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Combining Ability Type of Analysis for Triallel Crosses in Maize (*Zea mays* L.)

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Summary. Data on 30 three-way maize (*Zea mays* L.) hybrids formed from 5 inbred lines were subjected to the combining ability type of analysis. The relative importance of general and specific line effects in maize three-way hybrids was studied by the Ponnuswamy and Das (1973) method. It was also shown that this analysis provides the breeder with the basic information necessary to choosing proper breeding materials and in deciding the order in which they should be combined to get desirable three-way hybrids.

Introduction

A three-way cross symbolised by (AB)C has been defined as a cross between the line C and the unrelated F_1 hybrid (AB), lines A and B being called grand-parental or half-parental lines and line C being known as the (Full) parental line. The triallel cross (T. C.) has been defined by Rawlings and Cockerham (1962a) as a set of all possible three-way hybrids among a group of (Inbred) lines. Thus, given a set of v lines, the triallel will consist of a set of $\left[\frac{v(v-1)(v-2)}{2}\right]$ three-way crosses.

The well-known combining ability analysis of diallel cross (DC) has helped in understanding the nature of gene action in single cross hybrids, on which depends the breeding policy and selection procedure. It has helped in the evaluation of lines for their suitability in the development of hybrids and synthetic varieties. Methods such as the 'Triallel Analysis' and 'Double Cross Analysis' of Rawlings and Cockerham (1962 a, b), and Analysis of Partial Triallel Cross (P. T. C.) of Hinkelmann (1965), have made it possible to subject the double-crosses and three-way crosses to appropriate statistical and genetical analysis. However, not much attention has been paid to the development of methods for the evaluation of lines based on the results of the triallel experiments. Evaluation of lines is as important as the quantitative genetic analysis of a mating design to the breeder whose aim is to develop 'strains' or 'hybrids' which are in some way superior to those already in commercial use. Recently some attempts have been made by Ponnuswamy (1971) and Ponnuswamy and Das (1973) to develop suitable models and methods of analysis to study both the evaluation of lines and quantitative genetics aspects of Triallel.

The parameterization of the model in Ponnuswamy (1971) and Ponnuswamy and Das (1973) is different from that of Rawlings and Cockerham (1962a). In the former case the model has been developed on the lines of the combining ability model of diallel and is easily understood. The relationships between the parameters of the models in Rawlings and Cockerham (1962a) and Ponnuswamy and Das (1973) have also been established. In the case of Rawlings and Cockerham (1962a), both the average two-life specific effects and the two-line order effects involve dominance, whereas in Ponnuswamy and Das (1973) it is only the two-line specific effects of the second kind which involve dominance. This finding has resulted in the development of certain partial triallels which provide complete information on dominance. The parameterization in Hinkelmann (1965) and Ponnuswamy and Das (1973) is similar but Hinkelmann considers the reduced model consisting of only general line effects for the analysis of partial triallel cross. As pointed out earlier, both Rawlings *et al.* (1962a) and Hinkelmann (1965) consider only the quantitative genetic aspects of the triallel, whereas Ponnuswamy *et al.* (1973) consider both aspects.

The present investigation is an attempt to compare the relative importance of general and specific line effects in three-way hybrids involving five inbred lines of maize and show that the triallel experimental data can be used for the evaluation of lines by subjecting the data to the Analysis proposed by Ponnuswamy and Das. The concepts and formulae which are relevant to the present study are presented in the next Section.

Material and Methods

Methods for the Evaluation of Lines

The model, appropriate for the triallel experiment carried out in a randomized block design layout, is

$$y_{ijkl} = \mu + h_i + h_j + g_k + d_{ij} + s_{ik} + s_{jk} + t_{ijk} + r_l + e_{ijkl} \quad (1)$$

where y_{ijkl} is the yield of the cross $(ixj)k$ in the lth replicate, r_l is the lth replicate effect, μ is the general mean, h_i is the general line effect (g.l.e.) of the first kind, g_k is the g.l.e. of the second kind, d_{ij} is the two-line specific effect (t.l.s.e.) of the first kind (both i and j being grand-parents), s_{ik} is the two-line specific effect of the second kind (i being half-parent, k being parent), t_{ijk} is the three-line specific effect and e_{ijkl}'s are identically independently distributed normal variates with mean zero and variance σ^2. The least square estimates of the general and specific line effects are given by

$$\hat{\mu} = \bar{y}_{....} \tag{2}$$

$$\hat{h}_i = \left[\frac{(v-1)}{rv(v-2)(v-3)}\right] \times \left[y_{i...} + \left(\frac{2}{v-1}\right) y_{..i.} - \left(\frac{2}{v-1}\right) y_{....}\right], \tag{3}$$

$$\hat{g}_i = \left[\frac{2}{v(v-3)\,r}\right]\left[y_{..i.} + \left(\frac{1}{v-2}\right) y_{i...} - \left(\frac{1}{(v-2)}\right) y_{....}\right], \tag{4}$$

$$\hat{d}_{ij} = \left[\frac{(v-3)}{(v-1)(v-4)\,r}\right]\left[y_{ij..} + \left(\frac{1}{v-3}\right)(y_{i.j.} + y_{j.i.}) - \frac{2}{v(v-1)} y_{....} - \frac{(v^2-4v+2)\,r}{(v-3)}(\hat{h}_i + \hat{h}_j) - \left(\frac{r}{v-3}\right)(\hat{g}_i + \hat{g}_j)\right], \tag{5}$$

$$\hat{s}_{ij} = \left(\frac{D}{D_2}\right)\left[y_{i.j.} + \left(\frac{1}{D}\right) y_{j.i.} + \left(\frac{(v-3)}{D}\right) y_{ij..} - \frac{2(v-3)}{Dv} y_{....} - r(v-2)\,\hat{h}_i - \left(\frac{(v-3)\,r}{D}\right)\hat{h}_j - \left(\frac{r}{D}\right)\hat{g}_i - \left(\frac{D_1 r}{D}\right)\hat{g}_j\right], \tag{6}$$

$$\hat{t}_{ijk} = [\bar{y}_{ijk} - \bar{y}_{....} - \hat{h}_i - \hat{h}_j - \hat{g}_k - \hat{d}_{ij} - \hat{s}_{ik} - \hat{s}_{jk}] \tag{7}$$

where v is the number of lines.,

$$D = (v^2 - 5v + 5)\,, \quad D_1 = (v^3 - 7v^2 + 14v - 7)$$
$$D_2 = r(v-1)(v-3)(v-4)$$

$\bar{y}_{ijk.}$ is the mean of the cross $(ixj)k$, $y_{....}$ is the total of all the crosses, $y_{i...}$ is the total of all the crosses which involve line i as grand-parent, $y_{..i.}$ is the sum of all the crosses which involve line i as parent, $y_{ij..}$ is the sum of all the crosses which involve lines i and j as grand-parents, $y_{i.j.}$ is the total of all the crosses which involve line i as grand-parent and line j as parent; as usual, bar (—) above y's stands for the mean, average being taken over all the subscripts which are replaced by dots(.), and ($\wedge$) over the parameters stands for the estimates. The variances and covariances of these estimates and other related statistics for testing the hypothesis involving these parameters have also been worked out [c. f. Ponnuswamy and Das 1973]. For the sake of ready reference, the standard errors (SE) of the estimates are presented in the Appendix.

Comparisons of the performance of the individual lines as well as the combined performance of pairs or triplets of lines are of considerable interest. No doubt, comparisons, involving individual effects of general and specific effects of a set of lines with those of same other set, or the same set in different order, will provide sufficient information in this direction; and t tests can be easily devised to meet the situation. However, in the evaluation of lines, not only the general line effects of the particular line but also all the two-line and three-line specific effects involving that line should be considered together. This requires that all possible relevant comparisons be made, which is a very cumbersome and tedious procedure. Moreover, it is also desirable to know the relative importance of general and specific line effects. To facilitate comparison and also to determine the relative importance of the general and specific effects, the computation of certain statistics as given below is necessary.

$$\hat{\sigma}^2_{t_{ij}} = \left(\frac{1}{v-3}\right)\sum_{\substack{k \\ k\neq i\neq j}}^{v} (\hat{t}_{ijk})^2 - \left[\frac{(v^2-6v+7)}{r(v-1)(v-3)}\right]\hat{\sigma}^2, \tag{8}$$

$$\hat{\sigma}^2_{t_{i.j}} = \left(\frac{1}{v-3}\right)\sum_{\substack{k \\ k\neq i\neq j}}^{v} (\hat{t}_{ikj})^2 - \left[\frac{(v^2-6v+7)}{r(v-1)(v-3)}\right]\hat{\sigma}^2 \tag{9}$$

$$\hat{\sigma}^2_{t_{i..}} = \left(\frac{1}{(v-2)(v-3)}\right)\sum_{\substack{j \\ j\neq i}}^{v}\sum_{\substack{k \\ k\neq i\neq j}}^{v} (\hat{t}_{ijk})^2 - \left[\frac{(v^2-6v+7)}{r(v-2)(v-3)}\right]\hat{\sigma}^2, \tag{10}$$

$$\hat{\sigma}^2_{t..i} = \frac{2}{(v-2)(v-3)}\sum_{\substack{j \\ j,k\neq i}}^{v}\sum_{k>j}^{v} (\hat{t}_{jki})^2 - \left(\frac{(v^2-6v+7)}{r(v-2)(v-3)}\right)\hat{\sigma}^2, \tag{11}$$

$$\hat{\sigma}^2_{d_{i.}} = \left(\frac{1}{v-2}\right)\sum_{\substack{j \\ j\neq i}}^{v} (\hat{d}_{ij})^2 - \left[\frac{(v-3)^2}{r(v-1)(v-2)(v-4)}\right]\hat{\sigma}^2, \tag{12}$$

$$\hat{\sigma}^2_{s_{i.}} = \left(\frac{1}{v-2}\right)\sum_{\substack{j \\ j\neq i}}^{v} (\hat{s}_{ij})^2 - \left[\frac{(v-2)(v^2-4v+1)}{r(v-1)(v-3)(v-4)}\right]\hat{\sigma}^2, \tag{13}$$

$$\hat{\sigma}^2_{s_{.i}} = \left(\frac{1}{v-2}\right)\sum_{\substack{j \\ j\neq i}}^{v} (\hat{s}_{ji})^2 - \left[\frac{(v-2)(v^2-4v+1)}{r(v-1)(v-3)(v-4)}\right]\hat{\sigma}^2, \tag{14}$$

$$\hat{\sigma}^2_{g_i} = (\hat{g}_i)^2 - \left(\frac{2(v-1)}{rv^2(v-3)}\right)\hat{\sigma}^2, \tag{15}$$

$$\hat{\sigma}^2_{h_i} = (\hat{h}_i)^2 - \left[\frac{(v-1)^2}{rv^2(v-2)(v-3)}\right]\hat{\sigma}^2 \tag{16}$$

where $\hat{\sigma}^2$ is the estimate of error variance (cf. Ponnuswamy and Das 1973).

The relative magnitude of these statistics will indicate the relative importance of the general and specific effects and will also show whether there is much variability in the specific effects involving a particular line, a pair or triplet of lines. For example, the presence of relatively large variations in the specific effects involving a particular line would indicate that there are specific combinations of the line in question with certain inbreds which yield considerably more than would be expected on the basis of the average performance of the lines involved, and other combinations which yield much less than expected. On the other hand, if there is no variability in the specific effects associated with a line, say i, then it would appear that line i uniformly transmits its high-yielding (or low-yielding) ability to all of the crosses which involve line i. Suppose the variances $\hat{\sigma}^2_{d_i}$, $\hat{\sigma}^2_{s_i}$ and $\hat{\sigma}^2_{t_i}$ are substantially larger than $\hat{\sigma}^2_{s.i}$, $\hat{\sigma}^2_{t..i}$, then, in order to get a high-yielding combination, it may be better to use line i as a grand parent than as a parent. Of course these decisions should take into account the general and specific effects of the other lines too. In order to determine exactly the lines which should be considered, and the order in which they should be combined with the given line, the general and specific effects may be tested through the use of appropriate t test.

Thus the relative magnitude of the relevant statistics, for example, $\hat{\sigma}^2_{h_i}$ and $\bar{\sigma}^2_{g_i}$ as compared with those of $\hat{\sigma}^2_{s}$, $\hat{\sigma}^2_{d_i}$ and $\hat{\sigma}^2_{t_i}$ ($\hat{\sigma}^2_{s_i}$ & $\hat{\sigma}^2_{t..i}$), will provide sufficient knowledge to decide whether the general line effects alone are sufficient, or whether two-line and three line specific effects should also be taken into consideration in the evaluation of the breeding worth of lines. The information provided by these variances, supplemented by knowledge gained from the particular comparisons, should be adequate to determine whether it is advisable to go for synthetics by using specific lines, or to go for the development of hybrids, and if deciding on hybridization, which are the lines that should be considered and the order in which they should be combined in a three-way cross.

Methods to study the Quantitative Genetic Aspect of Triallel

Considering the set of lines as a random sample from an infinite population, and assuming the particular variance covariance structure for the parameters in model (1) [*viz.*, $E(h_i^2) = \sigma_h^2$, $E(h_i g_i) = \sigma_{gh}$ $E(g_i^2) = \sigma_g^2$, $E(d_{ij}^2) = \sigma_d^2$, $E(d_{ij}s_{ij}) = E(d_{ij}s_{ji}) = \sigma_{ds}$, $E(s_{ij}^2) = \sigma_s^2$, $E(s_{ij}s_{ji}) = \sigma_{ss}$, $E(t_{ijk}^2) = \sigma_t^2$, $E(t_{ijk}t_{ikj}) = E(t_{ijk}t_{jki}) = \sigma_{tt}$, $E(e_{ijkl}^2) = \sigma^2$ and all the other covariances being zeros], Ponnuswamy and Das (1973) have shown that the variances and covariances components of the general effects (*viz.* σ_h^2, σ_g^2 and σ_{gh}) are functions of additive and additive $\times$ additive type of epistasis only. The components σ_d^2 and σ_{ds} are functions of additive $\times$ additive type of epistasis only. σ_s^2 and σ_{ss} are the only two components which involve dominance component. The components σ_t^2 and σ_{tt} are functions of epistatic components other than additive $\times$ additive.

Thus, the non-significance of the three-line specific effects will provide positive evidence of the absence of all epistasis other than additive $\times$ additive. The pooled mean square of d effects and t effects when tested against error will show the absence of all types of epistatic gene action. Similarly, the pooled mean square of s and t effects when tested against error will provide an indirect test for the absence of all gene action other than additive, and additive $\times$ additive type of epistasis. Likewise, the non-significance of the pooled mean square of s, d and t effects when tested against error will show the absence of all types of non-additive gene action. However, for the estimation of all the nine design components, the number of lines should be at least 6.

Material for the Study

Handoo's (1964) data pertaining to 30 three-way hybrids formed from 5 inbred lines of maize constituted the material for the present study. The data were subjected to the analysis discussed above and the salient features of the results (presented in Tables 1 and 2) are now discussed.

Results and Discussions

We shall consider the results of the character 'mean grain yield per plant' for detailed discussion and briefly indicate the salient features of the results for the other characters.

Mean Grain Yield per Plant (in gms/at) 15% moisture)

The analysis of variance is presented in table 1, and the estimates of the general and specific effects and other related statistics for mean yield per plant are presented in table 2.

The analysis shows that the general line effects (both first and second kinds) as well as the two-line specific effects of the first kind are highly significant, the two-line specific effects of the second kind ($s'_{ij}s$) are significant, whereas the three-line specific effects are not significant. This shows the absence of all types of epistasis other than additive $\times$ additive. It is also evident that the nature of gene action is predominantly additive. However, because the number of lines was less than six, the magnitudes of

Table 1. *Analysis of variance for characters 1 to 7 (mean squares)*

Source	d. f.	Characters						
		Mean yield		Mean number of days		Mean ear		Mean plant height (cm.)
		gms./plant	kg./per ha.	to tassel	to silk	length (cm.)	girth (cm.)	
1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
General line effect of the first kind (h's elim. g's)	$v_1 = 4$	1471.41**	2632220**	3.631**	3.417**	3.798**	2.569**	109.18**
General line effect of the 2nd kind (g's elim. h's)	$v_1 = 4$	1865.71**	2859570**	56.322**	55.5430**	3.366**	4.181**	3084.37**
Two line specific effects of the first kind (d's elim. s's)	$v_2 = 5$	552.05**	457134*	2.135*	3.290**	2.144**	0.122NS	219.70*
Two line specific effects of the second kind (s's elim. d's)	$v_3 = 11$	270.73*	474425*	0.705NS	1.227NS	0.972*	0.279**	130.55NS
Three-line specific effects	$v_4 = 5$	58.46NS	155821NS	0.496NS	0.670NS	0.603NS	0.125NS	139.63NS
Crosses	$v_5 = 29$	506.49**	797579**	8.836**	9.133**	1.490**	0.863**	554.61**
Error	$v_6 = 177$	89.34	161057	0.907	0.947	0.521	0.096	89.62

where $v_1 = (v - 1)$, $v_2 = v(v - 3)/2$, $v_3 = (v^2 - 3v + 1)$, $v_4 = (v^2 - 6v + 7)/2$, $v_5 = [v(v - 1)(v - 2)/2 - 1]$ and $v_6 = v_5(r-1)$ r being the number of replications and v the number of lines.

** denotes significance at 1% level, * denotes significance at 5% level and NS stands for not significant.

Table 2. *The estimates of general and specific effects of lines and other related statistics (mean yield per plant)*

Lines	General line effects of first kind	General line effects of 2nd kind	Two line specific effect $[d_{ij}, s_{ij}]$ Lines 1	2	3	4	5
P_1	8.719	13.780	—	5.625 (6.650)	− .599 (−2.395)	3.058 (2.964)	−8.083 (−7.220)
P_2	−5.733	−9.646	5.625 (−1.859)	—	−5.975 (− .129)	−4.742 (−5.432)	5.092 (7.420)
P_3	6.499	6.020	− .599 (1.444)	−5.975 (3.420)	—	2.633 (−5.628)	3.942 (0.762)
P_4	−4.619	−6.173	3.058 (6.694)	−4.742 (−4.642)	2.633 (−1.088)	—	−.950 (−.963)
P_5	−4.866	−3.979	−8.083 (−6.280)	5.092 (−5.429)	3.942 (3.612)	− .950 (8.096)	—

Standard Errors:

$SE(\hat{h}_i) = 1.544$, $SE(\hat{g}_i) = 1.894$, $SE(\hat{h}_i - \hat{h}_j) = 2.417$, $SE(\hat{h}_i - \hat{g}_i) = 1.890$, $SE(\hat{g}_i - \hat{g}_j) = 2.989$
$SE(\hat{d}_{ij}) = 2.363$, $SE(\hat{s}_{ij}) = 2.745$, $SE(\hat{d}_{ij} - \hat{d}_{ik}) = 3.858$, $SE(\hat{d}_{ij} - \hat{d}_{kl}) = 2.728$
$SE(\hat{d}_{ij} - \hat{s}_{ij}) = 2.745$, $SE(\hat{d}_{ij} - (\hat{s}_{ij} + \hat{s}_{ji})/2) = 2.046$, $SE(\hat{s}_{ij} - \hat{s}_{ji}) = 3.661$, $SE(\hat{s}_{ij} - \hat{s}_{ik}) = 4.484$
$SE(\hat{s}_{ij} - \hat{s}_{ki}) = 3.661$, $SE(\hat{s}_{ij} - \hat{s}_{kl}) = 3.504$.

Figures in the bracket stand for (s_{ij}) effects.

Three-line specific effects.

$\hat{t}_{123} = 0.629$, $\hat{t}_{124} = 0.866$, $\hat{t}_{125} = -1.495$, $\hat{t}_{132} = 2.291$, $\hat{t}_{134} = -2.145$, $\hat{t}_{135} = -0.145$, $\hat{t}_{142} = -2.083$
$\hat{t}_{143} = .441$, $\hat{t}_{145} = 1.641$, $\hat{t}_{152} = -0.208$, $\hat{t}_{153} = -1.070$, $\hat{t}_{154} = 1.279$, $\hat{t}_{231} = -2.920$, $\hat{t}_{241} = 1.216$,
$\hat{t}_{251} = 1.704$

$SE(\hat{t}_{ijk}) = 1.930$

Note 1: Estimates for only 15 out of 30 parameters are given here, since when the number of lines is 5, the parameter $t_{ijk} = t_{lmk}$ for all i, j, k, m, $i \neq j \neq k \neq 1 \neq m$. Also for the estimation of σ_t^2 and σ_{tt}, v should be greater than 5 and hence genetic components could not be estimated in this case.

Note 2: Also when the number of lines $v = 5$, $SE(\hat{g}_i)$ and $SE(\hat{h}_i - \hat{g}_i)$ are equal, so also $SE(\hat{s}_{ij} - \hat{s}_{ji})$ and $SE(\hat{s}_{ij} - \hat{s}_{ki})$.

Lines	$\hat{\sigma}^2_{hi}$	$\hat{\sigma}^2_{gi}$	$\hat{\sigma}^2_{di}$	$\hat{\sigma}^2_{si.}$	$\hat{\sigma}^2_{s.i}$	$\hat{\sigma}^2_{ti..}$	$\hat{\sigma}^2_{t..i}$
P_1	73.638	186.301	25.767	27.866	19.879	−3.562	1.161
P_2	30.485	89.472	30.800	19.294	25.596	−3.125	−1.025
P_3	39.855	32.667	11.725	5.295	−3.389	−4.090	−6.288
P_4	18.953	34.532	5.439	12.772	35.120	−4.346	−2.787
P_5	21.295	12.259	28.116	39.117	26.180	−5.666	−4.146

different genetic components could not be worked out.

From the results presented in table 2, it is evident that lines P_1 and P_3 are significantly superior to the rest of the lines in their average performance. Also, there are no marked differences in the average performance of lines P_1 and P_3 as grand-parents or among the rest of the three lines both as parents and as grand-patents. Line P_1 is better than line P_3 in parental performance. Line P_1 performs better as parent than as grand-parent, while the reverse is true for line P_2; in the case of the others there are no marked differences.

The comparatively large magnitude of $\{\hat{\sigma}^2_{gi}\}$ and $\{\hat{\sigma}^2_{h_i}\}$ compared with $\{\hat{\sigma}^2_{di}, \hat{\sigma}^2_{si}, \text{and } \hat{\sigma}^2_{s.i}\}$ in all the lines except P_4 and P_5 shows that the general line effects are more important than the specific effects in lines P_1, P_2 and P_3, whereas for lines P_4 and P_5 the specific effects are more important.

Although lines P_1 and P_3 are similar in that both exhibit high general line effects, they attain their high average performance by entirely different means. The relatively low variations in the specific effects $[\hat{\sigma}^2_{d3.}, \hat{\sigma}^2_{s3.} \text{ and } \hat{\sigma}^2_{s.3}]$ associated with line P_3 indicate that line P_3 uniformly transmits its high-yielding ability to all its three-way crosses. On the other hand, the high variations associated with line P_1 show that there are specific combinations of line P_1 with certain inbreds which yield considerably more than would be expected and certain other combinations which yield much less than expected on the basis of the average performance. For this reason line P_3 is probably superior to line P_1 for inclusion in the production of a synthetic variety, line P_1 is probably superior to line P_3 if specific high-yielding combinations are desired. Also, since there are no specific effects involving lines P_1 and P_3, probably a cross involving both the lines might be used for the development of a synthetic variety.

If one is interested in developing superior three-way hybrids from the given material, P_1 and P_3 cannot be ignored as they are the only two lines which have high general effects, which means that a third line has to be selected from the remaining three lines which will have high positive interactions with lines P_1 and P_3. The significantly high negative values associated with the specific effects of line P_5 with line P_1, as well as the negative general effects of line P_5, indicate that line P_5 is not a desirable one. Lines P_2 and P_4 have both negative and positive interactions with lines P_1 and P_3. By considering the two-line specific effects, it can be shown that the triplets of lines (P_1, P_2 and P_3) or (P_1, P_3 and P_4) may be chosen and combined as (13)2 and (34)1, respectively, to produce superior three-way hybrids.

Comparison of the yields of the different inbred lines shows line P_3 is the highest yielder and line P_1 is the lowest yielder. This observation, and information on the average performance of lines P_1 and P_3 in the three-way hybrid Combinations, indicate that inbred line P_1 probably contains a large number of unfavourable alleles whereas line P_3 contains a larger number of favourable alleles. This aspect needs to be examined further.

Other Characters

The results for the character mean yield per hectare broadly agree with the conclusions drawn from character mean yield per plant. The results indicate that cross (13)2 is probably superior to other crosses.

The results pertaining to maturity characters, such as number of days to tassel, number of days to silk etc., show that lines P_2 and P_4 are always associated with early maturity and P_1 and P_3 with late maturity. They also indicate that it is possible to combine earliness of maturity and high-yielding potential in the three-way hybrid by forming crosses which include lines P_2 or P_4 with P_1 and P_3. It is evident from the results of the ear characteristics, such as mean ear length and mean ear girth, that the high-yielding potential associated with lines P_1 and P_3 can probably be ascribed to the large and lengthy ears associated with lines P_1 and P_3. The poor potential of line P_2 may be attributed largely to shorter ear length rather than smaller ear girth, the reverse being true for line P_5. An interesting point here is the absence of all epistasis other than additive × additive for all the characters considered.

Conclusions

As pointed out earlier, the analysis carried out indicates that it may be possible to develop synthetic varieties using the materials at hand. It also shows that it may be possible to exploit the highyielding potential, early maturity and other desired characteristics which are present in different lines, to obtain superior three-way hybrids by selecting the suitable lines and combining them in appropriate order.

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Appendix

The standard errors of the estimates are given below: —

$$SE(\hat{h}_i) = \left[\frac{(v-1)}{\sqrt{rv^2(v-2)(v-3)}}\right]\sigma,$$

$$SE(\hat{g}_i) = \sqrt{\frac{2(v-1)}{rv^2(v-3)}} \times \sigma,$$

$$SE(\hat{d}_{ij}) = \left[\frac{(v-3)}{\sqrt{r(v-1)^2(v-4)}}\right]\sigma,$$

$$SE(\hat{s}_{ij}) = \frac{(v-2)}{(v-1)} \times \sqrt{\frac{(v^2-4v+1)}{rv(v-1)(v-4)}} \times \sigma,$$

$$SE(\hat{t}_{ijk}) = \sqrt{\frac{(v^2-6v+7)}{r(v-1)(v-2)}} \times \sigma,$$

$$SE(\hat{h}_i - \hat{h}_j) = \sqrt{\frac{2(v-1)}{rv(v-2)(v-3)}} \times \sigma,$$

$$SE(\hat{g}_i - \hat{g}_j) = \frac{2\sigma}{\sqrt{rv(v-3)}}$$

$$SE(\hat{h}_i - \hat{g}_i) = \sqrt{\frac{3(v-1)}{rv^2(v-2)}}\,\sigma\,,$$

$$SE(\hat{d}_{ij} - \hat{d}_{ik}) = \sqrt{\frac{2(v-3)^2}{r(v-1)\,(v-2)\,(v-4)}} \times \sigma$$

$$SE(\hat{d}_{ij} - \hat{d}_{kl}) = \sqrt{\frac{2(v-3)}{r(v-1)\,(v-2)}} \times \sigma\,,$$

$$SE(\hat{s}_{ij} - \hat{s}_{ji}) = \sqrt{\frac{2(v-2)}{rv(v-3)}} \times \sigma\,,$$

$$SE(\hat{s}_{ij} - \hat{s}_{ik}) = \sqrt{\frac{2(v-2)\,(v^2-4v+1)}{rv(v-1)\,(v-3)(v-4)}} \times \sigma\,,$$

$$SE(\hat{s}_{ij} - \hat{s}_{ki}) = \sqrt{\frac{2(v^2-4v+1)}{rv(v-1)\,(v-4)}} \times \sigma\,,$$

$$SE(\hat{s}_{ij} - \hat{s}_{kl}) = \sqrt{\frac{2(v^2-3v+1)}{rv(v-1)\,(v-3)}} \times \sigma\,,$$

$$SE\left(\hat{d}_{ij} - \frac{\hat{s}_{ij} + \hat{s}_{ji}}{2}\right) = \sqrt{\frac{3(v-3)}{2r(v-1)^2}} \times \sigma\,,$$

$$SE(\hat{t}_{ijk} - \hat{t}_{ikj}) = \sqrt{\frac{2(v-4)}{r(v-1)}} \times \sigma\,,$$

$$SE(\hat{t}_{ijk} - \hat{t}_{ljk}) = \sqrt{\frac{2(v^2-6v+7)}{r(v-1)\,(v-3)}} \times \sigma\,,$$

$$SE(\hat{t}_{ijk} - \hat{t}_{ilm}) = \sqrt{\frac{2(v^3-11v^2+38v-39)}{r(v-1)\,(v-3)(v-4)}}\,\sigma\,,$$

$$SE(\hat{t}_{ijk} - \hat{t}_{lmk}) = \sqrt{\frac{2(v-5)\,(v^2-6v+7)}{r(v-1)\,(v-3)\,(v-4)}}\,\sigma\,,$$

$$SE(\hat{t}_{ijk} - \hat{t}_{lmn}) = \sqrt{\frac{2(v^3-11v^2+39v-41)}{r(v-1)\,(v-3)\,(v-4)}}\,\sigma\,,$$

where $SE(\hat{a} - \hat{b})$ stands for the standard error of the difference between $\hat{a}$ and $\hat{b}$.

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