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Fixed effect genetic analysis of a diallel cross in dry beans (*Phaseolus vulgaris* L.)*

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Summary. A full diallel cross among four diverse homozygous strains of dry edible beans (*Phaseolus vulgaris* L.) was evaluated for yield, protein content, and culinary quality traits in the F_2 and F_3 generations in two locations. Interpretation of diallel effects [Method 1 Model I] using a fixed-effect genetic model made it possible to combine data from two generations into a single analysis and quantify the relative contributions of additive and dominance genetic effects to general (GCA) and specific (SCA) combining abilities. GCA was found to arise from three potential sources: additive effects, dominance interactions at homozygous loci, and average dominance interactions in hybrids involving the parent in question. SCA was found to be a function solely of dominance. Additive effects were the primary determinant of GCA and were highly significant. Specific dominance interactions were significant for seed yield, cooked bean moisture content, and texture but not for protein content. Texture was the only trait for which the additive-dominance model failed to provide an adequate fit to the data, suggesting that texture is significantly affected by epistatic interaction. One cross ('Brazil-2' × 'Sanilac') was identified that exhibited a large heterotic effect for seed yield although the parents' additive effects were nonsignificant. Such a "nicking" effect was attributed to complementation between the two parents.

Key words: Combining ability – Genetic effects – Heterosis – Yield – Protein – Culinary quality

Introduction

The diallel mating design is used to estimate and compare the combining abilities or performances in hybrid combination of parental lines (Sprague and Tatum 1942). A knowledge of the general or specific combining ability effects and variances of a given set of lines forms a basis for studying the inheritance of complex traits and can be used as a tool in plant breeding.

Statistical analyses of diallel crosses have been the subject of many research papers since the procedure was developed. Jinks and Hayman (1953) and Hayman (1954a, b) approached the diallel analysis from the perspective of the fixed-effects model. Their work provided for the estimation of selected parental and progeny means and the testing of differences between them. These authors also expressed the variations among means in terms of variance components that were descriptive strictly of a population from which lines selected were sampled. The genetic interpretation of data using the Hayman-Jinks method is valid only if certain assumptions about parental material are true. Some of these are often untenable (Baker 1978).

Griffing (1956) developed diallel analyses in terms of both random and fixed-effect models and suggested that the choice of the correct model depended on the nature of parental material. Baker (1978) raised concerns as to the use of the random-effects model for the most commonly encountered type of parental set, i.e., a set of unrelated lines which often derive from broadly diverse genetic backgrounds. Eberhart and Gardner (1966) stated that plant breeders and geneticists were usually interested in genetic information about a particular set of parents and should use, in most cases, a fixed model. Until Cockerham (1980) suggested a fixed-effect method of genetic analysis, it appeared that the fixed-effect diallel model could not be used to extract genetic information other than

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estimates of combining abilities which were not subject to precise genetic interpretation. In using Griffing's analysis, many authors have ascribed significant general combining ability (GCA) effects solely to additive genetic effects and specific combining ability (SCA) effects to nonadditive gene action. Such interpretations are only qualitative in nature. It would also be desirable to quantify the contributions of additive and nonadditive genetic effects to GCA and SCA.

In dry beans (*Phaseolus vulgaris* L.), one of the plant breeder's concerns is to identify superior parental combinations both for yield and nutritional and culinary quality. In recent years we initiated a series of diallel crosses to study the combining ability of parental lines obtained from tropical germplasm research centers and commercial cultivars and breeding lines developed in the USA. In view of Baker's (1978) objections to the use of the random-effects model, the objective of our study was to adapt the fixed-effects method suggested by Cockerham (1980) and use it to determine the genetic effects influencing yield and food quality traits in a diallel cross of dry beans.

Materials and methods

Plant material

Parents chosen for this study were four homozygous strains that maximized the expression of the traits studied. They were (1) 'Brazil-2' (a tropically adapted bean with a beige testa), (2) 15-R-148 (a Red Mexican type maintained by the University of Wisconsin), (3) 'Sanilac' (a commercial navy bean cultivar), and (4) 'San Fernando' (a tropical cultivar representative of the Black Turtle Soup commercial class). The complete diallel cross (including reciprocals) was made in the winter of 1980–1981. F_1 progenies were advanced to the F_2 generation in the summer of 1981. A random sample of F_2 seed of each cross was advanced to the F_3 generation in Puerto Rico in the winter of 1981–1982. The F_3 seed was harvested in March 1982. A randomly drawn sample of 780 seeds from each parent and from the F_2 and F_3 generation of each cross was planted with 100 other entries in an 11×12 rectangular lattice with three replications at two locations: (1) the Crop Science Research Farm at East Lansing and (2) the Saginaw Valley Bean and Sugarbeet Research farm near Saginaw, Michigan, in May and June 1982, respectively. Parents were represented twice in each design. The experimental material was sown in the middle two rows of a four row plot. The outer two rows were borders and planted with the cultivar 'Seafarer'. Row length was 5 m and row width was 50 cm. Plants within rows were spaced 6 cm. Cultural practices were employed per seasonal recommendations at both sites. Mature plants were harvested in bulk and threshed from a 3 m section of the two center rows of each plot in late September and early October at East Lansing and Saginaw, respectively. Seeds were weighed and analyzed for moisture content using an electrical conductance meter. Yields (Mg/ha) were adjusted to a moisture content of 16%.

Quality assessment

A sample of dry beans from each replication was assessed for texture (kg force/100 g) and cooked bean moisture (%) as described by Hosfield and Uebersax (1980). Percent crude protein was determined using a Neotec Model 31 near infrared reflectance grain quality analyzer (GQA).

Statistical procedures

Data from each location were first subjected to an analysis of variance of the lattice design. In each case, the lattice resulted in a significant increase in precision efficiency. Subsequent analyses were performed using the adjusted means from the lattices. A two-way analysis of variance was used to partition the variation among adjusted means into components arising from the effects of genotypes, locations, and genotype × location (GL) interactions. Effects of locations and GL interactions were assumed to be random so the mean square for genotype and its components were tested using the GL mean square as an error term. The genotype sum of squares was partitioned into a contrast between the means of the F_2 and F_3 generations and into components associated with the diallel effects in each generation.

Combining ability analyses were performed using Griffing's (1956) Model I Method 1, in which all genotypic effects are considered fixed, and the parental lines comprise the population about which inferences are made. In order to obtain an interpretation of GCA and SCA effects in terms of the fixed effect genetic model, the estimators of GCA and SCA effects were solved in terms of the additive and dominance effects. In the diallel model,

$$Y_{ijk} = \mu + L_i + g_j + g_k + s_{jk} + r_{jk} + \varepsilon_{ijk} .$$

while in the genetic model (Cockerham 1980),

$$Y_{ijk} = \mu + L_i + A_j + A_k + \delta_{jj} D_{jj} + \delta_{jk} D_{jk} + \delta_{kk} D_{kk} + r_{jk} + \varepsilon_{ijk} ,$$

where:

μ is the population mean;
L_i is the effect of the *ith* location, $\sum L_i = 0$;
g_j is the GCA effect associated with the *jth* parent, $\sum_j g_j = 0$;
s_{jk} is the SCA effect associated with the cross between the *jth* female and the *kth* male parents, $s_{jk} = s_{kj}$, $\sum_k s_{jk} = 0$;
r_{jk} is the reciprocal effect associated with the cross between the *jth* female and *kth* male parent, $r_{jk} = -r_{kj}$, $\sum_k r_{jk} = 0$;
ε_{ijk} is the error term associated with the *jth* and the *kth* parent in the *ith* block;
A_j is the sum of the additive effects for genes in a gamete from the *jth* parent;
D_{jj} is the sum of the dominance effects associated with the *jth* parent;
D_{jk} is the sum of the dominance effects in the hybrid obtained by mating the *jth* and *kth* parents;
δ_{jj} is the expected proportion of loci homozygous for the allele derived from the *jth* parent, $\delta_{jj} = F/2$ in the case of populations derived by selfing where F is the inbreeding coefficient; and
δ_{jk} is the expected proportion of heterozygous loci, $\delta_{jk} = 1 - F$.

The usual estimator of the GCA effects of the *jth* parent has the following expectation:

$$\begin{aligned} E(g_j) &= E\{(\bar{Y}_{.j.} - \bar{Y}_{..j})/2p - \bar{Y}_{...}\} \\ &= (A_j - \bar{A}_{.}) + \delta_{jj}(D_{jj} - \bar{D}_p) + \delta_{jk}(\bar{D}_{j.} - \bar{D}_{..}) \end{aligned}$$

where effects are defined in Table 1.

Similarly, the expectation of the estimator of the SCA effect associated with the jk*th* cross is:

$$\begin{aligned} E(s_{jk}) &= E\{(\bar{Y}_{.jk} + \bar{Y}_{jk})/2 - \bar{Y}_{...} - g_j - g_k\} \\ &= \delta_{jk}(D_{jk} - \bar{D}_{j.} - \bar{D}_{.k} + \bar{D}_{..}) . \end{aligned}$$

Table 1. Definitions of terms used in the estimation of effects

Term	Definition
$\bar{A}. = \sum_{j}^{p} A_j/p$	Mean of additive effects
$\bar{D}_h = 2 \sum_{j<k}^{\frac{1}{2}p(p-1)} \sum D_{jk}/p(p-1)$	Mean of dominance interactions associated with hybrid progenies
$\bar{D}_p = \sum_{j}^{p} D_{jj}/p$	Mean of dominance interactions associated with the parents
$\bar{D}.. = \sum_{j}^{p} \sum_{k}^{p} D_{jk}/p^2$	Mean dominance interaction in the F_1 diallel population. $\bar{D}.. = \bar{D}_p/p + (p-1)\,\bar{D}_h/p$
$D_{hj} = \sum_{k \neq j}^{p-1} D_{jk}/(p-1)$	Mean dominance interaction associated with F_1 hybrid progeny of the *jth* parent
$\bar{D}_j. = \sum_{k}^{p} D_{jk}/p$	Mean of dominance interactions associated with progeny of the *jth* parent, $\bar{D}_j. = D_{jk}/p + (p-1)$

The diallel effects may be defined for any level of inbreeding of the hybrid population while the genetic effects are constant for a given population. Their relative contributions to the diallel effects change with inbreeding as manifested by changes in δ_{jj} and δ_{jk}. For selfed progeny, $\delta_{jj} = \delta_{kk}$ and $2\delta_{jj} + \delta_{jk} = 1$. Contrary to the common statement that GCA reflects only additive genetic effects, for the non-inbred (F_1) population, the GCA effect of a parent comprises its additive effect and the average dominance effects associated with that parent in hybrid combination with all others and with itself. With inbreeding, the GCA includes a genetic component associated with the set of dominance interactions within homozygous loci of the parent itself. In the biological sense, dominance effects arise from inter-allelic interaction present in heterozygotes. However, statistically it can be shown that dominance exists in homozygotes as well as heterozygotes (Falconer 1981). Cockerham (1980) discusses dominance effects for homozygous lines. The contribution of this component to GCA increases and the contribution of average dominance decreases in proportion to the level of inbreeding. The SCA effect associated with the *jkth* hybrid population is a linear function of the deviation of the dominance interaction associated with that particular pair of parents from the average effect of dominance associated with those parents in the closed parental set. The algebraic expression for the deviation, $D_{jk} - \bar{D}_j. - \bar{D}._k + \bar{D}..$, takes the form common to first order interaction terms. The contribution of this term to SCA is proportional to δ_{jk}. SCA should, therefore, decrease by a factor of one half with each generation of selfing. Failure of the population to conform to this rule implies occurrence of some other type of nonadditive gene action, i.e., epistasis. Given these definitions, it is apparent that nonsignificant SCA does not necessarily imply absence of appreciable dominance effects. If the parents exhibit consistent dominance relationships in combination with the others in the parental sample, then those effects will contribute to GCA rather than SCA. Only if there is fluctuation in the dominance relationships will there be significant SCA.

The analysis of genetic effects used ordinary least squares to fit a sequence of models to the adjusted F_2 and F_3 means.

Table 2. Estimate and expectations of the effects for fixed effect diallel analysis

Estimates	Expectation
μ	$\mu + 2\bar{A}. + \bar{D}_p$
$\bar{D}..$	$\bar{D}.. - \bar{D}_p = (p-1)(\bar{D}_h - \bar{D}_p)/p$
A_j	$(A_j - \bar{A}.) + (D_{jj} - \bar{D}_p)/2$
$\bar{D}_j$	$(\bar{D}_j. - \bar{D}..) - (D_{jj} - \bar{D}_p)$
	$= (p-1)\,[(D_{hj} - \bar{D}_h) - (D_{jj} - \bar{D}_p)]/p$
$\bar{D}_{jk}$	$D_{jk} - \bar{D}_j - \bar{D}._k + \bar{D}..$

The original design matrix was found to be singular due to the constraint $2\delta_{jj} + \delta_{jk} = 1$, so the model was adjusted to fit a set of altered parameters (Table 2). These parameters are subject to a great simplification provided an assumption is made that alleles identical in state exhibit no dominance effects, i.e., $D_{jj} = \bar{D}_p = 0$. The order of fitting parameters was: (1) average dominance ($\bar{D}..$), (2) additive effects (A_j), (3) average dominance effects of parents ($\bar{D}_j.$), and (4) specific dominance interactions (D_{jk}). The full genetic model accounted for 13 of the 19 degrees of freedom associated with variation among nuclear effects of genotypes in the diallel population. A residual genotypic sum of squares with six degrees of freedom was used to test the adequacy of the additive-dominance model.

Because the estimators of average dominance effects were strongly correlated with additive effects, estimates of the A_j's were obtained using a reduced model from which average dominance effects had been eliminated when found to be nonsignificant.

Results and discussion

In the two-way analysis of variance, significant differences were detected among locations and genotypes for all traits (Table 3). Genotypic effects accounted for 31 to 75% of the total variation among adjusted means. Partitioning of genetic variability into nuclear and reciprocal effects showed that nuclear variation constituted a major portion of the total variation (Table 3). Reciprocal differences were not significant for any trait. Of the total genotypic variability for yield, texture, cooked bean moisture, and percent crude protein, the contribution of nuclear effects was 89.9, 97.6, 75.0, and 97.5%, respectively. When nuclear variation was partitioned using the Griffing model, yield was the only trait that exhibited a significant difference between the F_2 and F_3 generations. Since heterosis for seed yield is common in beans, the observed inbreeding depression was expected. General combining ability (GCA) effects within the F_2 and F_3 generations were highly significant for all the traits. Specific combining ability (SCA) effects were significant for yield, texture, and cooked bean moisture but not for percent crude protein. This indicated that dominance as well as additive effects were important in trait expression (Table 3). The alternative partitioning of the nuclear

Table 3. Mean squares (MS) with sums of squares expressed as a percentage of the variation last partitioned (R_g^2)

Source	d. f.	Traits							
		Yield		Texture		Cooked bean moisture		Protein	
		MS (Mg/ha)	R_g^2 (%)	MS (kg/100 g)	R_g^2 (%)	MS (%)	R_g^2 (%)	MS (%)	R_g^2 (%)
Location	1	22.68**	61.4	671.5**	23.0	2.21*	4.8	57.38**	25.2
Genotype	31	0.37**	31.0	91.8**	75.1	1.00	66.8	5.10	69.4
Nuclear	19	0.54**	89.9	146.2**	97.6	1.22**	75.0	8.11**	97.5
Generation	1	0.76**	7.4	0.0	0.0	0.62	2.7	0.86	0.6
GCA/Gen	6	1.11**	64.9	330.5**	71.4	1.81**	46.8	24.7**	96.2
SCA/Gen	12	0.24*	27.7	66.1**	28.6	0.98*	50.6	0.41	3.2
$\bar{D}_{..}$	1	0.76**	7.4	0.0	0.0	0.62	2.7	0.86	0.6
A_j	3	2.20**	64.0	645.2**	69.7	3.40**	43.9	49.1**	95.5
$\bar{D}_{j.}$	3	0.03	0.9	15.8	1.7	0.22	2.8	0.35	0.7
D_{jk}	6	0.36**	21.1	102.7**	22.2	1.34**	34.6	0.59	2.3
Residual	6	0.11	6.7	29.6**	6.4	0.62	15.9	0.24	0.9
Reciprocal	12	0.10	10.1	5.6	2.4	0.65	25.0	0.34	2.5
Location × Genotype	31	0.09	7.6	2.6	1.9	0.42	28.4	0.41	5.4

*,** Denote significance at the 0.05 and 0.01 α-levels, respectively

variability into overall dominance ($\bar{D}_{..}$), additive (A_j), mean dominance of the *ith* parent ($\bar{D}_{j.}$), specific dominance (D_{jk}), and residual effects revealed that additive effects for all traits were highly significant and greater in magnitude than any other source of variation. The overall dominance was significant for yield only. Mean dominance effects of parents were not significant for any trait; however, specific dominance was significant for cooked bean moisture, yield, and texture. This is interpreted to mean that no parent exhibited a consistent dominance relationship across all others. Only texture showed a highly significant residual effect indicating that epistasis does, indeed, influence texture in this population. The partitioning of nuclear variability showed that additive effects (A_j) and specific dominance effects (D_{jk}) contributed most to variability for yield, texture, and cooked bean moisture. For percent crude protein the additive effect constituted 96% of the nuclear variability.

The average dominance effect for yield (Table 4) was 1.74 Mg/ha, confirming the occurrence of substantial heterosis in the population. The specific dominance effects associated with three of the four parents were significant, negative and of sufficient magnitude to offset the average dominance effect. These findings are indicative of inbreeding depression as the parental alleles reassociate in the inbred generations. The parent with the nonsignificant specific dominance effect was 'San Fernando' which had the greatest positive additive effect. Although the overall variation among average dominance effects of parents was not significant, these properties of 'San Fernando' (D_{44}) could result from the line carrying dominant genes that increased yield. Only one cross, 'Brazil-2' × 'Sanilac', exhibited significant dominance and thus, increased yield above the average level for hybrids. The predicted yield advantage of the F_1 of this cross above the population mean and based upon estimates of the average dominance effect and additive effects of the two parents would be 1.87 Mg/ha. The observed yield was 1.31 Mg/ha above this prediction (Table 4). In this case, neither the 'Brazil-2' or 'Sanilac' parent had a significant aggregate additive effect, perhaps because of balancing positive and negative gene effects. If the heterosis observed for this cross was, indeed, the result of repulsion-phase linkage of dominant genes, then it should be possible to select highly productive segregates from the populations. Selection would be enhanced if the observed "linkage" was a matter of association of alleles in a pure line rather than classical genetic linkage.

The single remaining significant genetic effect on yield was the negative additive effect of 15-R-148, a parent with high protein content. The negative relationship between additive effects on yield and protein content observed for this parent did not extend to the rest of the parental sample. 'Brazil-2' had the lowest additive effect on protein content but no significant effect on yield. 'San Fernando' increased yields in its hybrid progeny without a significant loss in average protein content.

All parents exhibited significant additive effects for cooked bean texture. 'Sanilac', a relatively soft bean, passed its softness to its progeny as indicated by its

Table 4. Estimates of mean dominance interaction ($\bar{D}$..), additive effect (A_j), and specific dominance interactions associated with progeny of the *j*th and *k*th parents (D_{jk}) with their standard errors and LSDs (0.05) for four traits measured on parents and F_2 and F_3 progeny of a four-parent diallel cross in dry beans grown in 1982

Source	Traits			
	Yield (Mg/ha)	Texture (kg/100 g)	Cooked bean moisture (%)	Protein (%)
Mean dominance ($\bar{D}$..)	1.74 ± 0.59**	− 0.32 ± 4.98	− 1.57 ± 1.13	− 1.85 ± 1.25
Additive (A_j)				
'Brazil-2' (1)	0.05 ± 0.05	2.42 ± 0.43**	− 0.43 ± 0.09**	− 1.16 ± 0.09**
15-R-148 (2)	− 0.37 ± 0.05**	− 1.06 ± 0.43*	0.00 ± 0.09	1.74 ± 0.09**
'Sanilac' (3)	0.08 ± 0.05	− 5.81 ± 0.43**	0.35 ± 0.09**	− 0.50 ± 0.09**
'San Fernando' (4)	0.24 ± 0.05**	4.45 ± 0.43**	0.07 ± 0.09	− 0.08 ± 0.09
LSD (0.05)	0.15	1.45	0.33	0.32
Specific dominance (D_{jk})				
D_{11}	− 1.69 ± 0.58**	3.05 ± 5.39	− 1.11 ± 1.22	− 0.28 ± 1.18
D_{12}	0.52 ± 0.43	12.48 ± 4.02**	− 1.86 ± 0.91	− 1.25 ± 0.88
D_{13}	1.31 ± 0.43**	− 5.77 ± 4.02**	0.18 ± 0.91	− 1.25 ± 0.88
D_{14}	− 0.14 ± 0.43	− 9.76 ± 4.02**	3.16 ± 0.91**	0.72 ± 0.88
D_{22}	− 1.55 ± 0.58*	9.85 ± 5.39	1.88 ± 1.22	0.09 ± 1.18
D_{23}	0.46 ± 0.43	− 4.68 ± 4.02	0.44 ± 0.91	0.82 ± 0.88
D_{24}	0.57 ± 0.43	− 17.65 ± 4.02**	− 0.46 ± 0.91	− 1.74 ± 0.88
D_{33}	− 1.82 ± 0.58**	− 21.94 ± 5.39**	2.35 ± 1.22	− 1.42 ± 1.18
D_{34}	0.05 ± 0.43	32.38 ± 4.02**	− 2.59 ± 0.91	1.86 ± 0.88*
D_{44}	− 0.47 ± 0.58	− 4.98 ± 5.39	− 0.09 ± 1.22	− 0.84 ± 1.18
LSD (0.05)				
$D_{jj} - D_{kk}$	1.55	14.67	3.36	3.24
$D_{jj} - D_{jk}$	1.73	16.41	3.76	3.62
$D_{jj} - D_{kl}$	1.34	12.71	2.91	2.80
$D_{jk} - D_{kl}$	1.34	12.71	2.91	2.80
$D_{jk} - D_{lm}$	1.34	12.71	2.91	2.80

*, ** Denote significance at the 0.05 and 0.01 α-levels, respectively

negative additive effect. The specific dominance effect associated with 'Sanilac' itself was negative, significant, and large in magnitude, suggesting that the parent is much softer than one would expect on the basis of its additive genetic effect. No other parent deviated from its expectation for the texture trait. 'San Fernando', a firm bean, had the largest positive additive effect on texture, but this firming influence was negated to a large extent by dominance effects in crosses with 'Brazil-2' and 15-R-148. When 'San Fernando' was crossed with 'Sanilac', the heterozygous progeny produced beans much firmer than expected. These unpredictable results may be due to structural and compositional complexity of the bean seed on which this trait is measured. Complex inheritance of texture was indicated by the significant mean square for residual (epistatic) genetic effects.

Two parents had significant additive effects on cooked bean moisture. The effects, while significant, were small in magnitude. Only one dominance effect was found to be significant. Hybrid progeny of the cross between 'Brazil-2' and 'San Fernando' retained over 3% more water in cooking than expected.

Essentially in this fixed-effect genetic analysis, the variation among effects of GCA in generations was partitioned into two components – one reflecting additive genetic effects (A_j) and the other average dominance effects associated with particular parents ($\bar{D}_{j.}$). Similarly, the sum of squares for SCA in generations was broken down into one component arising from specific dominance interactions (D_{jk}) and another from residual genetic effects, ostensibly epistatic in nature. In this regard, the major conclusions drawn from this study were four-fold: First, for this set of crosses, it is perfectly reasonable to make the usual interpretation of GCA as a function of only additive genetic effects and SCA as a function only of dominance interactions. Second, redefinition of diallel model effects in terms of fixed genetic effects allowed us to utilize information from two-inbred generations derived from a complex mating system to estimate cross-specific parameters that could be used to predict the mean performance of backcross or inbred populations derived from these parents. Third, genotypic variation for yield, cooked bean moisture, and protein content was ascribable to additive and dominance genetic effects with the additive portion being larger in all cases. Cooked bean texture exhibited significant levels of non-additive genetic variation other than dominance per se. Fourth, the analysis identified one cross ('Brazil-2' × 'Sanilac') that exhibited a large heterotic effect for yield although the average additive effects of the parents were small. Identification of such "nicking" phenomena could be achieved using bulk inbred populations from larger diallel or factorial matings. Selection for superior recombinants could then be practiced only in a few crosses.

While this technique offers some new possibilities for the analysis of diallel crosses, it does suffer from limitations. Because it requires that at least two inbred generations be evaluated simultaneously, more time is needed to develop the experimental materials. This requirement also doubles the already large number of populations that must be tested in a diallel design, thus, making it difficult to evaluate large numbers of parents. This problem could best be overcome by using a smaller number of elite lines for evaluation and establishing which crosses produced superior progeny.

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