

EXPERIMENTAL EVALUATION OF RELATIONSHIPS AMONG
POPULATIONS RESULTING FROM INTERGRADATION
AMONG CULTIVARS OF *ZEA MAYS* L.

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Manuscript received October 19, 1972

Revised copy received January 11, 1973

Transmitted by R. W. ALLARD

ABSTRACT

Populations were developed as intergradations among three maize cultivars, two adapted to North Carolina and one to Mexico, with the objective of testing whether diallel information could be used to identify the relationships among populations. The data substantiated theoretical observations that the technique would identify relationships among populations resulting from recent intergradations.

NUMERICAL taxonomic techniques (SOKAL and SNEATH 1963) utilize phenotypic differences based on multiple measurement criteria to discriminate among populations. The relative distances represent a criterion for assessing genetic relationships among populations. Measures which contribute primarily to discrimination are phenotypically stable and heritable. For a cultivated species such as maize, selective forces must be influenced by man. The acceptability (to man) of morphological types could have resulted in parallel evolution and in populations which were morphologically similar, or conversely, dissimilar. HANSON and CASAS (1968) investigated information available from hybrid population means to supplement numerical taxonomic information. They noted that if gene effects were additive at the gene level, or if only additive genetic effects were considered, hybrid means did not contribute new formation. However, non-additive gene effects (dominance and epistasis) contributed unique information for discrimination among populations. They developed coordinate positions for populations within a space utilizing variability among specific effects (non-additive gene effects) estimated from the diallel mating design. Distances between populations were shown to reflect weighted differences in gametic frequencies between populations. Thus, relative distances can be used to assess genetic relationships among populations. Grain yield per plant was selected as the measurement criterion. It is a complexly-inherited trait and, thus, contrasts with those used for numerical taxonomy. The character exhibits considerable non-additive effects when measured among populations.

HANSON and CASAS (1968) noted that with diverse populations the diallel information could yield a distorted spatial arrangement. CASAS, HANSON and WELLHAUSEN (1968) considered populations resulting from recent intergradations

between two base populations and concluded that information from the diallel mating design could be used to establish relationships among such populations. In contrast with the case involving diversity, we are dealing here with intergradation of gene frequencies and genotypic combinations. While gene frequencies represented a linear combination of gene frequencies for the base populations, gametic frequencies did not follow this pattern, resulting in terms which were ignored in the development. The objective of this research was to test whether the diallel information could be used to detect complicated intergradations which had been experimentally constructed. Three base populations were selected to represent a range of diversity.

MATERIALS AND METHODS

Three maize cultivars were selected from the study of MOLL *et al.* (1965): Jarvis and Indian Chief, two North Carolina cultivars, exhibited considerable heterosis while Zapalote Chico, a Mexican cultivar, failed to exhibit the level of heterosis expected. Maturities were within a two-week span. Crosses between cultivars were made reciprocally and composited. The following crosses were then made yielding nine populations:

$$\begin{aligned} (100)(100) &= (100) & (110)(110) &= (110) & (110)(101) &= (211) \\ (010)(010) &= (010) & (101)(101) &= (101) & (110)(011) &= (121) \\ (001)(001) &= (001) & (011)(011) &= (011) & (101)(011) &= (112) \end{aligned}$$

where (100), (010), and (001) represent populations corresponding to the three cultivars Jarvis, Indian Chief, and Zapalote Chico, respectively. We denote populations by numbers in parenthesis to represent the respective proportions of the three parents in each population. Each cross was made reciprocally between 40 plant plots and composited. The levels of recombination and/or sampling were similar among populations. A preliminary diallel study was completed with these nine populations to determine whether more detailed studies were warranted. The results of the preliminary study are reported here, but additional work was terminated because evidence for unusual gamete interactions was lacking.

Crosses for the nine parent diallels were made reciprocally, when possible, between 20 plant plots and reciprocal crosses were composited. The 45 crosses (which included the nine populations) were tested in a randomized block design with 10 replications grown at Clayton, Rocky Mount, and Plymouth, North Carolina Agricultural Experiment Stations in 1971. Plots consisted of 2 rows \times 10 hills each. Yield of ear corn was taken on 10 competitive plants.

RESULTS AND DISCUSSION

The spatial arrangement development by HANSON and CASAS (1968) identified coordinate positions, say $(x_{r1}, \dots, x_{r(n-1)})$ for the r^{th} of n populations, where the distance of the population from the average was defined as

$$R(r.) = [\sum_i (x_{ri})^2]^{1/2}$$

and from the r'^{th} population as

$$R(r,r') = [\sum_i (x_{ri} - x_{r'i})^2]^{1/2}, \quad 1 \leq i \leq (n-1).$$

These distances represent the basic parameters to be estimated from the data. Working with the expected sums of squares of specific effects (p_{rs}) estimated from the diallel, HANSON and CASAS (1968) obtained

$$E\sum_s (p_{rs})^2 = R^2(r.) + (n-1)(n^2 - n + 1)\sigma_{\epsilon}^2/n^2$$

where $\frac{2}{\sigma_{\epsilon}^2}$ represents the error variance of a phenotypic mean, P_{rs} , for the mating of the r^{th} and s^{th} populations. The specific effects are defined as

$$p_{rs} = P_{rs} - P_{r.} - P_{.s} + P_{..}, \sum_s p_{rs} = \sum_r p_{rs} = 0,$$

where $P_{r.}$ represents a marginal mean of the diallel, etc. The expectations were developed for $p_{rs} = p_{sr}$ or for no reciprocal crosses. Consider two subsets of the n populations and let $\{p_{as}\}$ represent the set of average specific effects for n_1 populations and $\{p_{bs}\}$ for n_2 different populations, $1 \leq s \leq n$. Then,

$$E \sum_s (p_{as} - p_{bs})^2 = R^2(a,b) + (n_1 + n_2)(n^2 - n + 1) \frac{2}{\sigma_{\epsilon}^2} / n_1 n_2 n.$$

Tests of significance follow from the variance ratio test with $(n-1)$ degrees of freedom for the treatment mean square. The error variances are

$$(n-1)(n^2 - n + 1) \frac{2}{\sigma_{\epsilon}^2} / n^2 \text{ and } (n_1 + n_2)(n^2 - n + 1) \frac{2}{\sigma_{\epsilon}^2} / n_1 n_2 n, \text{ respectively.}$$

The specific effects (p_{rs}) estimated for the diallel matings are presented in Table 1 with the analysis of variance according to GRIFFING (1956) given in Table 2. Highly significant variability among specific effects was found. Estimates for the distances [(100)-(010)], [(100)-(001)] and [(010)-(001)] relative to [(100)-(010)] were 1.00, .92 and 1.15, respectively, which are highly significantly different from zero. The positions of populations representing intergradation between two populations do not differ from that predicted from the respective positions of progenitor populations nor do the points corresponding to the average of the three parental and to the average of the six hybrid populations

TABLE 1

*Summary of specific effects (p_{rs}) in grams of unshelled grain per plant estimated from a diallel involving nine maize populations**

Population (r)	Population (s)									Marginal mean ($P_{r.}$)
	(100)	(010)	(001)	(110)	(101)	(011)	(112)	(121)	(211)	
(100)	-39.6	+13.7	+12.4	-2.1	+2.1	+6.8	+13.0	+0.6	-7.1	252.9
(010)	+13.7	-37.9	+21.7	-11.9	+13.7	+9.8	+5.9	-10.5	-4.2	265.4
(001)	+12.4	+21.7	-20.8	+10.0	-17.1	-14.2	-0.3	+0.0	+8.2	191.4
(110)	-2.1	-11.9	+10.0	-14.9	+9.3	+2.2	+15.2	-0.9	-6.8	260.8
(101)	+2.1	+13.7	-17.1	+9.3	-16.9	+7.8	-5.6	+3.8	+2.9	218.5
(011)	+6.8	+9.8	-14.2	+2.2	+7.8	-3.9	-9.9	-11.4	+13.0	219.2
(112)	+13.0	+5.9	-0.3	+15.2	-5.6	-9.9	-16.5	+0.6	-2.6	217.5
(121)	+0.6	-10.5	+0.0	-0.9	+3.8	-11.4	+0.6	+10.5	+7.3	239.0
(211)	-7.1	-4.2	+8.2	-6.8	+2.9	+13.0	-2.6	+7.3	-10.5	237.2
$P_{.s}$	252.9	265.4	191.4	260.8	218.5	219.2	217.5	239.0	237.2	233.5
ξ_{1s} :	-.194	-.345	+.434	-.428	+.369	+.326	+.334	-.063	-.338	
ξ_{2s} :	-.564	+.385	-.026	+.095	-.322	+.165	+.206	+.506	-.308	
ξ_{3s} :	+.404	-.356	+.198	+.140	-.140	+.083	-.438	+.526	-.395	

* p_{rs} estimates based on restriction, $\sum p_{rs} = 0$, so that $P_{rs} = [P_{rs} - P_{r.} - P_{.s} + P_{..}]$. $p_{rs} = p_{sr}$.

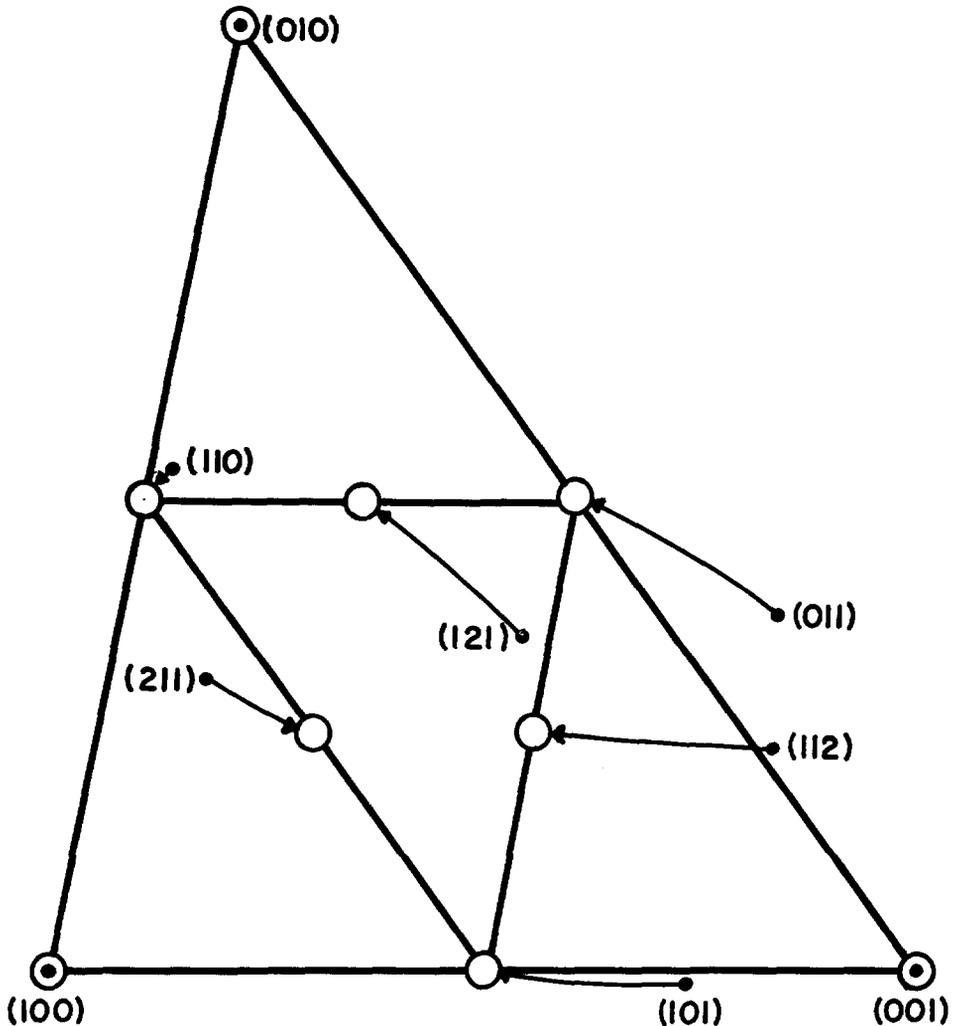


FIGURE 1.—Spatial representation (solid points) of the three base populations and intergradations from these populations utilizing $\{\xi_{1s}\}$ and $\{\xi_{2s}\}$ principal components where (100)=Jarvis, (010)=Indian Chief, and (001)=Zapalote Chico. Circles represent expected positions based on the estimated positions of the three base populations.

differ significantly. One concludes that the intermediate populations must be intermediate to their respective progenitor populations. The distances between parental populations can be estimated from the six intermediate populations, i.e., [(211)-(121)], [(101)-(112)] and [(112)-(011)] each estimate [(100)-(010)]/4, for example. The estimates for [(100)-(010)], [(100)-(001)] and [(010)-(001)] from the intermediate populations are 1.10, 2.23 and 2.06 which differ from zero but not from the previous estimates (at the .05 level of probability). The Zapalote parent (001) would appear to be out of place.

Principal components were selected for a graphic presentation. Positions should

TABLE 2

*Analysis of variance for the nine parent diallel (no reciprocals)
based on grams ear weight per plant*

Source variability	Degrees of freedom	Mean square
General	8	185,564**
Specific	36	6,475**
Genotype \times Env.†	88	1,444**
Pooled error	1187	905

** Significant at the .01 level of probability.

† $\hat{\sigma}_e^2 = 1444/30$.

reflect genetic differences primarily and environmental effects secondarily. The first three principal components, $\{\xi_{1s}\}$, $\{\xi_{2s}\}$ and $\{\xi_{3s}\}$, were calculated from the p_{rs} correlation matrix and were given in Table 1. They account for 51.0%, 20.4% 9.9%, respectively, of the variability. The residual variability from $\{\xi_{1s}\}$ and $\{\xi_{2s}\}$ was nonsignificant. The first two components were used for a spatial representation (Figure 1) where $\sum_i \xi_{is} p_{rs}$ gives a position for the r^{th} population in the i^{th} dimension. The intergraded populations fall in approximate intermediate positions and the Zapalote parent appears out of place, as noted in the original analyses. The relative distances for $[(100)-(010)]$, $[(100)-(001)]$ and $[(010)-(001)]$ in Figure 1 are 1.00, .90 and 1.23, but are .99, 1.74 and 1.59 when estimated from the six intermediate populations.

While the estimated positions for the average parental and average hybrid populations do not differ significantly, there appears to be a distortion proportional to the amount of Zapalote parent present but becoming critical only when intergradation approaches the Zapalote parent. Average recombination (HANSON 1962) in this material would be at least .47, noting that genes segregate independently for loci on different chromosome pairs following the population cross. Since considerable independent evolution and adaptation must have occurred for the Zapalote and the North Carolina populations, genetic differences could involve genes on the same or different linkage groups. The data support the theoretical observations of CASAS, HANSON and WELLHAUSEN (1968). These workers concluded that the diallel information could be used to test for possible intergradation among populations (see their formulas 1a and 1b). For this case, gene frequencies represent a linear combination of gene frequencies for the ancestral populations. The term ignored resulted from the failure of gametic frequencies to follow this linear combination. Linkage disequilibrium will contribute to this term. Even with the divergent populations used in this study, the term ignored in the theoretical development did not have major effects indicative of unique gamete interactions, except as possible proportionate effects.

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