis, Table 1) are high in populations A and B and decrease gradually from population C through the F_1's to the inbreds. Within inbreds, variation should only be due to environmental effects in the absence of mutations or other modifying phenomena.

Due to the importance and high specialization of the female inflorescence in maize, harvested ears from all populations were analysed 8 years after populations A, B and C were established. Questions that may be asked are: to what extent was it possible to maintain tripsacoid ear and kernel characteristics? and how do such traits relate to each other in populations of different degrees of tripsacoidy? Was it possible to generate a still more tripsacoid population derived from A, population D, and how does it differ from A? The variability range of ear types present in population A and some ears from population D are shown in Fig. 2.

Classified means for each ear and kernel trait measured are listed in Table 2. Population C is the maizoid population, and it is significantly different from all the other populations, with higher values for all traits, except kernel thickness, obviously indicating population C's similarity to modern maize. Kernels are thinner in modern maize because they are more crowded within the row on a highly condensed rachis, due to the polystichous condition, as opposed to the distichous *Tripsacum* inflorescence.

Coefficients of variation (C.V.) tend to be reasonably low for most traits (Table 3). They are high for some traits which thus indicate high variability within populations. Total number of kernels/ear is of course highest for the maizoid population C and very low for tripsacoid populations, which cause the overall phenotypic C.V. for this trait to be the highest of all, 629% among populations (Table 3). The degree of variability within one population is different from that within other populations. For example, pith diameter varies from zero to more than six mm within each tripsacoid population, while, within population C, the range was from 1.7 to 8.6 mm. Similarly obvious diversities between tripsacoid populations and the maizoid population can be observed for all traits which tend to assume very small values with increasing tripsacoidy (Table 4). Such "interactions" were confounded with a high range of variability within each sample of 20 ears, mainly for the tripsacoid populations, increasing the residual sums of squares in this type of experiment, generating corresponding C.V.'s higher than 40% (Table 3).

Comparing minimum to maximum ranges (Table 4), populations A and D seem to be similar, with a consistent tendency to more tripsacoidy towards population D because values tend to be smaller in D than in A. Population B tends to be different from populations A and D because some of its traits were significantly more maizoid than in populations A and D. Others were more tripsacoid than in population A but less so than in population D. This would support the idea that tripsacoid populations can be maintained and modified through selection.

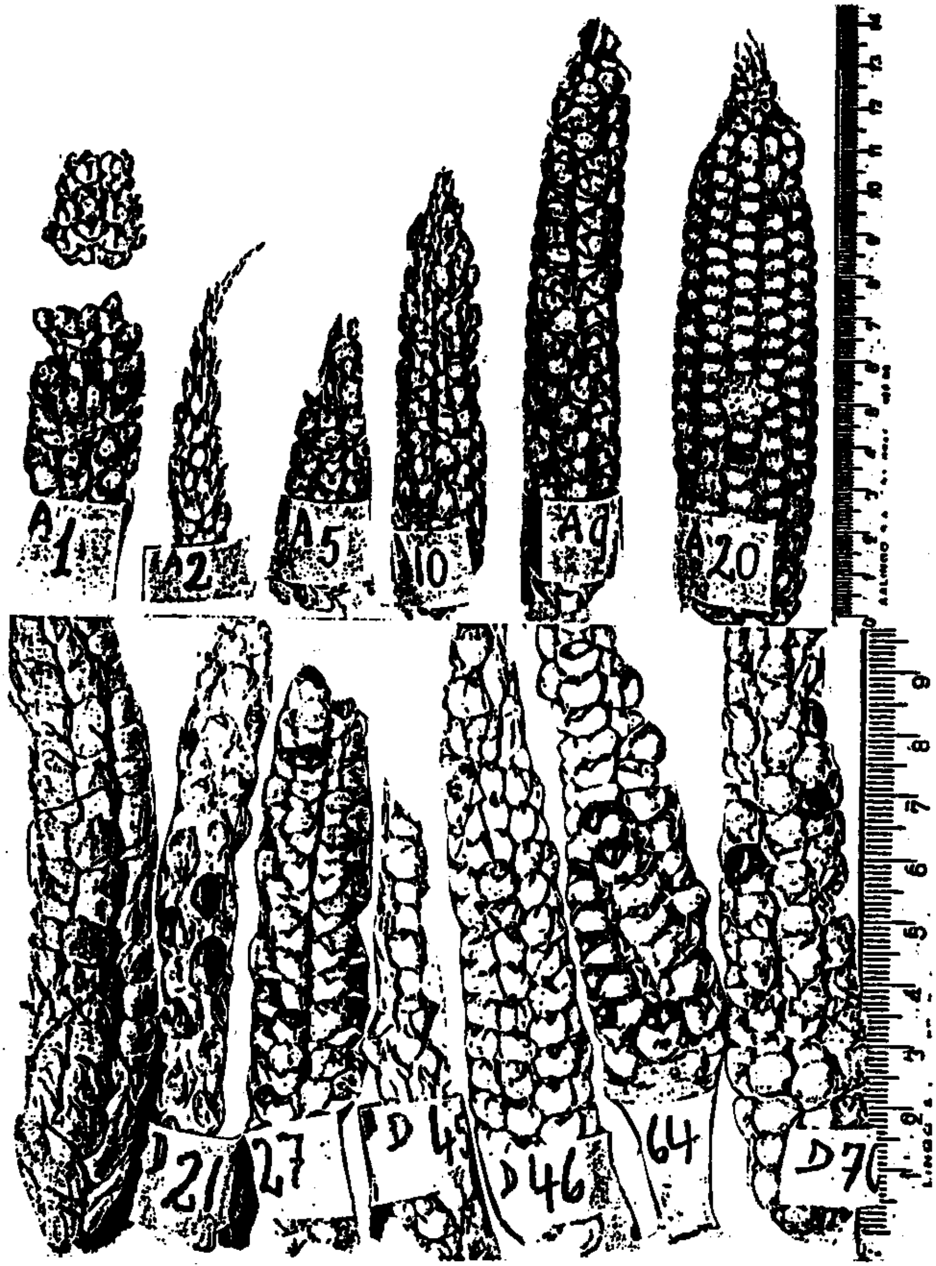

FIG. 2. **Population A ear samples showing (above) the range (left to right) from highly tripsacoid to maizoid ears. Ears from population D (below) are extremely tripsacoid. Tunicate ears and red pericarp Kernels derived from a tunicate maize and strawberry popcorn back-cross parents used early during the process of recovering maize form the male sterile *Zea* x *Tripsacum* cross descendents.**

TABLE 2. Post-harvest ear and caryopsis traits recorded from randomly sampled open pollinated ears of population A, B, C and D, grown in Urbana, 1985. Classification of means, using minimum significant differences (HSD) obtained from Tukey's studentized range test P ≤ .5 for df = 304.

	Variables and classified means						
Populations	ELE (1) (mm)	EDI (mm 10^{-1})	KRN (No.)	MKN (No.)	HTT (mm 10^{-1})	PDI (mm 10^{-1})	ELE (mm 10^{-1})
A	109.59b	233.24b	10.87b	12.86b	47.52ab	29.34b	78.81b
B	91.92c	224.84b	10.47bc	14.22b	43.51bc	23.86b	75.71b
C	149.42a	355.09a	14.04a	31.27a	50.39a	54.11a	98.44a
D	105.94b	204.87c	9.60c	12.52b	40.30c	23.56b	76.64b
HSD (Tukey)	10.42	16.57	0.94	2.79	4.24	5.87	3.51
	KWI (mm 10^{-1})	KTH (mm 10^{-1})	ETV (mm^3)	TKN (No.)	PHR —	KVE (mm^3)	
A	66.66a	53.29a	16,600.29b	143.80b	0.332b	140.78a	
B	62.09b	50.45a	12,731.91b	152.28b	0.299b	119.98b	
C	69.29a	43.01b	51,089.54a	445.92a	0.546a	146.18a	
D	61.34b	50.86a	12,708.57b	127.22b	0.321b	119.71b	
HSD (Tukey)	3.38	2.85	4,029.94	42.38	0.0793	12.62	

(1) ELE = Ear length, EDI = Ear diameter, KRN = Kernel row number, MKN = Maximum kernel number/row, HTT = Hard tissue thickness of cob, PDI = Pith diameter, KLE = Kernel length, KWI = Kernel width, KTH = Kernel thickness, ETV = Ear total volume, TKN = Total Kernel number estimate, PHR = Pith/hard tissue ratio, KVE = Kernel volume estimate.

(2) Means followed by same letter are not significantly different.

TABLE 3. Analysis of variance summary of post-harvest ear and caryopsis traits recorded from randomly sampled open pollinated ears of populations A, B, C and D, grown in Urbana 1985.

Variable	F	Mean	Std. Dev.	C.V. (%)	Variability among Populations: Phenotypic C.V. (%)
ELE (ear length)	74.8**	114.22 mm	25.52	22.3	193
EDI (ear diameter)	225.5**	254.51 mm10^{-1}	40.56	15.9	239
KDN (kernel row No.)	56.7**	11.25 rows	2.299	20.4	154
MKN (max. kernel No./row)	140.7**	17.72 kernels	6.836	3.85	458
HTT (hard tissue thickness)	14.6**	45.43 mm10^{-1}	10.37	22.8	87
PDI (pith diameter)	81.5**	32.72 mm10^{-1}	14.38	43.9	397
KLE (kernel length)	125.9**	82.40 mm10^{-1}	8.584	10.4	117
KWI (kernel width)	16.7**	64.84 mm10^{-1}	8.274	12.7	52
KTH (kernel thickness)	32.4**	49.40 mm10^{-1}	6.980	14.1	80
ETV (ear total volume)	285.1**	23,282.57 mm^3	9,866.28	42.3	226
TKN (total kernel No.)	173.4**	217.33 kernels	103.75	47.7	629
KVE (kernel volume)	16.0**	131.66 mm^3	30.896	23.4	297
PHR (pith/hard tissue ratio)	28.2**	0.3747	0.1941	51.7	275

** Significant at the 1% probability level.

Phenotypic correlation coefficients significantly different from zero are listed in Tables 5 and 6. They show that a tripsacoid trait like kernel thickness (KTH) in a maizoid population (c) is negatively correlated with maizoid traits, whereas the same trait in tripsacoid populations shows few significant, mostly positive, correlations.

TABLE 4. Minimum and maximum (range) of variable measurements. Post-harvest ear and caryopsis traits recorded from randomly sampled open-pollinated ears of tripsacoid populations A, B and D (highly tripsacoid) and C (maizoid), grown in Urbana, 1985.

Traits(1)	Minimum				Maximum			
	A	B	C	D	A	B	C	D
ELE	40	45	70	60	185	133	200	173
EDI	140	126	237	120	342	330	454	324
KRN	6	6	8	6	18	14	22	14
MKN	1	4	12	1	26	28	47	32
HTT	25	28	20	19	80	70	72	76
PDI	0	0	17	0	64	68	86	61
KLE	57	53	68	50	103	96	119	99
KWI	48	43	47	42	87	83	98	81
KTH	38	34	30	33	64	66	69	72
ETV	2141	3157	11541	2261	43573	34199	88462	37087
TKN	6	50	130	10	450	350	924	392
PHR (x10^4)	76	76	1864	66	6951	7000	9130	13421
KVE	72	47	79	44	224	206	246	207

(1) See Table 2 for trait designations and measurement units.

TABLE 5. Correlation matrices for highly tripsacoid maize populations A (above diagonal).and B (below diagonal).

POPULATION A - Traits(1)

		ELE	EDI	KRN	MKN	HTT	PDI	KLE	KWI	KTH	ETV	TKN	PHR	KVE
	ELE		.35	.33	.54	-(2)	.25	.28			.71	.58		
P	EDI	.25		.39	.75	-	.41	.43			.86	.78	.24	.30
O	KRN		.69		.22	-	.44				.46	.50	.27	
P	MKN	.76	.49	.35			.24	.46			.81	.93		.26
U	HTT										.22	.26	-.58	
L	PDI		.59	.41	.30	-.28			-.25		.42	.36	.87	
A	KLE	.29	.49	.22	.23						.43	.39	.44	
T	KWI			-.26						.40				.80
I	KTH				-.21			.31	.31					.69
O	ETV	.69	.84	.60	.74		.49	.48	.25			.87	.22	.24
N	TKN	.64	.67	.68	.91		.41	.27			.84			
	PHR		.51	.33	.28	-.57	.92				.40	.37		
B	KVE		.33					.64	.71	.76	.35			

(1) See Table 2 for trait designation.

(2) Correlations not listed were not significant at the 5% probability level.

Stepwise multiple regressions imply a multivariate model building. Variables are included following the stepwise forward procedure (Draper & Smith, 1981). Dependent variables are chosen for the purpose of best explaining the tripsacoid condition of each population (Table 7). Model building was not very efficient for the pith/hard tissue ratio (PHR), certainly because there simply is no pith, neither in *Tripsacum* nor in highly tripsacoid maize phenotypes. Equations for PHR explain therefore only 7,2% of total vari-

TABLE 6. Correlation matrices for maizoid populations C (above diagonal).and tripsacoid population D (below diagonal).

		POPULATION C - Traits[(1)]												
		ELE	EDI	KRN	MKN	HTT	PDI	KLE	KWI	KTH	ETV	TKN	PHR	KVE
	ELE		.47	[(2)]	.80	.35	.30	.33	.28	-.32	.79	.61		
P	EDI	.50		.62	.66	.64	.65	.84		-.48	.89	.75		
O	KRN	.42	.62		.32	.28	.61	.48	-.45	-.34	.49	.77	.37	-.30
P	MKN	.40	.76	.47		.44	.42	.53		-.55	.82	.84		
U	HTT				-.27		.42	.49	.27	-.27	.59	.43	-.34	
L	PDI	.39	.45	.54				.45			.58	.61	.68	
A	KLE		.38	.27	.25					-.43	.71	.58		
T	KWI													.73
I	KTH	.24				.29			.23		-.47	-.54		.64
O	ETV	.75	.90	.57	.73		.47	.36				.81		
N	TKN	.45	.78	.66	.95	-.24	.29	.29			.77		.25	-.26
	PHR	.30	.36	.49	.28	-.43	.89				.35	.36		
D	KVE	.32	.26			.27		.46	.64	.67	.29			

[(1)] See Table 2 for trait designation

[(2)] Correlations not listed were not significant at the 5% probability level.

TABLE 7. Stepwise, multiple regression analyses. Regression equations $\hat{y}$ = bo + bi xi + ... + bn xn; simplified (. $\hat{y}$ = bo ± xi ... xn). Variables are post harvest ear and caryopsis traits measured on 1985 harvested open - pollinated samples within populations A, B, C and D.

Population	Dependent variable ($\hat{y}$)		Y - intercept (bo)	Independent variables in regression equation (± xi ± .... ± xn)[(1)]	R^2 (%)
A	PHR[(2)]	=	+0.1332	+KRN	7
	ETV	=	-5019.6	+TKN + KLE + PDI	79
	TKN	=	-21.541	+ETV	77
B	PHR	=	-0.0305	+EDI - KTH	30
	ETV	=	-8853.5	+TKN + KVE + PDI + HTT	85
	TKN	=	+91.797	+ETV - KVE	79
C	PHR	=	+0.0120	+KRN + KTH	19
	ETV	=	-5151.7	+MKN + KLE + PDI + HTT	82
	TKN	=	+318.74	+ETV - KWI + PDI + KVE	81
D	PHR	=	-0.2238	+KRN	24
	ETV	=	-10127.1	+TKN + KVE + HTT + PDI	76
	TKN	=	+30.144	+EDI - HTT + ETV - KVE - PDI	75

1) regression coefficients omitted in equations shown

2) PHR = Pith/Hard Tissue Ratio
ETV = Ear Total Volume
TKN = Total Kernel No.
KRN = Kernel Row No.
KLE = Kernel Length
MKN = Maximum Kernel No./Row
PDI = Pith Diameter
EDI = Ear Diameter
KTH = Kernel Thickness
HTT = Hard Tissue Thickness
KVE = Kernel Volume Estimate
KWI = Kernel Width

ability present for the trait in population A, up to a maximum of 30.3% in population B. Nevertheless, responses still indicate differences or similarities among populations:

populations A and D appear thus to be of a similar nature, although quantitatively different because coefficients are different, but the independent variable in the PHR equation is the same, kernel row number (KRN). However, ear total volume (ETV) and total kernel number (TKN) are defined by more variables in population D, than in population A.

In population B, variability present for PHR is explained by the presence of ear diameter (EDI) plus kernel thickness (KTH), whereas the same response variable in population C is defined by kernel row number (KRN) instead of EDI. Also signs of regression coefficients are different for both equations, conditioning entirely different response surfaces. On the other hand, responses for ear total volume (ETV) are similar for populations B and D. Since the dependent variable first in the equation is the one most correlated with the response variable (highest partial R^2), it appears that population D has its own response for total kernel number (TKN) whereas either one or both of the other response variables are similarly defined in populations A and B. In short, regression equations show that all three populations represent different germplasm compositions, overlapping partially with each other in different areas (Table 7).

Morphological studies support the hypothesis that it has been possible to generate populations which differ significantly in kind and degree of tripsacoidy. Furthermore, polyacrylamide gel electrophoresis performed on backcross populations A, B and C, revealed bands which are observed exclusively in *Tripsacum dactyloides* extracts, along with bands from a purple (1974) stock of *Zea mays*.

Yield and combining ability tests of tripsacoid materials are only meaningful if preceeded by adaptation for acceptable yielding ability. This was done by crossing and backcrossing to inbreds 0h43, Mo17 and B73. Diallel crosses separately among BC_1's, BC_2's, and inbreds, tested in a 75-entry experiment, yielded results listed in Table 8. Controls (inbred F_1's) yielded on average more than backcross diallel crosses. However, differences were only significant when controls are compared with crosses among related BC's. Diallel crosses among relatives include the same inbred in the pedigree of both BC parents. For instance, the BC_1 cross (1 x 4) (Table 8) includes 75% 0h43 germplasm in either parent BC, with 25% population A germplasm in one parent and 25% population B in the other parent. In the BC_2 cross (1 x 4), 0h43 contribution to either BC is 87.5% germplasm. If inbreeding coefficients are 0.50 and 0.75 for above BC_1 and BC_2 populations, respectively, diallel crosses would be inbred by 37.50% and 43.75%, respectively (Li, 1955). Grain yields and ear lengths showed highly significant inbreeding depression effects (Figs. 3 and 5). Prolificacy was depressed in all backgrounds except B73 (Fig. 4), whereas ear length in B73 background was more depressed than in 0h43 or Mo17 background (Fig. 5). Thus, inbred B73 would appear to express the genetic load from *T. dactyloides* better than inbreds 0h43 and Mo17, since ear length was more reduced, prolificacy was higher, while grain yield inbred depression was similar in B73, 0h43, and Mo17 backgrounds.

Combining ability analyses were done separately for the BC_1 and BC_2 diallel cross sets. Differences due to general combining ability (GCA) were significant for prolificacy and ear length but not for yield (Table 9). Highest positive values for number of ears/plant were obtained for (B x B73) BC_1 and (A x B73) BC_2 diallel crosses. For ear length, most negative values were obtained for (A x B73), (B x B73), and (C x B73) BC_1 and BC_2 diallel crosses (Table 9 and Fig. 4, Fig. 5). There is a tendency of low or negative GCA values for ear length for population C diallel crosses (Table 9), which however is not confirmed if one considers only crosses among non-related BC's (Fig. 5).

TABLE 8. Average yields, number of ears (NE) per 35' x 30" plot (8.129 m^2) 35 plants/plot, and ear length (EL) recorded form a BC_1, BC_2 diallel cross yield test grown 1981 at Urbana UI experiment station. The first BC_1 cross below was: [(Oh43 x A) x Oh43] x [Mo17 x A) x Mo17].

BC_1 and BC_2 Crosses (only F_1's are shown)	Yield-BC_1 (g/plot)	NE-BC_1 (p/35 pl.)	EL-BC_1 (cm)	Yield-BC_2 (g/plot)	NE-BC_2 (p/35 pl.)	EL-BC_2 (cm)
1 (Oh43xA) x 2(Mo17xA)	5045	34.0	20.9	4694	35.0	20.9
1 (Oh43xA) x 3(B73xA)	5462	37.0	19.6	4375	39.0	18.7
1 (Oh43xA) x 4(Oh43xB)	3758	38.0	17.2	3229	26.7	17.9
1 (Oh43xA) x 5(Mo17xB)	4857	38.3	19.4	5030	35.0	19.7
1 (Oh43xA) x 6(B73xB))	4633	39.0	18.3	4525	32.3	19.4
1 (Oh43xA) x 7(Oh43xC)	3584	32.7	18.2	3562	27.7	19.9
1 (Oh43xA) x 8(Mo17xC)	4684	34.7	20.0	4541	38.3	20.3
1 (Oh43xA) x 9(B73xC)	5446	33.7	20.0	4671	32.0	20.0
2 x 3	4370	31.0	19.6	4305	42.0	18.6
2 x 4	4400	34.7	19.2	5179	33.3	21.0
2 x 5	3698	32.7	18.9	3023	29.7	19.0
2 x 6	5302	40.7	19.0	5141	34.0	18.7
2 x 7	4405	31.0	20.1	4619	33.7	19.2
2 x 8	3420	35.0	17.2	3908	37.3	18.4
2 x 9	4783	31.0	20.7	4543	44.7	17.1
3 x 4	4427	38.7	18.7	3751	26.0	20.2
3 x 5	5162	37.0	19.9	4915	41.7	18.1
3 x 6	4025	35.3	17.4	4361	39.7	17.7
3 x 7	5302	34.3	20.1	5117	44.7	18.2
3 x 8	5147	33.3	20.0	5887	45.3	19.1
3 x 9	4047	34.0	17.6	3309	30.3	16.6
4 x 5	4617	34.3	19.5	4512	34.7	20.3
4 x 6	4982	37.0	18.7	5117	34.7	20.3
4 x 7	3953	32.0	18.2	3504	33.3	17.9
4 x 8	4671	36.3	18.3	4219	36.3	18.3
4 x 9	3954	28.0	18.8	4835	35.3	19.3
5 x 6	5155	34.7	19.7	4931	37.0	19.1
5 x 7	3985	33.7	18.7	3887	30.0	19.6
5 x 8	3345	28.7	18.4	3437	28.3	18.4
5 x 9	4954	33.7	19.6	4733	34.7	20.4
6 x 7	4173	34.0	19.7	3616	36.3	17.4
6 x 8	4782	35.7	20.0	5199	45.3	17.2
6 x 9	3453	36.7	16.3	4307	34.7	16.9
7 x 8	4934	34.3	19.6	4808	32.7	20.1
7 x 9	4747	33.0	19.2	5003	33.7	19.8
8 x 9	5133	32.7	19.3	4947	36.7	18.9
MEAN	4521.32	34.46	19.06	4437.24	35.43	18.97
LSD (Tukey 0.05)	1803.21	------	2.389	1911.08	14.26	2.93
Oh43 x B73	5054.00	26.0	20.1			
Oh43 x Mo17	5677.67	32.0	22.3			
B73 x Mo17	5521.67	27.7	21.3			

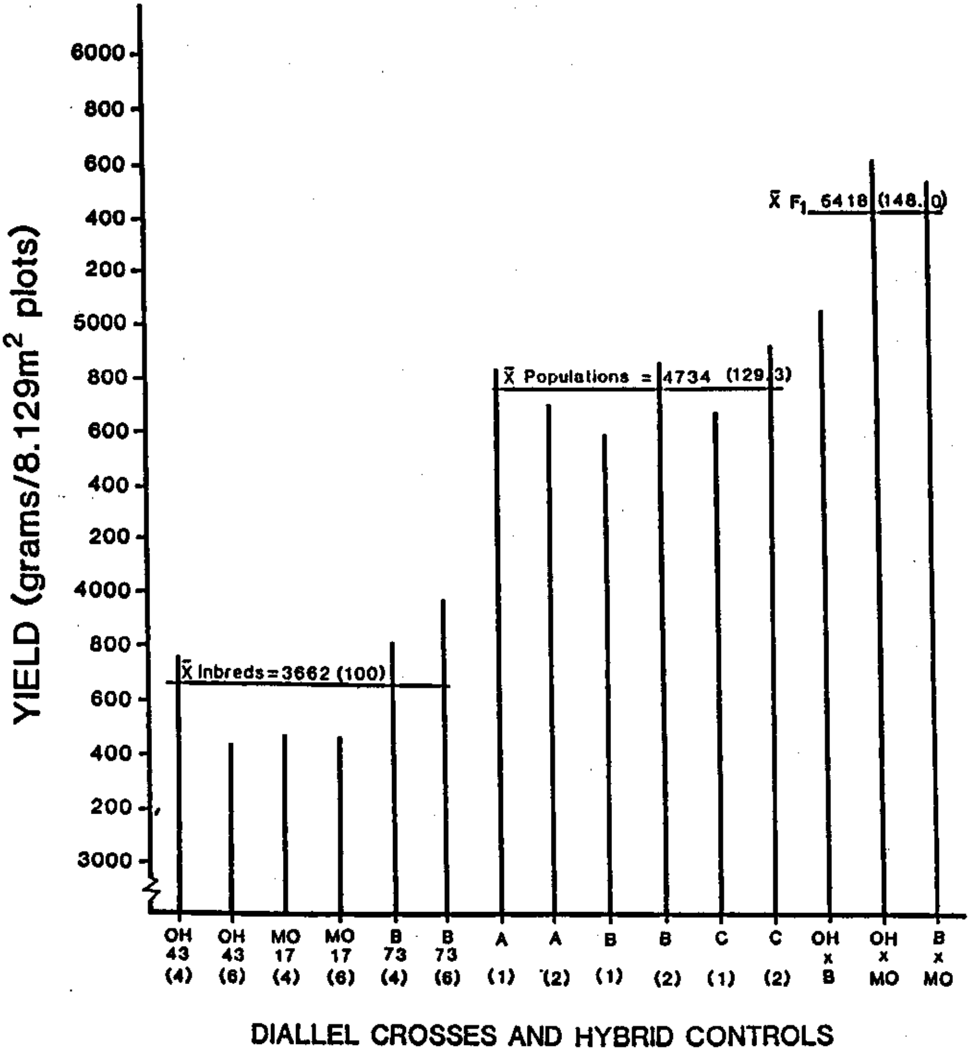

FIG. 3. Illustration of average grain yields of diallel crosses among backcross combinations involving tripsacoid recovered maize populations A, B and C. From left to right, the first group ("inbreds") has 75% or 87.5% gene frequency coming from only one of the elite maize lines, which was involved 4 times in diallel crosses with BC$_1$ and 6 times with BC$_2$ (as indicated below each line in parentheses). The second group ("populations") represents crosses where maize lines involved are different for each participating backcross. Crosses, where each population was involved only once (on one side) or twice (once on each side) are indicated with number 1 and 2 in parentheses.

Specific combining ability (SCA) was significant for grain yield, number of ears/plant and ear length, except for number of ears/plant among BC$_1$ diallel crosses (Table 8). Highly negative and positive SCA effects are evidently due to crosses among relatives and among non-relatives ("inbreds" or not), respectively. According to Griffing

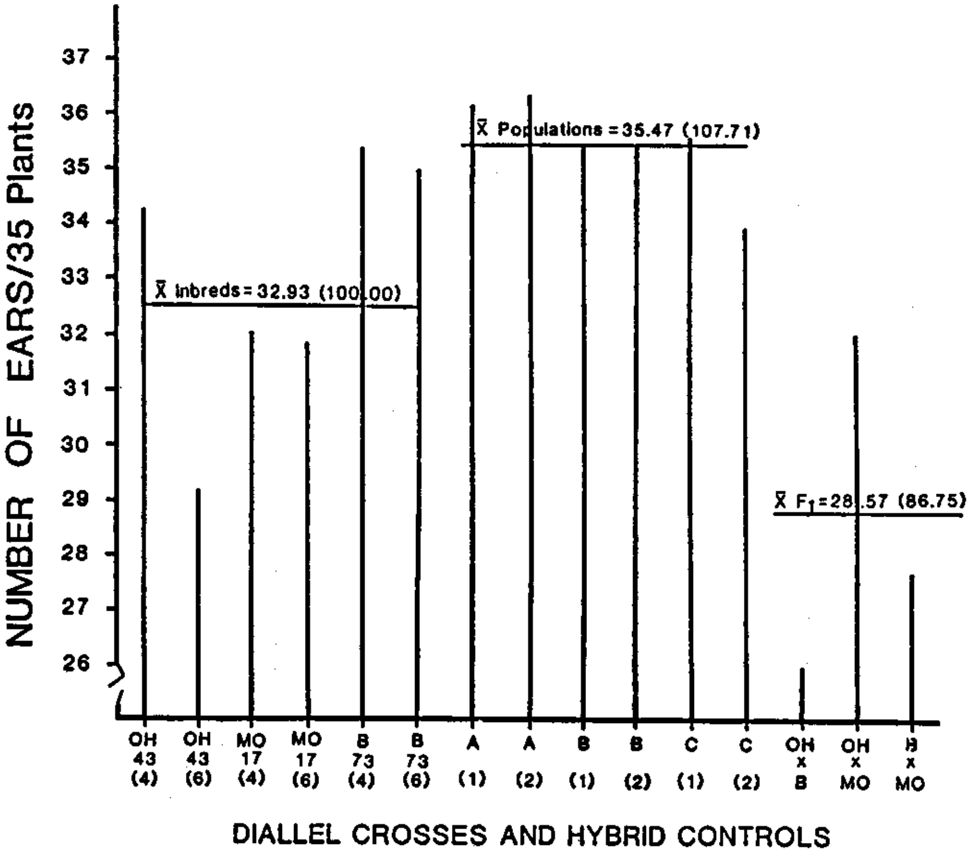

FIG. 4. Illustration of average number of ears/plants of diallel crosses among backcross combinations involving tripsacoid populations A, B and C.

(1956) and Gardner & Eberhart (1966), crosses among relatives should not be present in this kind of diallel. However, this apparent inconvenience turns out to be very informative in regard to differential behaviours of recurrent elite maize lines, as discussed earlier. Relevant results of the diallel experiment are illustrated in Fig. 3, 4 and 5. If one considers averages, grain yields appear more than a 1,000 kg/ha lower in crosses among BC's than in F_1 hybrid checks (Table 8). But the mean difference among non-related BC diallel crosses and F_1 hybrid checks (Fig. 3) is considerably less (-684 kg/ha). Considering specific BC diallel combinations (Table 8), BC_2 cross 3 x 8 (F_1's: (B73 x A) and (Mo17 x C)) yielded more (5,887 kg/ha) than anything else. Some other combinations yielded more than 5t/ha (Table 8).

Results suggest that backcross diallel tripsacoid combinations can be of surprisingly high specific combining ability, as good as some other exotic materials, when compared to results reported by Oyervides-Garcia et al. (1985). However, the breeding potential of tripsacoid material is expected to be different from any *Zea* sources, due to the uniqueness of genetic variability created with the introgression of *T. dactyloides* germplasm into *Z. mays*.

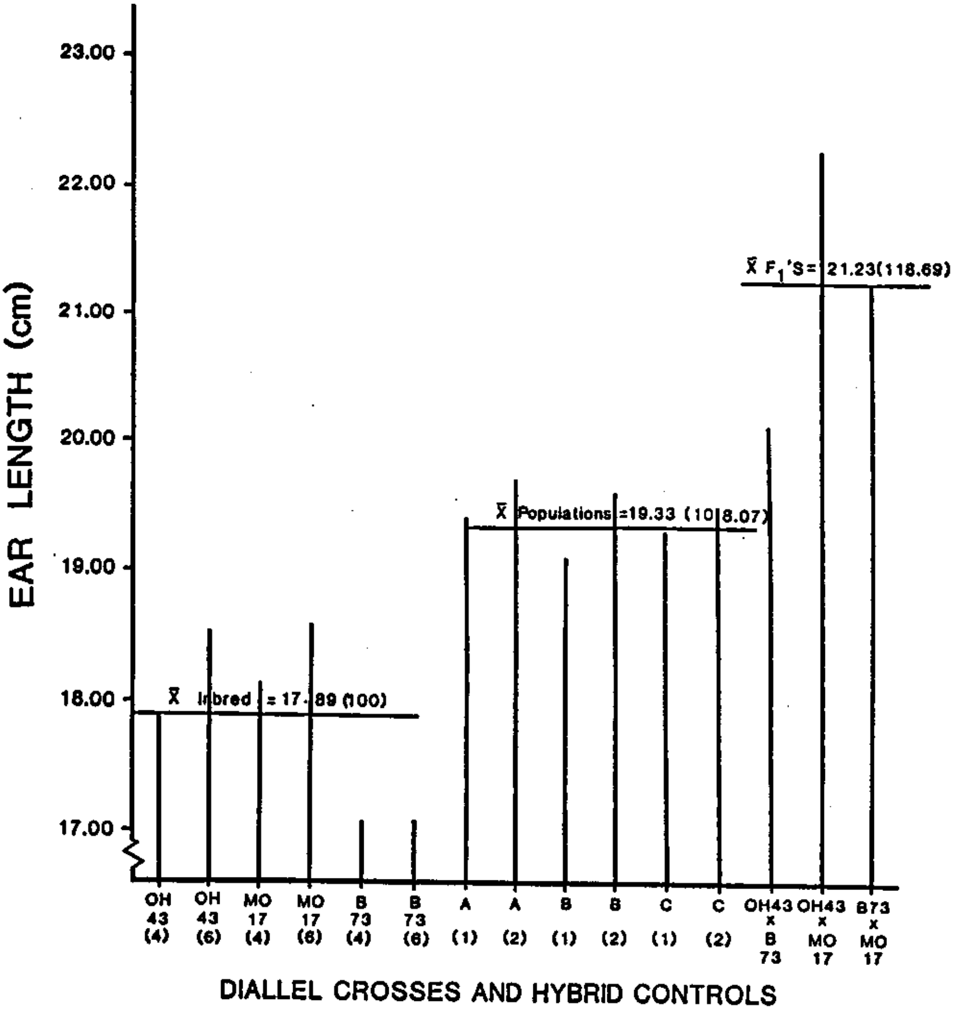

FIG. 5. Illustration of average ear lenght of diallel crosses among backcross combinations involving tripsacoid populations A, B and C.

Results such as reported in this paper may be sufficient to encourage breeders to consider broadening available germplasm bases by introgressing tripsacoid materials.

A convenient number of backcross and recombination generations, depending on the degree of tripsacoidy in the starting material, should yield breeding populations, without loss of potentially useful *Tripsacum* traits. At the same time, their yielding ability is high enough for starting a long-term population improvement scheme aiming at new source populations for inbred line extraction. One would desire to get from *Tripsacum* traits like resistance against drought and diseases and insect pests, more efficient plant architecture and flowering traits and perhaps unusual (for the maize plant) ways of reproduction.

TABLE 9. Estimates of general combining effects summarized from the BC_1 and BC_2 diallel analysis involving tripsacoid populations A, B and C.

Crosses	BC_1 diallel crosses			BC_2 diallel crosses		
	Yield (1) (kg/ha)	Ears/Plant (Nº)	Ear Length (cm)	Yield (kg/ha)	Ears/Plant (Nº)	Ear Length (cm)
1 A x Oh43	181	1.66	0.17	-124	-2.26	0.78
2 A x Mo17	-107	-0.81	0.46	-12	0.88	0.17
3 A x B73	253	0.71	0.07	75	3.41	-0.67
4 B x Oh43	-201	0.47	-0.53	-165	-3.07	0.47
5 B x Mo17	-61	-0.39	0.25	-147	-1.78	0.46
6 B x B73	48	2.47	-0.46	243	1.32	-0.72
7 C x Oh43	-155	1.53	0.16	-197	-1.16	0.04
8 C x Mo17	-8	-0.72	0.04	207	2.41	-0.14
9 C x B73	49	-1.86	-0.18	122	0.26	-0.40

(1) Differences among yield GCA effect estimates were non-significant ($P \leq 0.05$) in both BC_1 and BC_2 dialleles.

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