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Evaluation of an Exotic Maize Population Adapted to a Locality*

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Summary. An exotic *Zea mays* L. population ('Tuxpeno') was adapted to North Carolina conditions by first introducing genes for adaptability from two North Carolina varieties ([('Jarvis' × 'Indian Chief')'Tuxpeno']'Tuxpeno') including four generations of intermating, and then selecting for adaptability using maturity as the primary measure. The study evaluated selection for adaptability and the diversity available between adapted 'Tuxpeno' and the local varieties, 'Jarvis' and 'Indian Chief'. Analytical procedures were developed to quantify the diversity between populations and the complementation of local varieties by introduced germ plasms. The analyses utilized the specific effects available from the diallel mating design.

Three replicate selections responded similarly under simple recurrent mass selection (1/10) for the earliest disease-free plants initially and additionally for plant types (primarily height) in the final generation. The 1/4 local germ plasm permitted rapid adaptation of 'Tuxpeno' gene pool to local conditions. The adapted 'Tuxpeno' populations yielded similarly to the local populations with an average heterosis for grain yield of 28% when crossed to the local populations used as source of genes for adaptability. The diversity found between adapted 'Tuxpeno' lines and these local varieties based on genes affecting grain yield was 1.5 to 2.5 times that measured between the local varieties ('Jarvis' and 'Indian Chief'). Diversity lost through intergradation with local material was a reasonable investment. Yield genes introduced from 'Tuxpeno' complemented local gene pools through nonadditive, primarily dominance-associated, gene effects. Reassortment of major gene blocks apparently occurred leading to significant divergence among replicate selections involving both additive-associated and dominance-associated gene effects.

Key words: Genetic diversity-Convergent selection-Replicate selections-*Zea mays*

Introduction

Populations of maize (*Zea mays* L.) from Latin and South America represent sources of untapped germ plasm for the improvement of maize. Adapting an exotic population of maize to local growing conditions involves modifying characters such as maturity, plant height and disease susceptibility. Populations respond readily to selection for characters affecting adaptability (Compton et al. 1979; Genter 1976; Troyer and Brown 1972). Compton et al. (1979) suggested that mild selection pressure on intermixes of local and exotic populations should prevent loss of favorable alleles during adaptation.

When genes governing adaptability are introduced from local germ plasms, 3 to 4 generations of intermating are needed to merge linkage groups (Hanson 1959). What problems are introduced when linkage groups from local and exotic sources are recombined? If local germ plasms are used as source pools for adaptability genes, would a general shift back to local germ plasms be expected during adaptation? How can genetic differences between these local and introduced populations be quantified? The following study was initiated with the Rockefeller Foundation in Mexico with the objective to clarify these questions when adapting a modern Mexican race of maize to North Carolina.

Genetic diversity between populations is the differences in gene frequencies between populations. A measure of genetic diversity must reflect these differences. However, there is no experimental technique to measure genetic diversity with respect to genes affecting quantitative characters. Hanson and Casas (1968) and Casas et al. (1968) developed a spatial arrangement using information from diallel matings. Distances between populations reflected the

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weighting of differences in gene frequencies between populations by nonadditive genetic effects. They established that these spatial distances would permit a comparison of genetic diversities providing dominance of all affecting loci had unidirectional effects and divergence did not lead to noncompatible gametic combinations. Their technique will be used to evaluate the diversity between the exotic and the local populations used as source of genes for adaptability. An analysis quantifying the complementation of local germ plasms by an exotic population will be developed.

Materials and Methods

Populations

The Mexican race composite, 'Tuxpeno', is of recent origin (Wellhausen et al. 1952) but is tall and late when grown in North Carolina. Maturity was selected as the primary measure of adaptability. The ('Jarvis' × 'Indian Chief')F_4 population was crossed to the 'Tuxpeno' race, V520-C. The hybrid was intermated, and 150 selfed families were grown in North Carolina. The 18 earliest selfed lines were selected, and plants from remnant seed were backcrossed to V520-C and intermated for three cycles. Six cycles of recurrent phenotypic mass selection were then completed. Initially, populations had a high incidence of smutted plants. Only the 40 earliest, disease-free plants (with alternate pollinations) were intermated within a population of 400 plants. As selection proceeded, choice among early, disease-free plants became less restrictive. In cycle 6, attention was given to plant type (primarily height) among the 200 earliest plants. The incidence of smut was negligible in the test generation. Three replicate sets of adapted 'Tuxpeno' (T1, T2 and T3) were initiated in consecutive years. During the completion of T2 and T3 adaptation, T1 was subjected additionally to two cycles of selection for leaf width.

Evaluation

A 6-parent diallel mating design was established for 'Jarvis' (J), 'Indian Chief' (I), (J × I)F_2, T1, T2 and T3. Crosses were made reciprocally between 21-plant rows, and seed was composited. The diallel crosses were tested with 19 replications at Raleigh, NC in 1979. Adequate moisture was available during the growing season. The diversity measured in this environment was of such magnitude that further testing was judged unnecessary. That is, while genetic diversity between two populations is invariant, the analysis used to measure diversity depended upon the characters selected and the environment used for evaluation. The failure to establish genetic differences among populations signifies lack of genetic diversity among populations, inadequate measurement criteria, or the masking of genetic differences by environmental effects. If the diversity measured in an experiment answers the questions posed on genetic differences among populations, then no additional sampling of environments can change these conclusions. However, the establishment of breeding value of a population requires a multiple environment test.

Parents had similar plant types in that average flowering dates were within 5 days and plant heights within 0.2 m. Material was planted in nonbordered, 11 plant plots, 1.07 m rows with 0.46 m plant spacings. Two seeds were planted per hill and thinned randomly. At anthesis, the average number of plants per plot was 10.7 with no differences among treatments. Total plot yields of non-shelled grain were weighed in the field at harvest. For one replication, all plot yields were dried while in the remaining replications each 10th plot was dried. The correction for moisture was 17% with crosses within groups averaging 16% moisture and between groups 17% moisture. Its correlation with grain yield was 0.12. Kg/plant was obtained by dividing plot yield corrected for moisture by number of plants per plot at anthesis. Measurements were maximum width of leaf at the upper ear, height to base of tassel (PH), height to upper ear (EH), EH/PH, days from planting when 1/2 plants were in anthesis, number leaves above upper ear, ears/plant, and grain yield/plant.

Distance Analyses

Consider n local and m exotic populations and the v = (n + m)-parent diallel mating design with no reciprocal crosses. Consider next a function of genotypic values resulting when the rth population is mated to v reference populations, $x_{r1}, \ldots, x_{rs}, \ldots, x_{rv}$. A set of populations (r) can be placed in v dimensions based on their performances (x_{rs}) when mated to each of the v reference populations. Hanson and Casas (1968) used Cartesian distances within this spatial concept to develop measures of diversity among populations; that is,

$$D(r.) = [\sum_s (x_{rs})^2]^{1/2} \qquad 1.1$$

compares the rth population with the reference, $x_{r.} = 0$, and

$$D(r,r') = [\sum_s (x_{rs} - x_{r's})^2]^{1/2} \qquad 1.2$$

compares the rth and r'th populations.

Measurement criteria such as maturity, plant height and leaf width were modified by selection during adaptation. To measure diversity between populations, we based the x_{rs} deviations on specific effects of the diallel which involved primarily dominance-associated gene effects and thus, minimized the effects of major shifts associated with additive gene effects. Hanson and Casas (1968) used the phenotypic means (Y_{rs}), marginal means ($Y_{r.}$, $Y_{.s}$) and mean ($Y_{..}$) of the v-parent diallel to develop the phenotypic deviations:

$$p_{rs} = x_{rs} + \eta_{rs}$$
$$= (Y_{rs} - Y_{r.} - Y_{.s} + Y_{..}). \qquad 2.1$$

Note 4.2 and 5.1 (Appendix) for interpretation. The phenotypic deviations ($p_{r1}, \ldots, p_{rs}, \ldots, p_{rv}$) places the rth population in reference to the v populations but reflects deviations due to experimental errors (η_{rs}) in addition to x_{rs}. Distances estimated are identified as $\hat{D}_1(r.)$ and $\hat{D}_1(r,r')$.

The v-parent diallel can be reorganized into an m-parent diallel of populations in group A (say, exotic) with marginal means ($X_{r.}$), an n-parent diallel of populations in B (say, local) with marginal means ($Z_{.s}$) and the nm matings between groups (Y_{rs}) with mean ($Y_{..}$), Table 1. The m populations in A can be placed in n dimensions based on genotypic values when mated with the n populations in B. Consider the phenotypic deviations:

$$p'_{rs} = x'_{rs} + \eta'_{rs}$$
$$p'_{rs} = (Y_{rs} - X_{r.} - Z_{.s} + Y_{..}). \qquad 2.2$$

Note 4.1 and 5.2 (Appendix) for interpretation. Distances estimated are identified as $\hat{D}_2(r.)$ and $\hat{D}_2(r,r')$.

Experimental error deviations are associated with the estimation of distances. That is,

Table 1. Phenotypic means necessary for the complementation analysis

		Local (Group B)				Exotic (Group A)				
		1	2	..	n	1	2	..	m	Mean
Exotic	1	Y_{11}	Y_{12}	..	Y_{1n}	X_{11}	X_{12}	..	X_{1m}	$X_{1.}$
	2	Y_{21}	Y_{22}	..	Y_{2n}		X_{22}	..	X_{2m}	$X_{2.}$
		.	.						.	.
		.	.						.	.
	m	Y_{m1}	Y_{m2}	..	Y_{mn}				X_{mm}	$X_{m.}$
Local	1	Z_{11}	Z_{12}	..	Z_{1n}					
	2		Z_{22}	..	Z_{2n}					
					.					
					.					
	n				Z_{nn}					
Mean		$Z_{.1}$	$Z_{.2}$	..	$Z_{.n}$					

$Y_{rs} = \underline{f}_{1r} G \underline{f}'_{2s} + \epsilon_{rs}$; $X_{rs} = \underline{f}_{1r} G \underline{f}'_{1s} + \epsilon_{1r1s}$; $Z_{rs} = \underline{f}_{2r} G \underline{f}'_{2s} + \epsilon_{2r2s}$; $E\epsilon^2_{rs} = \sigma^2_{\bar{X}}$

Table 2. Deviations and expected errors corresponding with analytical procedures designed to establish spatial arrangements which reflect diversity among populations[a]

	Deviation	Composition of error $\left(k_i^2 \sigma^2_{\bar{X}}\right)$	
Analysis	(p_{rs})	$D^2(r.)$	$D^2(r,r')$
Diversity (1)	$(Y_{rs} - Y_{r.} - Y_{.s} + Y_{..})$[b]	$(v - v_1)(v^2 - v + 1)\sigma^2_{\bar{X}}/v_1 v^2$	$(v_1 + v_2)(v^2 - v + 1)\sigma^2_{\bar{X}}/v_1 v_2 v$
Complementation (2)	$(Y_{rs} - X_{r.} - Z_{.s} + Y_{..})$[c]	$(nm + m + n + 3)\sigma^2_{\bar{X}}/m$	$2n(m^2 + m - 1)\sigma^2_{\bar{X}}/m^2$

[a] Diallels are made without reciprocal matings

[b] Based on the $v = (n + m)$ – parent diallel with marginal means ($Y_{r.}$, $Y_{.s}$) and diallel mean ($Y_{..}$). The analysis was developed to compare the mean deviations of v_1 parents in group A (p_{as}) with mean deviations of v_2 parents in group B (p_{bs})

[c] For data as organized in Table 1 with an m-parent diallel of populations in group A with marginal means ($X_{r.}$), an n-parent diallel of populations in group B with marginal means ($Z_{.s}$) and the nm matings between groups (Y_{rs}) with mean ($Y_{..}$). The populations in A are plotted relative to their performances when crossed to the n reference populations (B)

$$E\sum_s p_{rs}^2 = D_1^2(r.) + k_i^2 \sigma^2_{\bar{X}}, \text{ and} \quad 3.1$$

$$E\sum_s (p_{rs} - p_{r's})^2 = D_1^2(r,r') + k_i^2 \sigma^2_{\bar{X}}, \quad 3.2$$

for example (Note 6.1, Appendix). The compositions of $k_i^2 \sigma^2_{\bar{X}}$ corresponding to the four distances are given in Table 2. Environmental error variances were corrected for in the estimates of distances.

$$\hat{D}_1(r.) = [\Sigma_s p_{rs}^2 - k_i^2 \sigma^2_{\bar{X}}]^{1/2}, \quad 3.3$$

for example.

The analysis of Hanson and Casas (1968) represents a diversity analysis among v populations. The distance of primary interest is $D_1(r,r')$ which estimates pair-wise distances between populations in $(v - 1)$ dimensions. Each distance reflects the weighting of differences in gametic frequencies between two populations by a set of $(v - 1)$ vectors reflecting non-additive genetic effects (Note 5.1, Appendix). The second analysis measures the complementation of reference populations (group B) by introduced populations (group A). $D_2(r.)$ is of primary interest and reflects weighting of differences in gametic frequencies between, say, the rth exotic population and the local populations by a set of n vectors reflecting the nonadditive gene effects expressed between exotic and local populations (5.2, Appendix).

Dividing relationships 3.1 or 3.2 by the appropriate $k_i^2 s^2_{\bar{X}}$ yield F ratios with $(v - 1)$ degrees of freedom for numerator. When p_{rs} deviations are standardized by $k_i s_{\bar{X}}$, $\hat{D} > \sqrt{F_\alpha - 1}$ is required for significance of $D_1(r,r')$ from zero based on α level of probability.

The test of the hypothesis that $D_2^2 = 0$ follows from the F distribution with n degrees of freedom for numerator. With standardized distances, different measurement criteria can be compared and/or combined. Each measurement criterion yields unbiased estimates for D^2. Combining information from different measurement criteria can be accomplished by calculating the average pooled sums of deviations squared based on standardized deviations. These standardized phenotypic distances squared estimate ($D^2 + 1$) with corresponding pooled degrees of freedom. A reduction in dimensionality can be accomplished by principal components (Sokal and Sneath 1968) where axes for p_{rs} are rotated and components removed until the residual variability in p_{rs} is nonsignificant.

Results

Each year, the three replicate selections completed in the proceeding year together with the (J × I)F_2 and V520-C populations were evaluated for maturity in ten replicate trials. Maturity was expressed as deviations from (J × I)F_2 maturity. Rapid convergence of the 'Tuxpeno' material to local maturities was found (Fig. 1). The standard error of the mean based on variability among the replicate selections tested in consecutive years was 0.59. Replicates had similar maturities at comparable selection stages. Selection for maturity was relaxed in the 6th cycle with emphasis on plant type, height primarily. The response to a 0.12 selection differential on selfed families was 3.6 days, and the response to mass selection (0.1 intensity) on both parents was 2.7 days per cycle for 5 cycles.

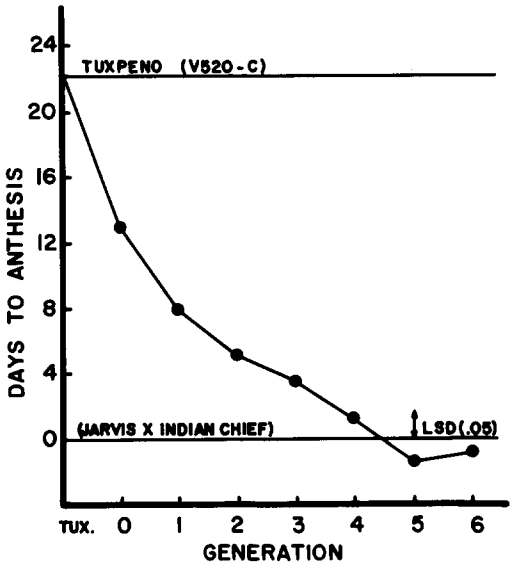

Fig. 1. Average days to anthesis for three Tuxpeno-derived lines relative to (J × I)F_2 when selected (1 in 10) for disease-free, early-flowering plants primarily during generations 0 to 5 and for reduced plant height in generation 6

The sixth cycle, tuxpeno-derived material had similar grain yields but was earlier and shorter than the North Carolina varieties (Table 3). The modified 'Tuxpeno' population which carried genes for adaptability introduced from local populations responded to selection for acceptable

Table 3. Characteristics of six maize populations used as parents in the 6-parent diallel

	Leaf width	Plant height	Days to anthesis	EH/PH	Number leaves	Ears/pl	Grain yield
	(cm)	(m)	(d)				(Kg/pl)
'Jarvis' (J)	11.82	2.36	80.0	0.667	7.02	1.12	0.217
'Indian Chief' (I)	10.72	2.34	82.2	0.671	6.79	1.28	0.195
(J × I)F_2	11.51	2.39	81.2	0.675	6.94	1.21	0.221
T1[a]	13.06	2.18	77.6	0.663	6.02	1.26	0.183
T2	10.91	2.34	79.0	0.677	6.21	1.26	0.226
T3	11.79	2.24	77.9	0.657	6.62	1.27	0.232
LSD (.05)	0.39	0.09	1.0	0.021	0.24	0.13	0.025

[a] Three replicate selections of 'Tuxpeno'-derived material

Table 4. Mean squares for the analyses of variance involving seven characters measured on 21 maize populations (19 replications)

Source variation	Degrees freedom	Leaf width	Plant height	Flowering	EH/PH	Number leaves	Ears/pl	Grain yield
		(cm)	(m)	(d)				(Kg/pl)
Populations	20	9.06**	0.1111**	37.96**	0.0016	1.40**	0.082**	0.0139**
General	5	31.08**	0.2800**	137.58**	0.0008	4.92**	0.174**	0.0076**
Specific	15	1.68**	0.0548**	4.75*	0.0018	0.22	0.052	0.0161**
Error	360[a]	0.36	0.0190	2.53	0.0011	0.14	0.038	0.0015

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

[a] Degrees of freedom was 340 for grain yield where only 18 replications were harvested

Table 5. Grain yields for the 6-parent diallel matings together with marginal means (kg/plant)

	Jarvis (J)	Indian Chief (I)	$(J \times I)F_2$	T1	T2	T3[a]	$Y_{r.}$
J	0.217	0.249	0.253	0.246	0.271	0.263	0.250
I		0.195	0.215	0.261	0.273	0.294	0.248
$(J \times I)F_2$			0.221	0.255	0.268	0.270	0.247
T1				0.183	0.239	0.221	0.234
T2					0.226	0.236	0.252
T3						0.232	0.253
$Y_{.s}$	0.250	0.248	0.247	0.234	0.252	0.253	0.247

$s^2_{\bar{x}} = 0.0000820$ (for Y_{rs} means); LSD (0.05) = 0.025

[a] Three replicate selections from the 'Tuxpeno'-derived material

Table 6. Standardized phenotypic distances among six maize populations together with estimates of distances based on pooled standardized distances among characters

Distance[a]	Phenotypic distances: Leaf width (1)	Plant height (2)	Date flowering (3)	Grain yield (4)	$\hat{D}_1(r,r')$ 1-3	1-4
1,2	1.57	1.39	1.21	2.78	0.98	1.55
1,3	1.16	0.78	1.18	2.05	0.34	0.94
1,4	2.24	1.05	1.02	2.72	1.18	1.62
1,5	1.65	1.44	1.36	2.77	1.10	1.61
1,6	2.37	1.54	1.11	2.91	1.44	1.85
2,3	1.20	1.20	1.22	1.13	0.68	0.64
2,4	2.54	2.36	1.42	4.54	1.92	2.77
2,5	2.01	2.51	1.25	4.25	1.72	2.55
2,6	3.05	2.74	1.20	4.82	2.25	3.06
3,4	1.70	1.51	1.64	3.56	1.27	2.03
3,5	1.58	1.58	1.91	3.24	1.37	1.95
3,6	1.91	1.80	1.30	3.79	1.36	2.18
4,5	2.40	0.93	1.08	1.73	1.26	1.30
4,6	1.89	1.07	1.36	1.15	1.09	0.99
5,6	2.02	0.78	1.84	1.06	1.30	1.14
Required for Significance:	1.49[b] 1.75	1.49[b] 1.75	1.49[b] 1.75	1.49[b] 1.75	0.83[c] 1.04	0.75 0.92

[a] 1 = 'Jarvis'; 2 = 'Indian Chief'; 3 = $(J \times I)F_2$; 4 = T1; 5 = T2; 6 = T3

[b] Based on $\sqrt{F}$ ratio for 5 and 360 degrees of freedom and 0.05 and 0.01 levels of probability

[c] Based on $\sqrt{F\text{-}1}$ for 15 and 360 degrees of freedom, respectively, and 0.05 and 0.01 levels of probability

plant types. The diallel analyses according to Griffin (1956) are summarized (Table 4). Analyses were based on 19 replications except for grain yield for which one replication was discarded due to abnormal variability. Highly significant differences were found among populations for all characters except EH/PH. The heterosis for grain yield between Jarvis and Indian Chief was 21% (Table 5), which is comparable to other estimates (Hanson and Moll 1973, Moll et al. 1965), and between the adapted 'Tuxpeno' lines and 'Jarvis' and 'Indian Chief' was 21% and 35%, respectively.

Diversity Relationships

Three of the six plant measurements together with grain yield had significant specific effects (Table 4). Thus, these

four characters will contribute information to a diversity analysis. The $p_{rs} = (Y_{rs} - Y_{r.} - Y_{.s} + Y_{..})$ deviations identified in Table 2 and 2.1 were calculated for the four measurement criteria. The $\hat{D}_1(r,r')$ calculated (Table 6) estimate distances between populations based on p_{rs} deviations standardized by $k_i s_{\bar{X}}$ (Table 2). As an example, let us consider grain yield data and the distance between 'Jarvis' and 'Indian Chief'. The p_{rs} deviations were calculated from data in Table 5, and

$$\{\sum_s (p_{1s} - p_{2s})^2\}^{1/2} = \{(-0.036 + 0.002)^2 + \ldots +$$

$$(0.007 - 0.040)^2\}^{1/2} = 0.0809,$$

or in standard units,

$$= 2.78$$

where $k_i s_{\bar{X}} = .0291$ (Tables 2, 5). These standardized phenotypic distances estimate $[D^2(r,r') + 1]^{1/2}$.

The information from the three plant measures was pooled. For example, the estimated distance between 'Jarvis' and 'Indian Chief' (Table 6) based on plant characteristics is,

$$D(1,2) = \{(1.57^2 + 1.39^2 + 1.21^2)/3 - 1\}^{1/2} = 0.98,$$

with 15 degrees of freedom. $\bar{T}$ was plotted in the two-dimensional plot based on estimated distances among J, I and (J × I)F_2 so that the distances between J-$\bar{T}$, I-$\bar{T}$ and (J × I)-$\bar{T}$ had minimum variation from the corresponding estimated distances. Similarly, the mean for the native populations ($\bar{JI}$) was plotted in the two-dimensional plot for T1, T2 and T3 populations. The diversity relationships among populations based on leaf width, plant height and flowering data are presented in Figure 2 while the diversity relationships for the combined information using the three plant characteristics and grain yield are presented in Figure 3.

The patterns of relationships among populations were quite similar for measurement criteria. 'Indian Chief' showed a greater diversity with adapted 'Tuxpeno' than 'Jarvis'. 'Tuxpeno' lines diverged significantly during selection. The average distance among 'Tuxpeno' selections was 74% that found between 'Jarvis' and 'Indian Chief' (Table 6). The distances estimated between exotic and the two local varieties were 1.5 times that observed between the two local varieties.

Complementation

Complementation between gene pools for grain yield is of primary interest. The data (Table 5) were rearranged per

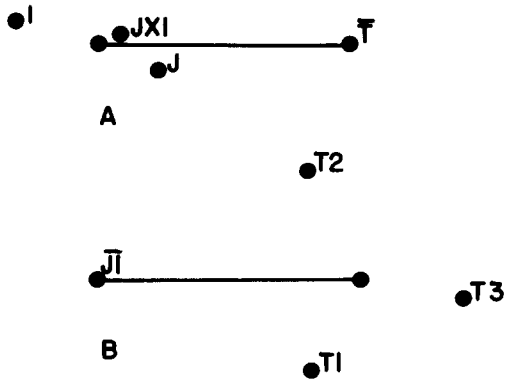

Fig. 2. Diversity relationships with reference to the $\bar{JI} - \bar{T}$ axis based on pooled information from three plant characters placing average Tuxpeno adapted ($\bar{T}$) relative to Jarvis (J), Indian Chief (I) and (J × I)F_2 (A) and placing average Jarvis-Indian Chief complex ($\bar{JI}$) relative to the Tuxpeno replicates (B)

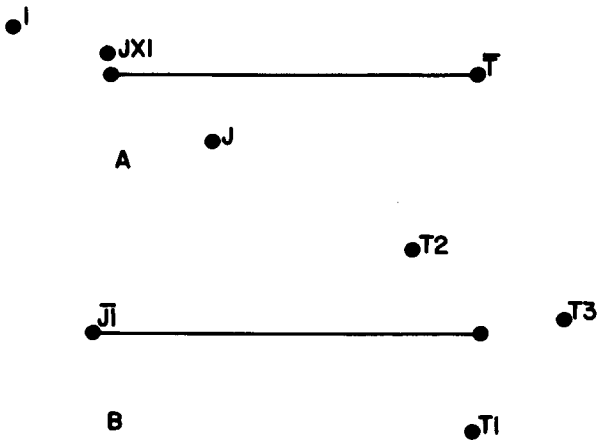

Fig. 3. Diversity relationships with reference to the $\bar{JI} - \bar{T}$ axis based on pooled information from three plant characteristics and grain yield placing average Tuxpeno adapted ($\bar{T}$) relative to Jarvis (J), Indian Chief (I) and (J × I)F_2 (A) and placing average Jarvis-Indian Chief complex ($\bar{JI}$) relative to the Tuxpeno replicates (B)

Table 1, and p'_{rs} deviations were calculated as indicated in Table 2 or 2.2. Estimates for standardized $D_2(r.)$ were obtained using both local and introduced populations as reference populations (Table 7). The comparable distances between a line in group A and the mean of group B, D(r,b), based on the diversity analysis for grain yield are also given. Estimates for $D_2(r.)$ were about 1.5 times larger than for $D_1(r,b)$. 'Indian Chief' had a significantly greater deviation from $\bar{T}$ than 'Jarvis' reflecting greater complementation due to nonadditive gene effects between 'Tuxpeno' and 'Indian Chief'. The $D_2(r.)$ distances between local and introduced populations were about 2.5 times that found between 'Jarvis' and 'Indian Chief'. A major complementation of local material by the introductions was found relative to that available between the local populations.

Table 7. Estimates of standardized distances between local populations and the adapted 'Tuxpeno' germ plasms and between adapted 'Tuxpeno' populations and local germ plasms based on complementation and diversity analyses. Analyses based on grain yield measure[a]

Comparison[b]	Complementation $\hat{D}_2(r.)$	Diversity $\hat{D}_1(r,b)$
J – I	2.49	2.59
J – $\bar{T}$	4.68	3.15
I – $\bar{T}$	7.57	5.39
(J × I)F_2 – $\bar{T}$	5.82	4.11
T1 – $\bar{JI}$	6.02	4.14
T2 – $\bar{JI}$	5.74	3.87
T3 – $\bar{JI}$	6.62	4.46

[a] All estimates of distances are highly, significantly different from zero

[b] The local populations are identified as J = 'Jarvis', I = 'Indian Chief' and the adapted 'Tuxpeno' populations as T1, T2 and T3

Discussion

Cress (1966) concluded that heterosis did not necessarily reflect genetic diversity between two populations. However, Hanson and Casas (1968) demonstrated that their diversity analysis, which utilized the specific effects in a v-parent diallel, gave a reasonable basis for comparing genetic diversities providing dominance was unidirectional and types of gene interactions were distributed among population crosses. We have constructed examples of diallel matings using an unidirectional dominance model and examined the correlations between $D_1(r,r')$ and a measure of genetic diversity based on differences in gene frequencies (q_{ri}), $[\sum_i (q_{ri} - q_{r'i})^2]^{1/2}$. The correlations increased when the number of loci was increased or the difference in gene frequencies between populations were increased. With v = 6, and 6 or more loci, the correlations ranged between .96 and .99 being essentially one with distinct differences among populations. Hanson and Moll (1973) using this diversity analysis reconstructed the genetic relationship among nine populations resulting from intergradation among three maize populations. In our study (J × I)F_2 was intermediate to 'Jarvis' and 'Indian Chief'. These results support their (1968) conclusion that for measures such as grain yield, $D_1(r,r')$ permits the comparison of relative genetic diversities between recently integrated or closely related populations. However, distortion of genetic relationships will occur when genes having unique interactions are associated with specific population crosses.

In contrast to the diversity analysis, the complementation analysis involves the nonadditive gene effects between the exotic vs. local gene pools (Note 4.1, 4.2, Appendix). If similar types of epistasis are expressed among population crosses, the $\underline{I}\,\underline{f}'_2$. in 4.1 should be zero and the standardized distances, $D_2(r.)$ and $D_1(r,b)$ in 5.1 and 5.2, should be similar noting that $D_1(r,b)$ is between the rth population in A and the average of the n populations in B and $(\underline{f}_{1r} - \underline{f}_{2.}) = (\underline{f}_r - \underline{f}_b)$. The standardized $D_2(r.)$ estimates were 1.5 times larger than those for $D_1(r,b)$, Table 7. A set of unique gene complexes was introduced from Tuxpeno which gave favorable (Note heterosis, Table 5) dominance-associated gene interactions with the local gene pools. 'Jarvis' and 'Indian Chief' contributed equally to the adapted 'Tuxpeno' background, yet 'Indian Chief' had significantly greater distances from $\bar{T}$ than Jarvis (Tables 6, 7, Fig. 3) indicating further the importance of unique epistatic combinations in gene expression.

Replicate selections of 'Tuxpeno' diverged significantly even though effective population size of 80 was maintained. The divergence between 'Tuxpeno' lines as determined from all measures (Table 6) was about 74% that found between 'Jarvis' and 'Indian Chief'. Apparently, major blocks of genes assorted during adaptation involving both additive (Note low grain yields for T1, Table 3) and nonadditive gene effects (Table 6).

'Jarvis' and 'Indian Chief' normally exhibit 20 to 24% heterosis (Moll et al. 1965; Hanson and Moll 1973), being 21% in this study. Major diversity was expressed between adapted 'Tuxpeno' lines and the two local varieties, being 1.5 (Table 6) and 2.5 (Table 7) times that found between these two local varieties. The genetic background of adapted 'Tuxpeno' is at least 25% 'Jarvis-Indian Chief' depending upon the shifts associated with selection. 'Tuxpeno' is sufficiently genetically diverse from 'Jarvis' and 'Indian Chief' so that intergradation with 'Jarvis' and 'Indian Chief' to obtain a gene pool for adaptation leaves considerable residual diversity.

Grain yields of the adapted populations as determined here and in preliminary trials were similar to local populations. From the results of this study, one concludes that yield genes involving nonadditive or dominance-associated gene effects were introduced from Tuxpeno which augmented the local gene pools. 'Tuxpeno' is one of the many modern races available (Wellhausen et al. 1952). Valuable gene pools are likely available requiring only the adaptation of the gene pool to an area. Characters associated with adaptability were highly heritable within the population created by crossing 'Tuxpeno' to a local population and then backcrossing to 'Tuxpeno'.

Appendix

Consider n local populations together with m exotic populations. Populations are each at gene frequency equilibrium. Identify the gametic types for all loci, say w types, found in the (n + m) populations. Let $\underline{G}$ be a w × w matrix of genotypic values resulting from the pairwise union of

the w gametic types. Consider next the gametic frequencies for the rth population, $\{f_{ir}\}$, corresponding to the array of gametic types, noting that a frequency is zero if the gametic type is not present in a population, and express the frequencies as a 1 × w row vector ($\underline{f}_r$). The vectors associated with the rth exotic population will be identified as $\underline{f}_{1r}$ and with the sth local population as $\underline{f}_{2s}$ with mean frequencies within exotic and local groups being $\underline{f}_{1.}$ and $\underline{f}_{2.}$, respectively, and $(m\,\underline{f}_{1.} + n\,\underline{f}_{2.})/(n+m) = \underline{f}_{.}$. The genotypic mean for the union of the rth exotic and sth local variety is

$$\sum_i\sum_j f_{1ir} f_{2js} G_{ij} = \underline{f}_{1r}\underline{G}\,\underline{f}'_{2s},$$

in matrix notation where the prime designates the transpose of a matrix.

The (i, j) element of $\underline{G}$ can be expressed as a linear combination of effects,

$$G_{ij} = u + a_i + a_j + I_{ij},$$

of a constant, u, gametic effects, a_i and a_j, and a gamete-gamete interaction effect, I_{ij}. The matrix $\underline{G}$ can be expressed as a sum of three w × w matrices,

$$\underline{G} = \underline{U} + \underline{A} + \underline{A}' + \underline{I},$$

where the elements of $\underline{U}$ are the constant u, $\underline{A}$ represents a collection of w (identical) row vectors ($\underline{A}_1$) whose respective elements are a_i effects, and $\underline{I}$ represents the matrix of I_{ij} effects. To specify the model, we require $\underline{A}\,\underline{f}'_{.} = \underline{I}\,\underline{f}'_{.} = \underline{0}$ where $\underline{f}_{.}$ is the row vector of mean gametic frequencies for the (n + m) populations. Because the model is based on gametic effects, a_i reflects additive-associated gene effects while with no epistasis I_{ij}'s are non-zero if and only if dominance is present. Otherwise, $\underline{I}$ reflects dominance-associated effects and some additive-associated epistatic effects.

We will examine in detail the phenotypic deviation (2.2):

$$p'_{rs} = x'_{rs} + \eta'_{rs} = (Y_{rs} - X_{r.} - Z_{.s} + Y_{..})$$

$$\begin{aligned} E(p'_{rs}) &= (\underline{f}_{1r}\underline{G}\,\underline{f}'_{2s} - \underline{f}_{1r}\underline{G}\,\underline{f}'_{1.} - \underline{f}_{2.}\underline{G}\,\underline{f}'_{2s} + \underline{f}_{1.}\underline{G}\,\underline{f}'_{2.}) \\ &= (\underline{f}_{1r} - \underline{f}_{2.})(\underline{U} + \underline{A} + \underline{A}' + \underline{I})(\underline{f}_{2s} - \underline{f}_{1.})' \\ &= (\underline{f}_{1r} - \underline{f}_{2.})[\underline{I}\,\underline{f}'_{2s} + (n/m)\,\underline{I}\,\underline{f}'_{2.}] \\ &= (\underline{f}_{1r} - \underline{f}_{2.})\underline{B}'_{2s} = x_{rs},\ 1 \leqslant s \leqslant n, \end{aligned} \qquad 4.1$$

noting that $(\underline{f}_{1r} - \underline{f}_{2.})\underline{U} = (\underline{f}_{1r} - \underline{f}_{2.})\underline{A} = \underline{A}'(\underline{f}_{2s} - \underline{f}_{1.})' = \underline{0}$ and the restriction $\underline{I}\,\underline{f}'_{.} = \underline{0}$. For the phenotypic deviation 2.1:

$$\begin{aligned} E(p_{rs}) &= (\underline{f}_r - \underline{f}_{.})\underline{I}\,\underline{f}'_s \\ &= (\underline{f}_r - \underline{f}_{.})\underline{B}'_{1s} = x_{rs},\ 1 \leqslant s \leqslant v, \end{aligned} \qquad 4.2$$

Substituting 4.2 into 1.2 yields

$$D_1(r,r') = \{\sum_i [(\underline{f}_r - \underline{f}_{r'})\underline{B}'_{1i}\}^{1/2},\ 1 \leqslant i \leqslant (v-1), \qquad 5.1$$

where $\underline{B}_{1i}$ result from the reduction of the $\underline{B}_{1s}$ to (v − 1) row vectors; that is, the v × v, x_{rs} deviations in 2.1 yield a singular matrix with rank (v − 1), Hanson and Casas (1968). Substituting 4.1 into 1.1 yields

$$D_2(r.) = \{\sum_s [(\underline{f}_{1r} - \underline{f}_{2.})\underline{B}'_{2s}]^2\}^{1/2},\ 1 \leqslant s \leqslant n, \qquad 5.2$$

for the complementation analysis.

One is dealing with phenotypic deviations. Thus, for example,

$$\begin{aligned} E\sum_s (p_{rs} - p_{r's}) &= E\sum_s (x_{rs} - x_{r's} + \eta_{rs} - \eta_{r's})^2 \\ &= D_1^2(r,r') + k_i^2\,\sigma_X^2 \end{aligned} \qquad 6.1$$

where η_{rs} is the error deviation associated with a phenotypic deviation and is composed of errors (ϵ_{rs}) associated with means and marginal means, $E(\epsilon_{rs}^2) = \sigma_X^2$. The error compositions associated with the four distances are summarized in Table 2. The complexity of error variances result because the analysis is based on no reciprocal crosses, $\epsilon_{rs} = \epsilon_{sr}$.

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