

EVALUATION OF PARTIAL VS. COMPLETE DIALLEL
CROSSES IN UPLAND COTTON,
GOSSYPIUM HIRSUTUM L.

By

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EVALUATION OF PARTIAL VS. COMPLETE DIALLEL

CROSSES IN UPLAND COTTON,

GOSSYPIUM HIRSUTUM L.¹

ABSTRACT

Eight commercial cultivars of upland cotton (Gossypium hirsutum L.), their 28 F_1 's (ignoring reciprocals), 24 of their 28 possible F_2 's and 24 selected Bc's were planted in a randomized complete-block design with four replications, at a single location in 1975. Three fiber characters, 2.5% and 50% span lengths and uniformity index, as measured on remnant samples from the parents and their F_1 's in that experiment were studied herein. These data were used to compare Griffing's complete diallel design to several partial diallel designs, i.e., the factorial partial diallel (FPD) design 4 with four crosses (FPD4) per line and the circulant partial diallel (CPD) design with sample sizes (= number of crosses per line) of three (CPD3) and five (CPD5). Points of comparison included detection of GCA and SCA, estimates of narrow- and broad-sense heritabilities and of average degree of dominance, selection of lines based on relative GCA effects, and relative magnitudes of the average standard errors of the difference of GCA effects. The Jinks-Hayman method of analyzing a complete diallel was compared to Griffing's analysis on the basis of detection

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of additive and dominance variation and on the relative size of their estimates of heritability and degree of dominance. Computer simulation was used to study the distribution of estimates of heritability and average degree of dominance and the relationships of those estimates between the complete and the partial diallels.

The complete and all partial diallels detected significant GCA effects for all three fiber characters while detection of SCA effects was less consistent. The range of variation in GCA, SCA, and error mean squares became progressively smaller as sample size increased from three to four to five. The same was true for broad- and narrow-sense heritabilities and for average degree of dominance. Detection of GCA variance components was less certain than for GCA effects especially when sample size was small. Since the CPD and FPD designs did not have the same sample sizes, a clear case could not be made for one partial diallel design over the other. Accuracy of estimation appeared to be more a function of increasing sample size than of different designs. Estimation of average degree of dominance by partial diallels was much less reliable than for heritability, especially for small sample sizes and for traits with low heritability. Mistakes in selection relative to the complete diallel based on ranking of parental GCA effects increased as sample size and heritability declined. The standard errors of the difference between GCA effects in the FPD4 design were generally smaller than in the CPD3 or CPD5 designs. However, fewer errors in selection were actually made with the CPD5 design than with the FPD4. The Jinks-Hayman analysis in another data set indicated that the average degree of dominance for 2.5% span length was essentially in the complete dominance range

while the other two traits showed overdominance. In Griffing's analysis, all three traits were in the partial dominance range. Both analyses detected significant GCA or D in every case. Griffing's analysis detected significant SCA only for 2.5% span length, while the Jinks-Hayman method detected significant H_1 and H_2 for all three traits. No consistent differences for heritability estimates were noted between the two analyses. The Jinks-Hayman analysis estimated dominance higher than did Griffing's, but it is not known whether the Jinks-Hayman analysis was overestimating that parameter, Griffing's was underestimating it, or both. In the simulation studies, increased environmental variation generally reduced the size of skewness and kurtosis of the distribution of heritability estimate. Smaller sample sizes increased standard deviations for estimates of heritability and degree of dominance. When environmental variation is small, heritability tends to be overestimated, but not when the variation is large. For both values of environmental variance, the mean degree of dominance tends to be biased upwards. When environmental variation is large, some dominance will tend to be estimated even where none exists in the genetic system. The CPD5 design exhibited higher correlations for degree of dominance and heritability with the complete diallel than did the FPD4 which in turn was higher than the CPD3. The correlations for heritability were generally higher than for degree of dominance indicating that heritability is more accurately estimated with partial diallels than is degree of dominance. When environmental variation increased, the heritability correlations declined in general while those for degree of dominance declined in every case. The decline for dominance also appeared to be greater than for heritability.

Estimates of degree of dominance obtained with partial diallels appear particularly unreliable when sample size is small, environmental variance is large, or heritability is low.

Additional index words: Fiber length, Uniformity index, Combining ability, Heritability, Degree of dominance, Simulation.

INTRODUCTION

General and specific combining ability are important parameters in the improvement of crop performance. The estimation and analysis of combining ability provide the plant breeder with a means to select potentially desirable lines or combinations of lines for particular purposes. It also provides estimates of genetic parameters from which inferences can be derived about the types of gene action controlling the traits in question.

A diallel crossing system is frequently used to obtain estimates of combining ability. A complete diallel cross, without reciprocals or selfs, requires $p(p - 1)/2$ single crosses among p inbred lines. When a large number of lines is available for study, the number of crosses may be too large for simultaneous evaluation by a complete diallel.

Partial diallel crosses have been proposed as a means for the breeder to cope with many potential parents. At the same time, a higher intensity of selection among parents can be practiced; and it can thus give greater precision in estimating the variance components for general combining ability. To estimate the specific combining ability for a particular cross, one has no alternative other than to study that actual cross. A few papers using the partial diallel cross have been reported in maize (Zea mays L.), flax or linseed (Linum usitatissimum L.), barley (Hordeum vulgare L.), alfalfa or

lucerne (Medicago sativa L.), and wheat (Triticum aestivum L.). The present study will report on use of the technique in cotton, Gossypium hirsutum L.

The purpose of this study was to compare a complete diallel mating design, using Griffing's (14) method of analysis, and two partial diallel systems in estimating genetic parameters and general combining ability effects for three characters in cotton. Computer simulation was also used to investigate the distribution and compare estimates of heritability and average degree of dominance for the Griffing analysis vs. partial diallel crosses. Jinks-Hayman (16, 19) diallel estimates, commonly used in plant breeding, were also compared to estimates derived by the Griffing analysis.

LITERATURE REVIEW

Complete Diallel Crosses

The two main approaches to analyses of diallel crosses which have been widely utilized by plant and animal breeders are those described by Griffing (13, 14) and by Jinks and Hayman (16, 17, 18, 19). Hayman (16) has presented methods for measuring additive and dominance variation, for describing relative dominance among lines, and for testing the validity of certain assumptions in his analysis. His experimental materials include parents and a set of F_1 's (with or without reciprocals), and the set of parental inbreds usually represent the population of inference.

Kempthorne (21) has criticized the Jinks-Hayman analysis for being too restricted in scope of inference. He argued that interpretation of the diallel cross should be made in terms of a larger population from which the homozygous parents were derived. Despite this criticism, the Jinks-Hayman method remains an important tool for the plant breeder to detect a particular set of inbred lines which produce superior hybrids or to detect an inbred line or lines which have breeding value for the production of varieties.

In 1960, Hayman (17) presented a method for estimating genetic parameters when inbred lines are considered a random sample from a population, and he also showed how the variances for combining abilities derived by Griffing's method (14) were related to his genetic

components. Because estimation of variance components is subject to large sampling errors, those estimates would likely not be close to population values when the number of parents were small. Hayman (18) considered a fixed-effect model to be more appropriate if the number of parents was less than 10.

Griffing (14) developed analyses for four diallel methods: including or excluding parents and/or reciprocals. Fixed or random effects are allowed in each method. The fixed model provides estimates of general combining ability (GCA) effects for the parents and of specific combining ability (SCA) effects for the particular crosses studied. The random model allows estimates of GCA and SCA variance components. The former is concerned with combining abilities for the individual parents used in the experiment; the latter is more concerned with drawing inferences from estimates of variance components about the population from which the parents were sampled.

Partial Diallel Crosses

A method for constructing a partial diallel cross design was first proposed by Brown, as cited in Kempthorne (22). Kempthorne and Curnow (23) elaborated on Brown's method and presented a method of analysis. In their "circulant partial diallel" (CPD) design, either the number of parents, p , or the sample size (= the number of crosses per line), s , must be even while the other is odd. Fyfe and Gilbert (12) proposed two other designs, a "triangular" and a "factorial partial diallel" (FPD) which they claim are better balanced and give more information per mating about GCA than the CPD design of Kempthorne and Curnow (23). However, these designs are restricted to those cases where the number

of parents is not a prime and (for a given number of parents) only one value of s is possible; in contrast, more than one value of s can be chosen in the case of the CPD designs.

There is a correspondence between partial diallel crosses (PDC) and the partially balanced incomplete block (PBIB) designs with two plots per block and two associate classes. Various methods of constructing PDC designs are based on the utilization of PBIB designs. In the case of complete diallel crosses, all comparisons between GCA effects for any two parents will have the same variance (a balanced property); whereas, in the PDC there are at least two different standard errors for comparisons. Average variances over all comparisons of GCA effects are used for determining the efficiency of different designs. Mathur and Narain (26) presented tables for several PDC together with average variances for various combinations of p and s .

Comparisons Among Various Diallel Designs

Fyfe and Gilbert (12) demonstrated that the average variance of the difference between two GCA's in their factorial design 4 was smaller than that in the CPD design. Kearsey (20) compared five experimental designs and concluded that the CPD design involved rather laborious computations and that the Jinks-Hayman method provided more information on variance components. However, he did not compare standard errors of variance components. Thus, conclusions about the precision of estimates cannot be made.

Murty et al. (27) compared CPD sets where $s = 3, 5, 7,$ and 9 from a set of 10 linseed genotypes. They found variation due to SCA was significant for all characters; whereas, GCA was significant for

most characters considered at all values of s . A tendency was noted for GCA effects to be overestimated with a decrease in s . For all characters the average standard error of the difference between two GCA's increased sharply as s was reduced below $p/2$ for all characters. Although the precision of GCA effect estimates decreased with diminishing values of s , their results showed that PDC with $s = p/2$ may be adequate to screen parents for GCA effects. They observed that the ranks of parents remained more or less the same based on GCA estimates (for values of s equal to or greater than $p/2$). Anand and Murty (1) carried out the same type of experiment as Murty et al. (27) with a different set of parents, but their results were very similar.

Anand and Rana (2) compared the efficiency of the FPD design of Fyfe and Gilbert (12) in a 10×10 diallel cross of linseed with wide genetic diversity. They found that PDC design 4 gave large and significant GCA estimates for most of the characters and no significant variation due to nonadditive effects was noted for any character. The latter is contrary to the findings of Murty et al. (27) and of Anand and Murty (1), who showed that rearrangement of parents had little effect on their rank based on GCA effects.

Somayajulu et al. (31) studied combining ability for grain yield in 23 wheat cultivars using the CPD design with $s = 4$. They found non-additive genetic variation was predominant and considerable agreement between the estimation of GCA effects based on F_1 vs. F_2 generations. They concluded that the design was reliable for estimating GCA effects.

The conclusions, especially in relation to nonadditive genetic effects, by Murty et al. (27), Anand and Murty (1), and probably also Somayajulu et al. (31), are likely not correct because the computer

program written for their CPD design contained errors (5). From a complete diallel among 12 parents, Bray (5) analyzed his data using the method of Kempthorne and Curnow (23) with several values of s . Twenty random samples were analyzed for each s for each character. He demonstrated that estimates of variance components for any one sample with small values of s may depart greatly from that of the complete diallel. The precision of the heritability estimates was poor for most characters, and conclusions regarding presence vs. absence of GCA and SCA were rarely correct in the smaller partial dialles. He believes one cannot generalize an optimum value of s because different characters respond differently.

Dhillon (8), citing his Ph.D. investigation on sampling in a diallel cross of 20 parents, found that results from a PDC of $s = 11$ to 15 corresponded to the complete diallel. The ratio of GCA to SCA variance components exhibited upward bias in the PDC, but it generally agreed with the complete diallel. Moreover, for characters with high heritabilities but low degrees of dominance, the PDC gave reliable estimates for s as small as five. The characters (for which nonadditive gene action was more important) were more liable to misinterpretation in small partial diallels. He judged that the CPD design of Kempthorne and Curnow (23) was slightly inferior to the FPD of Fyfe and Gilbert (12).

Chaudhary et al. (6) compared four sets of partial diallels using Kempthorne and Curnow's method (23) with the complete diallel in barley. Analyses of variance showed significant GCA and SCA mean squares for all characters in all four partial sets and in the complete diallel. In general, dominance gene action appeared to predominate. The rankings

of parents based on GCA effects in the four sets of partial diallels were very dissimilar to that in the complete diallel, but the rankings were similar between the partial diallel sets with $p = 12$, $s = 5$ and with $p = 12$, $s = 3$. The other two sets (with $p = 8$) were also alike. This suggests that the CPD design is not very reliable in selecting cultivars with high GCA.

Dhillon and Singh (9) evaluated 20 diverse maize parents in four environments using the CPD design with different partial diallel sizes. Their results showed that GCA mean squares for most traits were significant in most environments regardless of s and agreed very well with the complete diallel. For SCA mean squares, variation existed from character to character and from environment to environment, i.e., there were no consistent agreements between the PDC and the complete diallel. In most cases, there was no overestimation of nonadditive gene action. The estimation of GCA effects became more unpredictable as s decreased. In general, the average standard errors of the difference between GCA effects increased rapidly for $s < 7$. For traits with low heritability, estimates of narrow-sense heritability (H_n) in the partial diallels were not comparable with that from the complete diallel in any environment. On the other hand, for high heritability traits, H_n was in general erratic with environment for $s \leq 5$. There was good agreement with "true" GCA variance component of estimates with CPD for $s \geq 5$, but not for the SCA variance component.

Dhillon and Singh (10) also reported another similar study, but here they compared the FPD of Fyfe and Gilbert (12) with Griffing's method 4 (14). Analyses of variance showed agreement between the partial and the complete diallel. Correlation coefficients for GCA

effects between the two were high for all characters. Estimates of average standard errors of the difference between GCA effects in the FPD were larger than in the complete diallel. Broad-sense heritability estimates in the FPD showed close agreement with the complete diallel for all traits, except grain yield; but H_n did not, especially for low values of s . He concluded that the FPD was, on the whole, reliable but that it depended on sample size, the genetic nature of the characters involved, and the number of environments used to evaluate the materials.

MATERIALS AND METHODS

Experimental Procedures

The fiber data used in the present study were measured on remnant samples from an irrigated experiment conducted by Mamaghani (24). The eight commercial cultivars of upland cotton used in his experiment included '6111', 'Acala 1517-70', 'Stoneville 7A', 'Deltapine Land 16', 'Lankart LX 571', 'Lockett 4789-A', 'Westburn 70', and 'Paymaster 202' (coded as 1 through 8, respectively, in Figure 7). These eight parents, the 28 F_1 's (excluding reciprocals), 24 of the 28 possible F_2 's, and 24 selected Bc's were planted on 5 June 1975 at Perkins, Oklahoma on a Teller loam soil (a fine-loamy, mixed, thermic Udic Argiustolls). The experimental design was a randomized complete-block with four replications. Two independently assigned rows of each F_2 and a single row of all other entries were included in each replication. Plots were single rows 7.1 m long and 1.0 m apart, and plants within a row were 20-30 cm apart. Plants bordering alleys or skips in the row were not harvested. The number of plants sampled varied from plot to plot (usually from 20 to 25), but not more than 30 plants were harvested from any single row. Three mature bolls were harvested from the central portion of each plant, and fiber from those bolls was measured in the Cotton Fiber Laboratory at Oklahoma State University. The following characters from those samples were analyzed: 2.5% and 50% span lengths (measured on the digital fibrograph in inches) and uniformity index (the ratio

of 50% to 2.5% span length expressed as a percentage).

Partial Diallel Cross Designs

Two partial diallel methods were studied. The first was the circulant partial diallel (CPD) cross design of Kempthorne and Curnow (23) with two sampling levels where the number of crosses per line, s , equaled three and five. From the complete diallel table, the crosses sampled for $s = 3$ and $s = 5$ are illustrated in Table 1. The factorial partial diallel (FPD) cross design 4 of Fyfe and Gilbert (12) was also studied. The number of parents $p = km$ where $k \geq 2$ and $m \geq 2$ and both must be integers. For $p = 8$, $k = 4$ and $m = 2$. Each parent can be denoted as ab , where $1 \leq a \leq k$ and $1 \leq b \leq m$. The crosses being sampled are of the type $ab \times ac$ or $ab \times cb$ with $s = k + m - 2 = 4$. The crosses utilized herein for this design are also illustrated in Table 1.

Statistical Analyses

A preliminary test for homogeneity of variances was conducted in each replication for all three fiber characters using the Q-test (11). Because each row had an unequal number of plants, the Q-value was calculated as

$$Q = \frac{\bar{v} \sum_{i=1}^k v_i s_i^4}{\left(\sum_{i=1}^k v_i s_i^2 \right)^2}$$

where

$$\bar{v} = \frac{\sum_{i=1}^k v_i}{k}$$

and

$v_i = n_i - 1$ ($i=1, \dots, k$). Then, $k\bar{v} (kQ-1)/2$ is asymptotically chi-square with $k-1$ degrees of freedom.

Griffing's method 4 vs. parital diallel cross methods. The original F_1 individual plant data for the three fiber characters were converted to row means which were all used in all subsequent analyses. Parental, F_2 , or backcross data were not used in these comparisons. Analyses of variance for combining ability and estimation of GCA and SCA effects followed Griffing's method 4, model I (fixed effects). However, model II (random effects) was also used to derive estimates of variance components, heritability, and degree of dominance.

The analyses of the partial diallel followed the procedures outlined by Kempthorne and Curnow (23) for the CPD and by Fyfe and Gilbert (12) for the FPD design 4. Models I and II were also used for the same purposes in the partial diallels as described above for Griffing's analysis. Estimates of GCA effects were calculated as:

$$\hat{g}_i = \sum_j a^{ij} Q_j$$

where a^{ij} is the ij^{th} element of the inverse matrix and $Q_i = Y_i - 2Y_{..} / p$ where $Y_{..}$ is the total of cross means.

Assuming that parents are inbred with a coefficient of inbreeding of one, then heritability estimates in the broad- (H_b) and narrow-senses (H_n) based on plot means were calculated as follows:

$$H_b = (2\hat{\sigma}_g^2 + \hat{\sigma}_s^2) / \hat{\sigma}_p^2 \quad \text{and} \quad H_n = 2\hat{\sigma}_g^2 / \hat{\sigma}_p^2$$

where

$$\hat{\sigma}_p^2 = 2\hat{\sigma}_g^2 + \hat{\sigma}_s^2 + \hat{\sigma}_e^2 \text{ and } \hat{\sigma}_g^2, \hat{\sigma}_s^2, \text{ and } \hat{\sigma}_e^2$$

are variance components for GCA, SCA, and experimental error, respectively. Average degree of dominance (\hat{d}) was estimated as

$$\left(\hat{\sigma}_s^2 / \hat{\sigma}_g^2 \right)^{1/2}$$

The average variance of the difference between two GCA effects for the CPD design was

$$2 \left[p a^0 / (p-1) - 1/2s(p-1) \right] (\sigma_s^2 + \sigma_e^2/r)$$

where a^0 is the element of the diagonal of the inverse matrix. The same estimate for the FPD design 4 is $2 \left[\bar{D} - \bar{ND} \right] \sigma_e^2/r$ where \bar{D} is the average of the diagonal terms of the inverse matrix and \bar{ND} is the average of the non-diagonal terms of that matrix. Spearman's rank correlation method (30) was used to calculate correlations among parental ranks based on their GCA estimates between the partial and complete diallels.

Twelve random samples of partial diallels were taken from the complete diallel by rearranging the positions of parental lines within the diallel table, and the same analysis was then conducted for each of the 12 samples.

Jinks-Hayman method vs. Griffing's analysis. The procedures of Jinks and Hayman (16, 19) were used to analyze the same F_1 data used in the previous section plus that of the parents. An analysis of variance of $(W_r - V_r)$ values was conducted for each trait; the test showed no

significant differences among $(W_r - V_r)$ values over arrays which suggested that the additive-dominance model was adequate in this population for these traits (25). No further tests of the basic assumptions of the diallel analysis (7) were made because the intention of this study was to compare estimation procedures, and the fiber properties themselves were only of secondary interest. Each replication was treated as a separate experiment, and the environmental components for parents (E_0) and F_1 progenies (E_1) were estimated from the variation among plants within a plot. The estimates of the Jinks-Hayman parameters D , H_1 , H_2 , F , E_0 , and E_1 (16, 19) were obtained for each trait in each replication; then, the mean over replicates for each of those estimates was taken. Standard errors of the mean were then calculated from the variation of the estimates in each replication around the overall mean. This analysis by individual replicates was recommended by Nelder (28) to reduce bias in the standard errors of the parameters estimated.

A narrow-sense heritability based on plot means [following Crumacker and Allard (7)] was estimated as $H_n = 1/4 D / (1/4 D + 1/4 H_1 - 1/4 F + E)$ where $E = (E_0 + E_1)/2$. Average degree of dominance was estimated as $(H_1/D)^{1/2}$. Each ratio was calculated in each replicate and then averaged over replicates; t-values were used for setting confidence limits on the overall means again using variation of the estimates in each replication around the overall mean to calculate a standard error of the mean.

Simulation studies of the diallel. In a computer simulation study, the complete diallel consisted of $p(p-1)/2$ crosses with $p = 8$.

In generating the F_1 hybrids, it was assumed that parental lines were completely homozygous at all loci and that there were no interallelic interactions (i.e., epistasis). Ten loci, two alleles per locus, each locus having an additive value equal to two (in homozygous dominants) or zero (in homozygous recessives), were used in combination with different gene frequencies, f , of 0.2, 0.5, and 0.8 and with dominance effects, δ , of 0, 1, and 2 at each gene frequency (except at $f = 0.8$ which lacked $\delta = 0$ and 2). Two levels of environmental standard deviations, σ_E , of 1.5 and 6.5 were used with each of these combinations.

Genotypes were randomly assigned to the eight parents either as recessive or dominant homozygotes at each locus independently. Then, genotypic value was assigned to the F_1 progeny resulting from that cross and summed over all 10 loci. A single phenotypic value of the F_1 progeny was generated for each cross to represent a mean over replicates. The phenotypic values were obtained by adding a random value obtained from a normal distribution with zero mean and variance of σ_E^2 . The random environmental components were generated through the use of the subprogram GAUSF(N); whereas, genotypes of parents were obtained through the subprogram RANF(0) which generates a random number uniformly distributed as (0,1). Those two subprograms were made available through the generosity of Dr. J. P. Chandler (Computer Sci. Dep., Oklahoma State University). The error mean square was derived from a chi-square variable using the formula (15) $X_V^2 = v[1 - 2/(9v) + \text{Nor} \sqrt{2/(9v)}]^3$ where Nor is a standardized normal variate which is generated by GAUSF(N), and v is the degrees of freedom for the X_V^2 statistic. The error mean square is then $X_V^2 \sigma_E^2 / (vr)$ where r is the number of replications.

Estimates of narrow-sense heritability and of the average degree of dominance were calculated from variance components from each sample for each type of diallel. Means, standard deviations, skewness, kurtosis, and correlations between full and partial diallels for those estimates were calculated from 200 samples and used to compare the partial with the complete diallel (Griffing's analysis).

RESULTS AND DISCUSSION

Homogeneity of variance was tested for the three fiber characters by replications using the Q-test (11). Because the results were not significant in one or more replications for each character, diallel analyses were conducted.

Detection of GCA and SCA

Analyses of variance for the complete diallel (Table 2) indicated highly significant differences among entries and GCA effects (Model I) for all three fiber traits. Only 2.5% span length also exhibited significant SCA effects. All the partial diallels were in agreement with the complete diallel for 2.5% span length with respect to significance of GCA effects (Table 3). Thirty-four of the 36 partial diallels also exhibited significant SCA effects. Thirty-three of 36 partial diallels displayed significant GCA effects for 50% span length while 35 to 36 did so for uniformity index. Eleven of 36 partial diallels detected significant SCA effects for 50% span length while 5 to 36 did so for uniformity index. The complete diallel did not detect significant SCA effects for the latter two traits. These results suggest that SCA effects are more sensitive to sampling variation than are GCA effects. In detecting significance of GCA, the complete diallel (CD7) was equivalent to CPD5 which was better than FPD4 which was in turn better than CPD3. However, the differences among the partial diallels were very small, for their ability to detect the presence vs. absence of

GCA effects.

Figs. 1 through 3 show the distribution for the GCA, SCA, and error mean squares estimate in the various diallels for 2.5% and 50% span lengths, and uniformity index, respectively. The GCA mean squares were generally smaller in the partial diallels than in the complete diallel. This is because the expected mean square for GCA has a coefficient that varies directly with the size of s . As s increased from 3 to 4 to 5 in the CPD3, FPD4, and CPD5, respectively, the mean squares for GCA, SCA, and error displayed a narrowing range of variation and tended to more closely correspond to that of the complete diallel.

When the test for GCA mean squares was based on Model II (the random model), the loss of power of the test was more obvious with small s (Table 3). Relative to Model I, a greater proportion of the samples were significant at the 0.05, but not the 0.01, probability level. For the CPD3 design, only 17 of 36 GCA components were significant over all three traits while 28 of 36 were for the FPD4 and 35 of 36 were for the CPD5 design. The test for SCA mean squares in Model II is the same as in Model I.

Estimates of Heritability and Degree of Dominance

Estimates of narrow-sense heritability were 0.65 for 2.5% span length, 0.28 for 50% span length, and 0.35 for uniformity index, respectively, in the complete diallel (Fig. 4). Again, the estimates in the partial diallels showed wider variation for small values of s in all three traits, an intermediate amount of variation for FPD4, and the least variation for CPD5. Therefore, the likelihood of obtaining a fairly accurate estimate of heritability is low for very small sample

sizes even for relatively highly heritable characters like 2.5% span length. If the CPD and FPD designs had the same sample sizes, a clear case could be presented for one design or the other. However, the trends indicated in Figs. 1 through 4 suggest that accuracy of estimation is more a function of increasing sample size than of one design being better than the other. Admittedly, only 12 samples are a limited basis to come to such a conclusion. It also appears that going from $s = 3$ to $s = 4$ causes a much greater reduction in variation among samples than going from $s = 4$ to $s = 5$.

The estimates of broad-sense heritability (Fig. 5) showed, in general, less sensitivity to sampling than did those for narrow-sense, especially for 2.5% span length and uniformity index. However, the same trends are evident for ranges in the estimates in the CPD3 to FPD4 to CPD5 designs. From simulation studies, Pederson (29) concluded that partial diallels should be preferred to the complete diallel as far as efficient (the amount of information per unit of measurement) estimation of heritability is concerned. This could be taken as one of the advantages of partial diallel crosses if highly heritable traits are estimated and if a suitable value of s is used. Certainly, a value of $s = 3$ would appear too small for our group of eight parents. Whether a researcher would be satisfied with estimates obtained with $s = 4$ or $s = 5$ would likely be a subjective decision.

All three characters expressed a degree of dominance in the partial dominance range in the complete diallel analysis (Fig. 6). This is defined as \hat{d} greater than zero (no dominance), but less than one (complete dominance), assuming gene frequency is one-half. The results indicate that estimates of average degree of dominance were very variable

between samples for characters with low heritability and especially for smaller sample sizes. For $s = 3$, \hat{d} ranged from 0.4 to 2.5 for 2.5% span length, zero to infinity for 50% span length, and zero to 2.5 for uniformity index. Relatively few cases showed close agreement with the complete diallel. Lack of dominance was shown by some samples of $s = 3$ and $s = 4$ in the lower heritable traits. This was due to negative estimates of SCA variance components which were interpreted to be estimates of zero. Dhillon and Singh (9) also found that negative estimates of the SCA component occurred more frequently for characters with low genotypic variation. When s increased from 3 to 4 to 5, variation of \hat{d} became markedly less.

Ranking of Parents Based on GCA Effects

Rankings of the parents based on their GCA effects in the complete vs. the three partial diallels are shown in Fig. 7. The number inside each symbol indicates the number of samples of a given parental line falling in that rank (vertical scale) out of 12 samples while the top scale indicates the "true" parental rank based on the complete diallel. Assuming the researcher intended to retain the half of the eight lines with higher GCA effects and discard the lower half, how many mistakes would he have made using the partial diallels relative to the complete diallel? For 2.5% span length, where $s = 5$, the top and bottom three parents would have been differentiated without mistakes; where $s = 4$, the top three and bottom two would have been handled correctly; where $s = 3$, only the top and bottom two would have been identified without errors in every case. For uniformity index, when $s = 5$, the top three and bottom two would have been identified without error; and when $s = 4$

or 3, the top two and bottom one would have been selected without error in every case. For 50% span length, when $s = 5$ or 4 , it was only the top and bottom one; and when $s = 3$, it was the top one only. Mistakes become more frequent as sample size decreased from 5 to 4 to 3 and as heritability declined from high (2.5% span length) to moderate (uniformity index) to low-moderate (50% span length).

Spearman's rank correlations between CPD5 and the complete diallel (Fig. 8) were all over 0.90 for 2.5% span length, 11 of 12 ranged between 0.86 and 0.98 for uniformity index, but only 7 were 0.86 or higher for 50% span length. (A correlation of 0.86 or higher was significant at the 0.01 level of probability; 0.71 to 0.85 was significant at the 0.05 level.) In correlations with FPD4, 10 of 12 gave a correlation over 0.90 for 2.5% span length, only 2 of 12 fell between 0.86 and 1.00 for 50% span length while 11 of 12 did so for uniformity index. In the case of CPD3, only 5 of 12 were within the range of 0.86 to 1.00 for 2.5% span length, 2 of 12 for 50% span length, and 6 of 12 for uniformity index. This suggests (as did the data in Fig. 7) that smaller sample sized partial diallel crosses cannot be relied upon with much confidence to select among parents based on GCA effects. Bray (5) also observed that for small values of s , the partial diallel cross frequently leads to incorrect selections, especially for characters of low heritability. However, if the partial diallel cross is restricted to characters of high additive variation only, its use would be fairly limited.

For a given partial diallel design, estimates of the average standard errors of the difference between GCA effects have been observed (1, 10, 27) to increase with a decrease in the value of s . This trend

was generally supported for CPD3 vs. CPD5 in the present data (Table 4). Two exceptions for uniformity index were noted where slightly smaller average standard errors were observed for $s = 3$ than $s = 5$. A large increase in the average standard error of the difference when s is small will reduce sensitivity of detecting differences among lines. All partial diallels have larger average standard errors of the difference than the complete diallel because the complete diallel is the most balanced design (with only one standard error for comparing any two GCA effects). The FPD4 design had much smaller average standard errors of the difference for 2.5% span length, slightly smaller for 50% span length (except one sample), and 6 of 12 were slightly smaller (with two ties) for uniformity index than for the CPD5 design. The range of variation in the average standard errors of the difference was also smaller in the FPD4 design for all traits than for the CPD5 which in turn was smaller than for the CPD3 which suggests that this design tends to be somewhat more sensitive to detection of differences among GCA effects. This may be due to the better balance of the FPD4 design (12). Therefore, the FPD4 design may be preferred over the CPD because of its smaller average standard errors. However, disadvantages of the former design are that the numbers of parents cannot be a prime and the numbers of crosses per line are rather restricted. Also, inspection of the data in Fig. 7 showed that fewer mistakes in selection would be made with the CPD5 design than with the FPD4.

Partial diallel crosses have a defect in that detection of differences among parental lines does not have the same accuracy for each comparison because more than one standard error is involved. However, this should not be considered a serious hindrance to the use of partial

diallels because they are of primary value in the initial stages of parental screening. Precise comparisons among GCA effects are not extremely important. What is important is that most of the better lines are retained and most of the poorer ones are discarded. Furthermore, when large numbers of lines are evaluated, the differences among the standard errors would tend to be quite small so that the average standard error of the difference between GCA effects could be used with some confidence.

Parameters Estimated by the Jinks-Hayman Analysis

All estimates of genetic and environmental parameters, except for F, were significantly different from zero for all characters (Table 5). F was significant only for 50% span length.

With respect to significant dominance effects, these results did not correspond to those from Griffing's analysis (Table 2) which showed significant SCA effects for 2.5% span length only. The differences in these results may be partly associated with the estimates of environmental variation which were smaller in the Jinks-Hayman method because they were based on variation within plots. Both analyses detected significant GCA's or D's for every character.

Estimates of narrow-sense heritability and average degree of dominance were all significantly different from zero (Table 6). The Jinks-Hayman analysis gave a lower estimate of heritability for 2.5% span length (0.48 vs. 0.65), but higher for 50% span length (0.38 to 0.28) and uniformity index (0.49 to 0.35), than did Griffing's method (Fig. 4). The Jinks-Hayman estimate of heritability for 2.5% span length was essentially equivalent to that for uniformity index while it

was almost twice as large when estimated by Griffing's analysis. The Jinks-Hayman degree of dominance showed complete dominance for 2.5% span length and overdominance for the other two traits; whereas, Griffing's method showed partial dominance for all three (Fig. 6).

The Jinks-Hayman analysis provides six statistics from which the components D , H_1 , H_2 , F , E_0 , and E_1 can be obtained; whereas, Griffing's method and the partial diallels provide estimates of additive, non-additive, and environmental variation (20). It is doubtful how much confidence one can place in the estimates of F because its value can change greatly from one year to the next (3) which would in turn be capable of influencing the estimates of heritability and degree of dominance quite significantly. Estimates of heritability and degree of dominance are of basic importance in plant breeding programs. The Jinks-Hayman method requires more labor to acquire those estimates, but there is no proof one way or the other which method gives the more reliable estimates. The Jinks-Hayman method tends to estimate degree of dominance higher than does the Griffing analysis. Baker and Verhalen (3) obtained overdominance estimates for 50% span length and uniformity index in two years and a high degree of partial dominance in one year and complete dominance the next for 2.5% span length using the Jinks-Hayman analysis; but their analysis for combining ability over years for the same data (4) using the Griffing analysis showed the three traits were controlled by partially dominant genes. Judging from their two references (3, 4) and the present results for heritability, complete agreement does not exist between the two techniques in ranking the three traits; however, 2.5% span length appeared to have the highest estimate. Whether the Jinks-Hayman or Griffing analysis is more

accurate cannot be determined from such scanty evidence.

Estimation of Genetic Ratios in Simulation Studies

In studying the distribution of a parameter estimate, two statistics used for measuring departure of the distribution from the normal curve are skewness and kurtosis (30). A negative (positive) skewness indicates the curve has a long tail to the left (right). A curve with a positive kurtosis has longer tails and a sharper peak than normal; whereas, negative kurtosis indicates shorter tails and a flatter top.

All mean estimates of heritability exhibited downward bias when $\sigma_E = 1.5$ and almost all the mean estimates did so when $\sigma_E = 6.5$. Increasing environmental variation markedly reduced the size of skewness and kurtosis of the distribution of heritability estimate. Some of the distributions changed from negative to positive skewness, most of the kurtosis became negative; and the amount of bias also tended to be smaller when σ_E was larger (Tables 7 and 8).

For a given gene frequency, the standard deviation of the heritability estimate appeared to increase with level of dominance. This trend was evident in both environments, but the changes were less with the larger σ_E . It should also be noted that CPD3 in general has the largest standard deviation and CPD5 the smallest. The effect of changing dominance level on skewness and kurtosis depended on gene frequency and environmental variation.

For $\delta = 1$ and $\sigma_E = 1.5$, the standard deviation of the heritability estimate declined with a decreasing gene frequency for all diallels. At those levels of δ and σ_E , skewness and kurtosis were largest at $f = 0.5$ for both the complete and partial diallels of CPD5 and FPD4.

When $\delta = 1$ and $\sigma_E = 6.5$, there is little change in the magnitude of the three statistics from $f = 0.2$ to $f = 0.5$; but the change was marked from $f = 0.5$ to $f = 0.8$ for all diallels.

Frequency distributions for heritability (given $f = 0.5$ and $\sigma_E = 1.5$) are shown in Fig. 9 as an example. The histograms indicate that the CPD5 design had the closest resemblance to the complete diallel at all three levels of dominance.

In contrast to the heritability estimates, the mean estimate for average degree of dominance tended to be biased upwards in all diallels in both environments (Tables 9 and 10). The amount of bias depended upon the environmental variation, gene frequency, and level of dominance. The bias tended to be larger as σ_E increased, except for the case of complete dominance. The complete diallel did not always give the best estimates (indicated by mean estimates) nor did it consistently have smaller standard deviations than the partial diallels. The mean estimate for average degree of dominance indicated that a character will always be estimated to have some degree of average dominance when σ_E is large even when the trait in reality it actually has no dominance at all. However, there were also a large number of zero estimates among the 200 samples. This occurred most frequently when $\delta = 0$ and $\sigma_E = 6.5$ and slightly less often when $\sigma_E = 1.5$. The chance of obtaining zero values ranged from 50 to 55% in the complete diallel and CPD5 and from 56 to 69% in the other partial diallels. Therefore, the larger diallels have a slightly greater chance of making wrong conclusions about degree of dominance. With partial dominance, large σ_E and $f = 0.2$ and 0.8 , the complete and the partial diallels did not always give good estimates. The chance of obtaining zero or undefined estimates was about 50% in the

complete diallel, about 60 to 70% in the CPD3, and substantially lower in CPD5 and FPD4 for $f = 0.5$. The chance of obtaining zero estimates was reduced greatly when dominance is complete.

The frequency distributions for the average degree of dominance showed positive skewness and kurtosis in all diallels (Fig. 10 for $f = 0.5$ and $\sigma_E = 1.5$) and in both environments (Tables 9 and 10). The effect of increasing level of dominance on increasing the standard deviation at a fixed gene frequency was similar to that for the heritability estimates at $\sigma_E = 1.5$ and at $\sigma_E = 6.5$ with $f = 0.5$; but for $\sigma_E = 6.5$ with $f = 0.2$, the relationship no longer held. When $\delta = 1$ and $\sigma_E = 1.5$, there was an increase in standard deviation, skewness, and kurtosis with increasing gene frequencies from 0.2 to 0.5. From $f = 0.5$ to 0.8, $\hat{\sigma}_d$ continued to increase while skewness and kurtosis declined. When $\sigma_E = 6.5$, the changes in those statistics were more erratic and seemed to follow no pattern.

Correlations of the estimates of heritability and average degree of dominance between the complete and partial diallels indicated that the CPD5 design had higher correlations in general with the complete diallel than did the FPD4 design which in turn had generally higher correlations than the CPD3 design (Table 11). A high correlation indicates high effectiveness of the partial diallel. When σ_E is large, the complete diallel is still considered to give no worse estimate of heritability or of average degree of dominance than the partial diallel, even though a few cases may be noted where the standard deviation of \hat{d} is larger. The estimate is generally more accurate in the complete diallel due to larger number of crosses per line. A high correlation with the complete diallel should thus be regarded as an indication of a "good" estimate.

Although most of the correlations were significant, about 70% of the average degree of dominance correlations would be considered too low to be of practical importance (i.e., around 0.6 or lower). Also, these correlations are undoubtedly inflated due to environmental correlations because samples for the partial diallel crosses were derived as subsamples from the complete diallel.

It is of interest to know what changes in the correlations occur when environmental variation changes and gene frequency is fixed or when the environment is fixed and gene frequency changes. In the first situation, changes in the correlations for heritability in general declined from σ_E of 1.5 to 6.5. The correlations for degree of dominance declined in every instance when σ_E was increased from 1.5 to 6.5, and the decline appeared more drastic than it did for heritability. In the second situation, when environmental variation was held constant and gene frequency declined from 0.8 to 0.5, five of the six heritability correlations increased as did four of six for degree of dominance. When σ_E was held constant and gene frequency changed from 0.5 to 0.2, no trends were evident in the heritability correlations, but 14 out of 18 dominance correlations increased.

The correlations for heritability were largest for $\delta = 0$ and $\sigma_E = 1.5$ at both gene frequencies. This would be expected to also be true for $f = 0.8$ had those calculations been made, but this would not be true for average degree of dominance.

A smaller correlation for average degree of dominance, in comparison to heritability, does not necessarily mean that the partial diallel, especially with relatively large s , would be less effective than the complete diallel in estimating dominance. The reason for the

low correlations may be that the overall distributions for the complete and partial diallels do not conform very well, especially for small sample sizes. Nevertheless, the complete diallel can be considered to give the "best" estimate of average degree of dominance when environmental variation is low or heritability is high because the standard deviation is then the smallest.

The relative sizes of the correlations calculated herein suggest that the estimation of average degree of dominance by partial diallel crosses (especially for small values of s , in a highly variable environment or when a character has low heritability) is not very reliable. This in agreement with the conclusions derived from the fiber data previously analyzed, but this should not seriously hinder use of partial diallel cross methods since accurate estimates of average degree of dominance in partial diallels are not as important as those for heritability or GCA. The FPD4 may be as efficient as (but not more efficient than) the CPD in estimating average degree of dominance, but it could be more efficient in estimating heritability under certain conditions, namely, for traits controlled mainly by additive effects. Since, in the present study, the value of s was not the same in both partial diallel methods, clearcut conclusions regarding the efficiency of the two methods cannot be made. Earlier results implied that the number of crosses per line were more critical than was the particular partial diallel chosen for use.

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Fig. 3. Mean squares for GCA, SCA, and error for uniformity index for three partial diallels vs. the complete diallel (Bars indicate mean values).

Fig. 4. Estimates of narrow-sense heritability for three fiber characters in three partial diallels vs. the complete diallel (Bars indicate mean values).

- Fig. 5. Estimates of broad-sense heritability for three fiber characters in three partial diallels vs. the complete diallel (Bars indicate mean values).
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Table 1. Crosses utilized in the CPD3, CPD5, and FPD4 designs.

Parents	Parents						
	2	3	4	5	6	7	8
1†	y	<u>x</u> y	x y	x y	x	<u>x</u>	
2		y	<u>x</u> y	x	x y	x	<u>x</u>
3			y	<u>x</u>	x	x y	x
4					<u>x</u>	x	x y
5					y	<u>x</u> y	x y
6						y	<u>x</u> y
7							y

† = Parental code is given in the Materials and Methods.

x = crosses in CPD3 (circulant partial diallel, sample size 3) design.

x = crosses in CPD5 (circulant partial diallel, sample size 5) design (plus those in CPD3 design).

y = crosses in FPD4 (factorial partial diallel, sample size 4) design.

Table 2. Analyses of variance for combining ability in complete diallel crosses of three fiber characters (Model I).

Sources	df	Mean squares		
		2.5% SL ($\times 10^{-4}$)	50% SL ($\times 10^4$)	Unif. index
Entry	27	59.71**	9.94**	5.30**
GCA	7	44.83**	5.73**	3.42**
SCA	10	4.46**	1.35	0.59
Error	81	0.94	0.79	0.38

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

Table 3. Number of instances in 12 partial diallel samples vs. the complete diallel which exhibited significant F-tests for GCA and SCA (Models I and II) at two levels of probability (α) for three fiber characters.

Model	Fiber character	α	GCA				SCA			
			CPD3 ⁺	CPD5	FPD4	CD7	CPD3	CPD5	FPD4	CD7
I	2.5% span	0.05	--	--	--	--	2	--	2	--
		0.01	12	12	12	1	9	12	9	1
	50% span	0.05	4	--	1	--	3	4	2	--
		0.01	6	12	10	1	--	--	2	--
	Uniformity	0.05	--	--	--	--	2	1	2	--
		0.01	11	12	12	1	--	--	--	--
II	2.5% span	0.05	2	1	6	--	2	--	2	--
		0.01	1	11	6	1	9	12	9	1
	50% span	0.05	3	3	1	--	3	4	2	--
		0.01	3	8	5	1	--	--	2	--
	Uniformity	0.05	--	1	--	--	2	1	2	--
		0.01	8	11	10	1	--	--	--	--

⁺CPD3 and CPD5 = the circulant partial diallel, sample sizes 3 and 5, respectively. FPD4 = the factorial partial diallel, sample size 4
CD7 = the complete diallel.

Table 4. Average standard errors of the difference between GCA effects in 12 partial diallel samples and the complete diallel for three fiber characters.

Sample no.	2.5% span length ($\times 10^{-2}$)				50% span length ($\times 10^{-2}$)				Unif. index			
	CPD3	CPD5	FPD4	CD7	CPD3	CPD5	FPD4	CD7	CPD3	CPD5	FPD4	CD7
1	2.53	1.52	0.69	0.56	1.46	0.88	0.66	0.51	0.47	0.53	0.53	0.33
2	2.87	1.52	0.77		1.66	0.86	0.67		0.91	0.60	0.47	
3	2.16	1.52	0.75		1.20	0.74	0.72		0.56	0.51	0.51	
4	3.53	2.06	0.88		1.33	0.89	0.84		1.10	0.54	0.56	
5	3.22	1.44	0.85		1.77	0.84	0.76		0.52	0.45	0.53	
6	2.85	1.50	0.92		1.31	0.68	0.81		0.67	0.60	0.53	
7	2.16	1.52	0.89		1.42	0.85	0.81		0.59	0.43	0.55	
8	3.07	1.62	0.76		1.49	0.78	0.74		0.85	0.44	0.53	
9	2.70	1.70	0.78		1.70	0.95	0.62		0.54	0.58	0.45	
10	1.93	1.71	0.79		1.05	0.84	0.72		1.21	0.60	0.50	
11	3.29	1.37	0.77		1.97	0.86	0.67		1.40	0.61	0.47	
12	2.66	1.54	0.75		1.82	0.91	0.77		0.89	0.62	0.53	
Range	1.60	0.69	0.23	--	0.92	0.27	0.22	--	0.93	0.19	0.11	--

Table 5. Mean estimates of genetic and environmental components for the three fiber characters based on a fixed model using the Jinks-Hayman method.

Parameter	2.5% span length ($\times 10^{-3}$)	50% span length ($\times 10^{-3}$)	Uniformity index
D	2.845**	0.634**	4.089**
H ₁	2.970**	1.469*	6.767*
H ₂	2.548**	1.113**	4.751*
F	0.346	0.470*	2.996
E ₀	0.102**	0.027**	0.109**
E ₁	0.124**	0.037**	0.176**

*, ** Significantly different from zero at the 0.05 and 0.01 levels of probability, respectively.

Table 6. Mean estimates of heritability and degree of dominance for the three fiber characters based on a fixed model using the Jinks-Hayman method.

Fiber character	Heritability	95% conf. limit	Degree of dominance	95% conf. limit
2.5% span length	0.48	0.34-0.62	1.03	0.78-1.28
50% span length	0.38	0.18-0.49	1.50	1.07-1.94
Uniformity index	0.49	0.42-0.56	1.24	0.82-1.66

Table 7. Mean estimates of heritability (\hat{H}_n), standard deviation ($\hat{\sigma}_h$), skewness (sk), and kurtosis (ku) at selected gene frequencies (f) and dominance levels (δ) in simulation for $\sigma_E = 1.5$.

F	δ	H_n	Statistics	CPD3	CPD5	FPD4	CD7
0.2	0	0.85	\hat{H}_n	0.80**	0.82**	0.81**	0.82**
			$\hat{\sigma}_h$	0.12	0.09	0.10	0.09
			sk	-1.91	-1.29	-1.35	-1.42
			ku	5.23	1.93	1.80	2.49
	1	0.87	\hat{H}_n	0.81**	0.83**	0.82**	0.83**
			$\hat{\sigma}_h$	0.13	0.09	0.11	0.09
			sk	-1.80	-0.97	-1.39	-1.08
			ku	4.37	0.51	2.09	0.85
	2	0.84	\hat{H}_n	0.77*	0.78**	0.79**	0.79**
			$\hat{\sigma}_h$	0.19	0.16	0.17	0.14
			sk	-2.17	-2.26	2.33	-1.94
			ku	5.52	6.57	7.08	4.76
0.5	0	0.90	\hat{H}_n	0.85**	0.86**	0.86**	0.87**
			$\hat{\sigma}_h$	0.10	0.08	0.08	0.07
			sk	-1.92	-1.52	-2.04	-1.73
			ku	5.15	2.38	6.66	4.80
	1	0.81	\hat{H}_n	0.75**	0.76**	0.76**	0.76**
			$\hat{\sigma}_h$	0.17	0.13	0.13	0.12
			sk	-1.69	-1.91	-1.46	-1.94
			ku	3.70	5.79	3.35	6.04
	2	0.62	\hat{H}_n	0.53**	0.53**	0.55**	0.54**
			$\hat{\sigma}_h$	0.28	0.22	0.24	0.20
			sk	-0.52	-0.76	-0.76	-0.79
			ku	-0.86	-0.09	-0.28	0.23
0.8	1	0.66	\hat{H}_n	0.57**	0.59**	0.60**	0.60**
			$\hat{\sigma}_h$	0.20	0.17	0.17	0.15
			sk	-0.99	-0.88	-0.75	-0.69
			ku	0.58	0.70	0.46	0.46

*, ** Significantly different from "true" value at 0.05 and 0.01 levels of probability, respectively.

Table 8. Mean estimates of heritability (\hat{H}_n), standard deviation ($\hat{\sigma}_h$), skewness (sk), and kurtosis (ku) at selected gene frequencies (f) and dominance levels (δ) in simulation for $\sigma_E = 6.5$.

f	δ	H_n	Statistics	CPD3	CPD5	FPD4	CD7
0.2	0	0.23	\hat{H}_n	0.21*	0.22	0.21*	0.22
			$\hat{\sigma}_h$	0.15	0.13	0.14	0.12
			sk	0.16	0.31	0.44	0.26
			ku	-1.06	-0.72	-0.14	-0.55
	1	0.33	\hat{H}_n	0.30**	0.29**	0.29**	0.29**
			$\hat{\sigma}_h$	0.17	0.15	0.17	0.14
			sk	-0.12	0.06	0.16	0.10
			ku	-0.72	-0.61	-0.74	-0.50
	2	0.41	\hat{H}_n	0.40	0.41	0.39	0.41
			$\hat{\sigma}_h$	0.20	0.16	0.17	0.15
			sk	-0.32	-0.33	-0.16	-0.24
			ku	-0.76	-0.36	-0.58	-0.34
0.5	0	0.32	\hat{H}_n	0.28**	0.28**	0.27**	0.28**
			$\hat{\sigma}_h$	0.17	0.14	0.16	0.13
			sk	0.06	-0.09	-0.11	-0.11
			ku	-0.80	-0.38	-0.70	-0.24
	1	0.31	\hat{H}_n	0.28*	0.28**	0.29	0.29*
			$\hat{\sigma}_h$	0.18	0.16	0.16	0.15
			sk	0.31	0.06	0.17	0.09
			ku	-0.43	-0.61	-0.75	-0.71
	2	0.28	\hat{H}_n	0.27	0.27	0.24**	0.26
			$\hat{\sigma}_h$	0.19	0.16	0.17	0.15
			sk	0.16	0.08	0.30	0.12
			ku	-1.02	-0.88	-0.59	-0.64
0.8	1	0.13	\hat{H}_n	0.14	0.12	0.14	0.11*
			$\hat{\sigma}_h$	0.15	0.10	0.11	0.09
			sk	0.78	0.75	0.78	0.79
			ku	-0.48	-0.19	0.43	0.14

*, ** Significantly different from "true" value at 0.05 and 0.01 levels of probability, respectively.

Table 9. Mean estimates of average degree of dominance (\hat{d}), standard deviation ($\hat{\sigma}_d$), skewness (sk), and kurtosis (ku) at selected gene frequencies (f) and dominance levels (δ) in simulation for $\sigma_E = 1.5$.

f	δ	d	Statistics	CPD3	CPD5	FPD4	CD7
0.2	0	0.00	\hat{d}	0.11**	0.07**	0.09**	0.07**
			$\hat{\sigma}_d$	0.23	0.11	0.13	0.10
			sk	4.82	1.99	1.93	1.77
			ku	32.21	4.46	5.47	3.50
	1	0.31	\hat{d}	0.30	0.31	0.33	0.33
			$\hat{\sigma}_d$	0.30	0.17	0.21	0.14
			sk	2.70	0.49	1.08	0.64
			ku	13.80	0.37	2.39	0.48
	2	0.50	\hat{d}	0.53	0.57**	0.58	0.58**
			$\hat{\sigma}_d$	0.37	0.34	0.70	0.33
			sk	1.78	2.36	10.04	2.85
			ku	5.50	8.24	123.32	12.10
0.5	0	0.00	\hat{d}	0.08**	0.06**	0.08**	0.06**
			$\hat{\sigma}_d$	0.12	0.09	0.11	0.09
			sk	1.63	1.52	1.70	1.51
			ku	2.92	2.00	3.54	2.93
	1	0.50	\hat{d}	0.57*	0.59**	0.58**	0.58**
			$\hat{\sigma}_d$	0.49	0.40	0.33	0.30
			sk	3.43	5.53	3.54	4.75
			ku	21.44	44.00	24.45	34.08
	2	1.00	\hat{d}	1.36**	1.31**	1.53**	1.25**
			$\hat{\sigma}_d$	1.55	0.87	2.02	0.74
			sk	4.84	2.86	5.45	3.94
			ku	30.90	10.87	38.67	26.61
0.8	1	0.57	\hat{d}	0.56	0.61	0.62	0.63**
			$\hat{\sigma}_d$	0.52	0.47	0.45	0.31
			sk	2.04	3.83	2.07	2.52
			ku	9.01	28.45	6.65	12.51

*, ** Significantly different from "true" value at 0.05 and 0.01 levels of probability, respectively.

Table 10. Mean estimates of average degree of dominance (\hat{d}), standard deviation ($\hat{\sigma}_d$), skewness (sk), and kurtosis (ku) at selected gene frequencies (f) and dominance levels (δ) in simulation for $\sigma_E = 6.5$.

f	δ	d	Statistics	CPD3	CPD5	FPD4	CD7
0.2	0	0.00	\hat{d}	0.44**	0.37**	0.35**	0.26**
			$\hat{\sigma}_d$	1.29	0.89	0.79	0.45
			sk	6.97	5.01	4.83	2.20
			ku	63.57	32.72	34.95	5.37
	1	0.31	\hat{d}	0.68	0.42**	0.48*	0.38*
			$\hat{\sigma}_d$	2.62	0.73	0.76	0.48
			sk	8.94	4.51	2.82	1.86
			ku	90.49	33.58	11.27	6.66
	2	0.50	\hat{d}	0.49	0.53	0.52	0.46
			$\hat{\sigma}_d$	0.81	0.91	0.75	0.41
			sk	3.28	8.03	2.85	1.12
			ku	14.25	83.94	10.62	1.84
0.5	0	0.00	\hat{d}	0.42**	0.33**	0.42**	0.35**
			$\hat{\sigma}_d$	0.93	0.50	0.80	0.50
			sk	4.85	1.88	4.15	2.24
			ku	34.83	3.78	25.35	7.20
	1	0.50	\hat{d}	0.64	0.55	0.57	0.68*
			$\hat{\sigma}_d$	1.11	0.67	0.83	1.24
			sk	2.83	1.94	3.64	7.67
			ku	10.15	5.44	22.51	73.95
	2	1.00	\hat{d}	0.93	1.13	1.33	1.38*
			$\hat{\sigma}_d$	1.20	1.40	2.56	2.50
			sk	2.87	8.11	7.78	10.00
			ku	11.11	88.98	70.48	117.70
0.8	1	0.57	\hat{d}	0.46	0.94**	0.53	0.88**
			$\hat{\sigma}_d$	0.86	1.69	0.81	1.22
			sk	2.69	4.40	1.76	2.52
			ku	8.41	25.32	2.74	8.52

*, ** Significantly different from "true" value at 0.05 and 0.01 levels of probability, respectively.

Table 11. Correlation coefficients for heritability and average degree of dominance between the partial diallels and complete diallel at selected gene frequencies (f), dominance levels (δ), and environmental variations (σ_E) in simulation.

f	δ	σ_E	Heritability			Dominance		
			r_{73^+}	r_{75}	r_{74}	r_{73}	r_{75}	r_{74}
0.2	0	1.5	0.81**	0.96**	0.93**	0.51**	0.74**	0.61**
		6.5	0.67**	0.89**	0.79**	0.12	0.65**	0.38**
	1	1.5	0.64**	0.91**	0.86**	0.31**	0.81**	0.69**
		6.5	0.65**	0.91**	0.85**	0.13	0.59**	0.50**
	2	1.5	0.78**	0.93**	0.86**	0.58**	0.87**	0.61**
		6.5	0.64**	0.92**	0.84**	0.26**	0.60**	0.57**
0.5	0	1.5	0.86**	0.96**	0.94**	0.42**	0.71**	0.66**
		6.5	0.72**	0.90**	0.84**	0.07	0.58**	0.46**
	1	1.5	0.71**	0.93**	0.77**	0.49**	0.92**	0.55**
		6.5	0.67**	0.91**	0.82**	0.06	0.47**	0.36**
	2	1.5	0.54**	0.88**	0.74**	0.35**	0.74**	0.36**
		6.5	0.62**	0.90**	0.73**	0.13	0.33**	0.04
0.8	1	1.5	0.65**	0.91**	0.83**	0.33**	0.81**	0.64**
		6.5	0.63**	0.85**	0.71**	0.17*	0.27**	0.27**

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

r_{73^+} = linear correlation between CD7 and CPD3, r_{75} = correlation between CD7 and CPD5, and r_{74} = correlation between CD7 and FPD4.

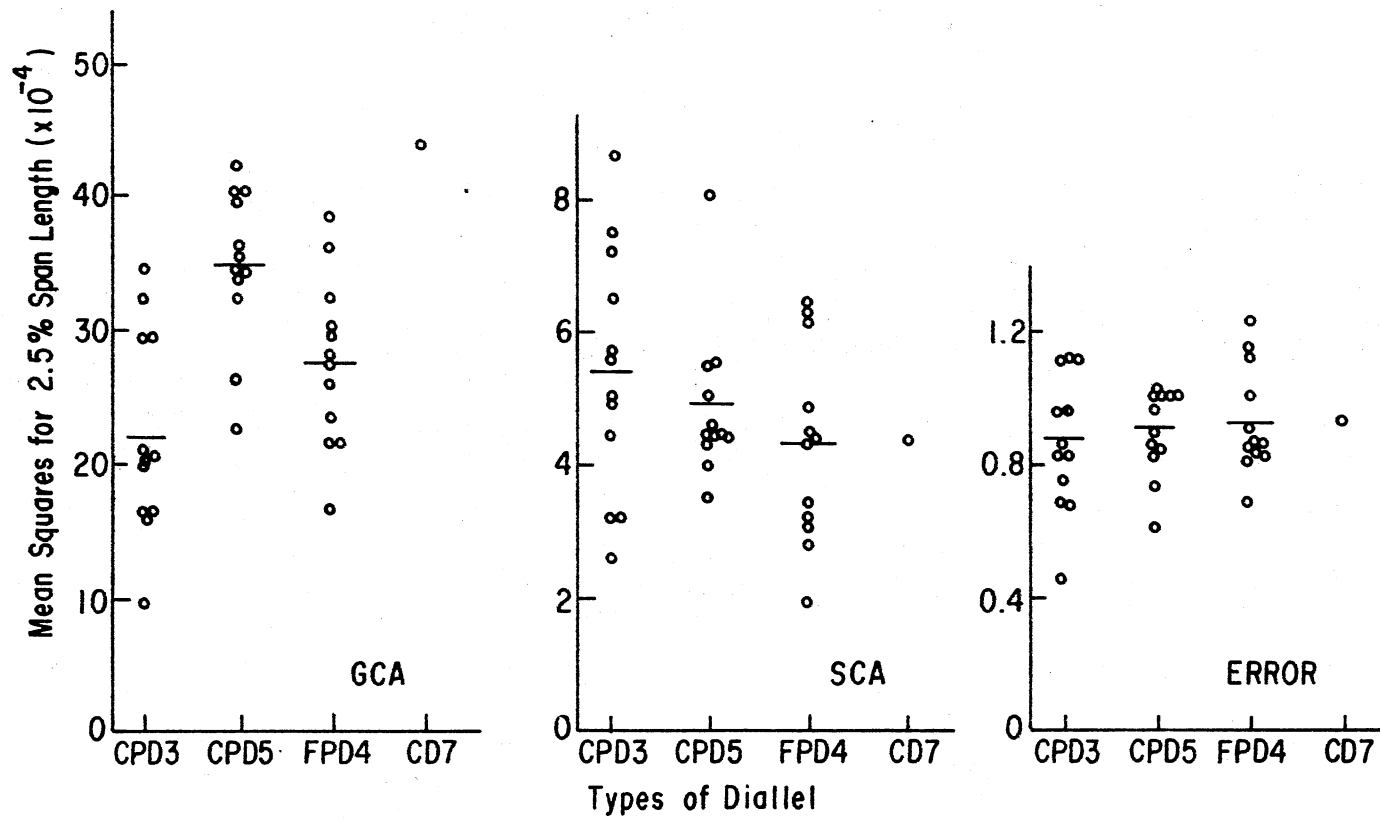


Fig. 1. Mean squares for GCA, SCA, and error for 2.5% span length for three partial diallels vs. the complete diallel (Bars indicate mean values).

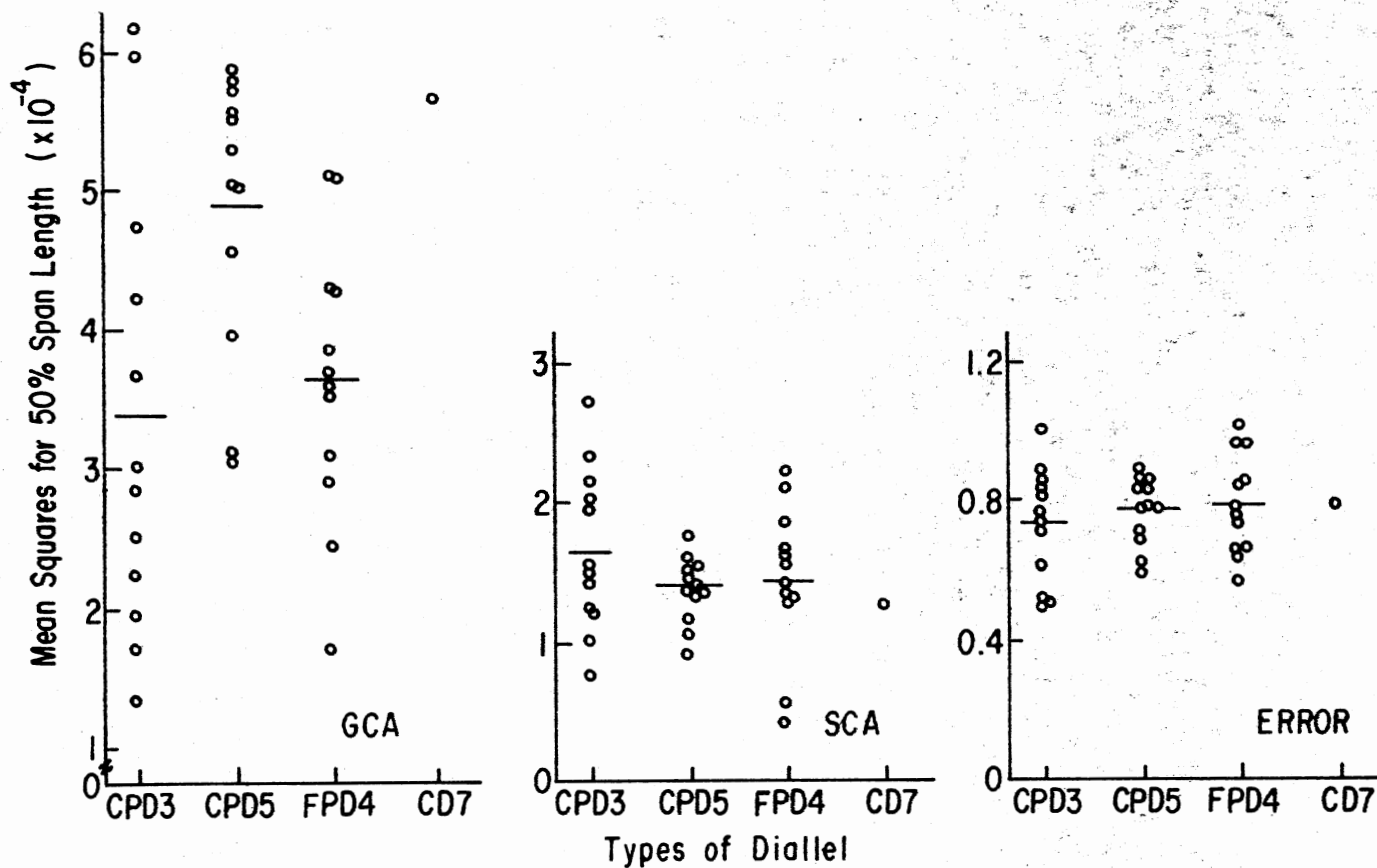


Fig. 2. Mean squares for GCA, SCA, and error for 50% span length for three partial diallels vs. the complete diallel (Bars indicate mean values).

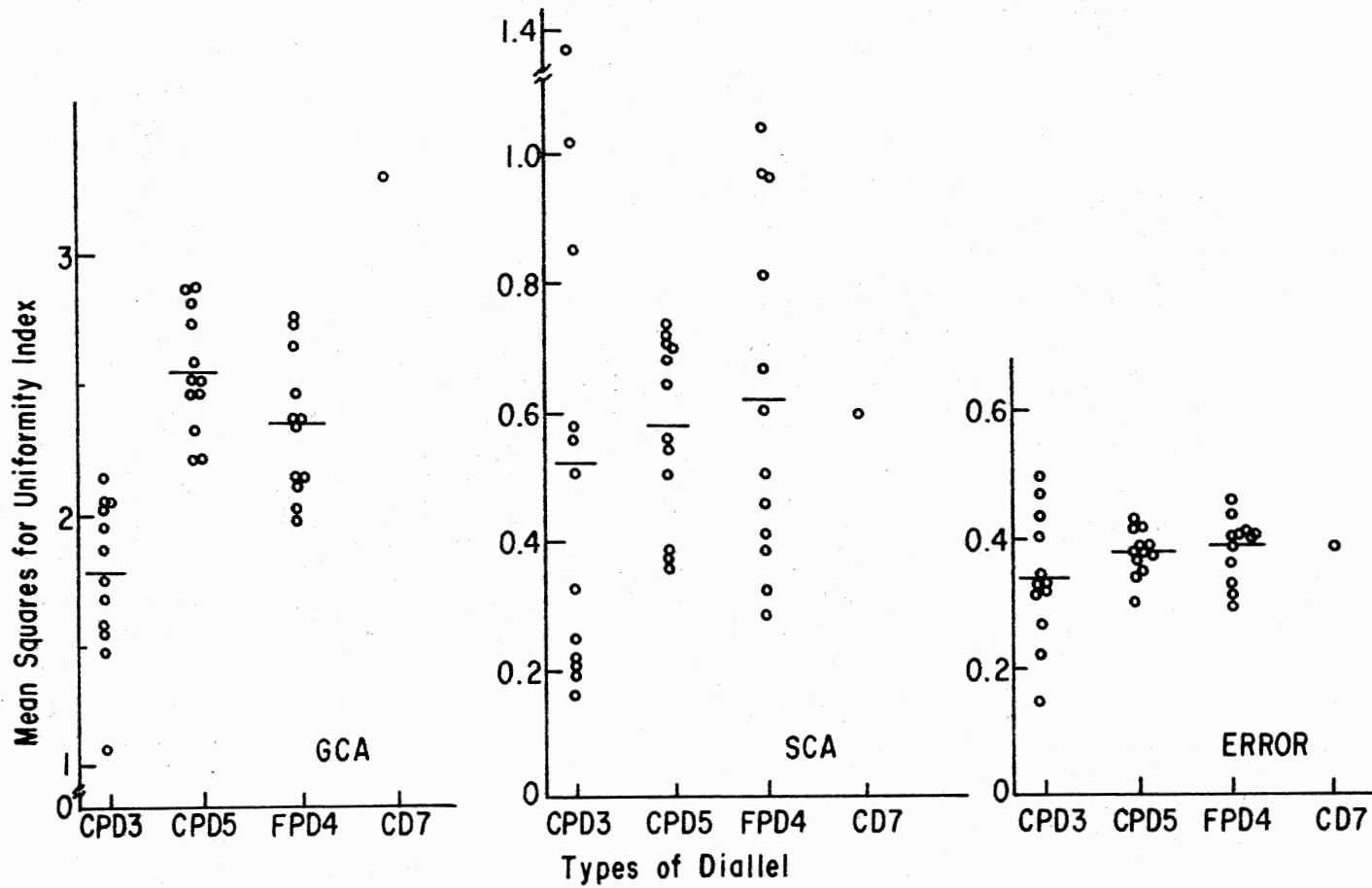


Fig. 3. Mean squares for GCA, SCA, and error for uniformity index for three partial diallels vs. the complete diallel (Bars indicate mean values).

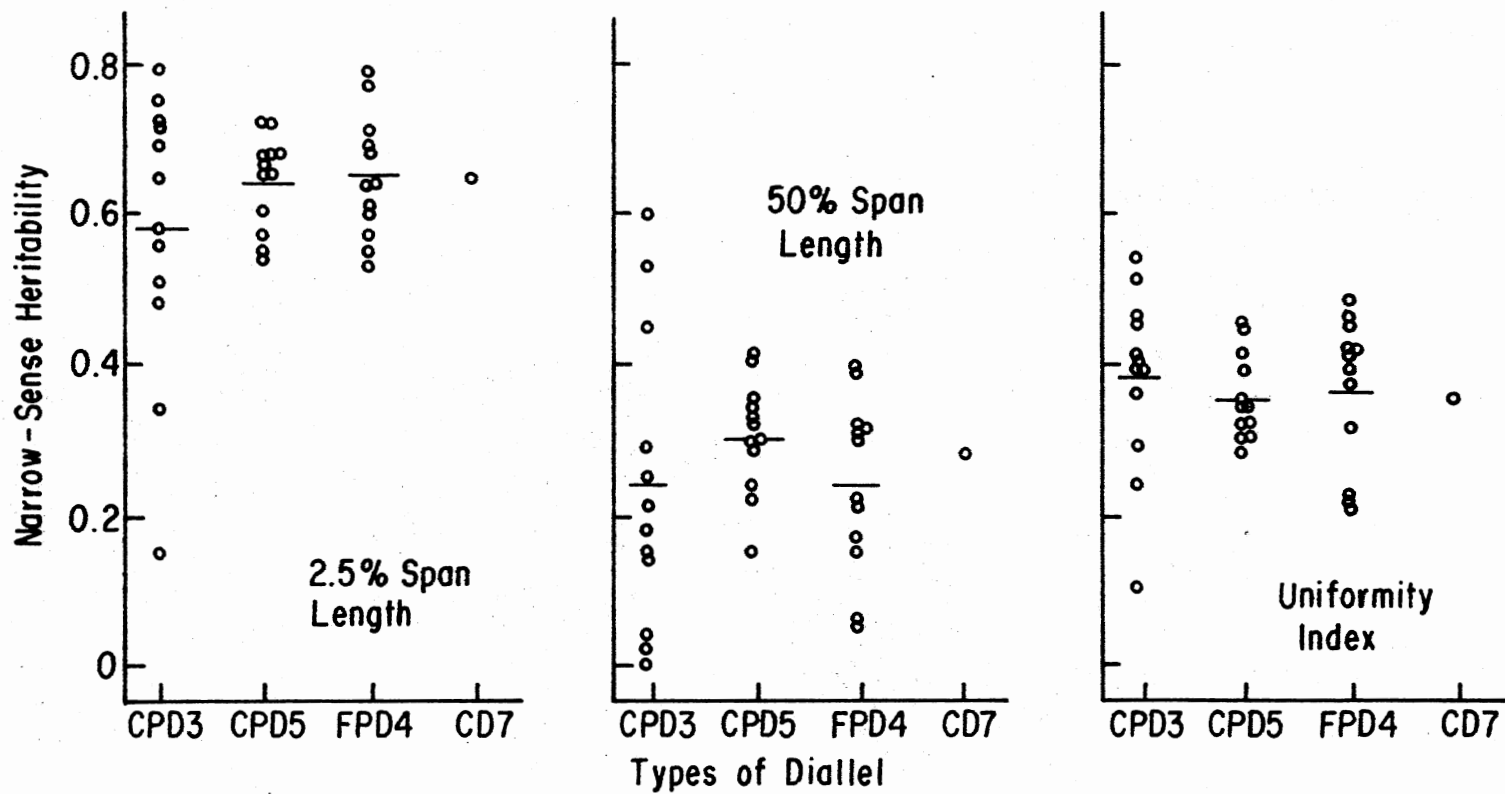


Fig. 4. Estimates of narrow-sense heritability for three fiber characters in three partial diallels vs. the complete diallel (Bars indicate mean values).

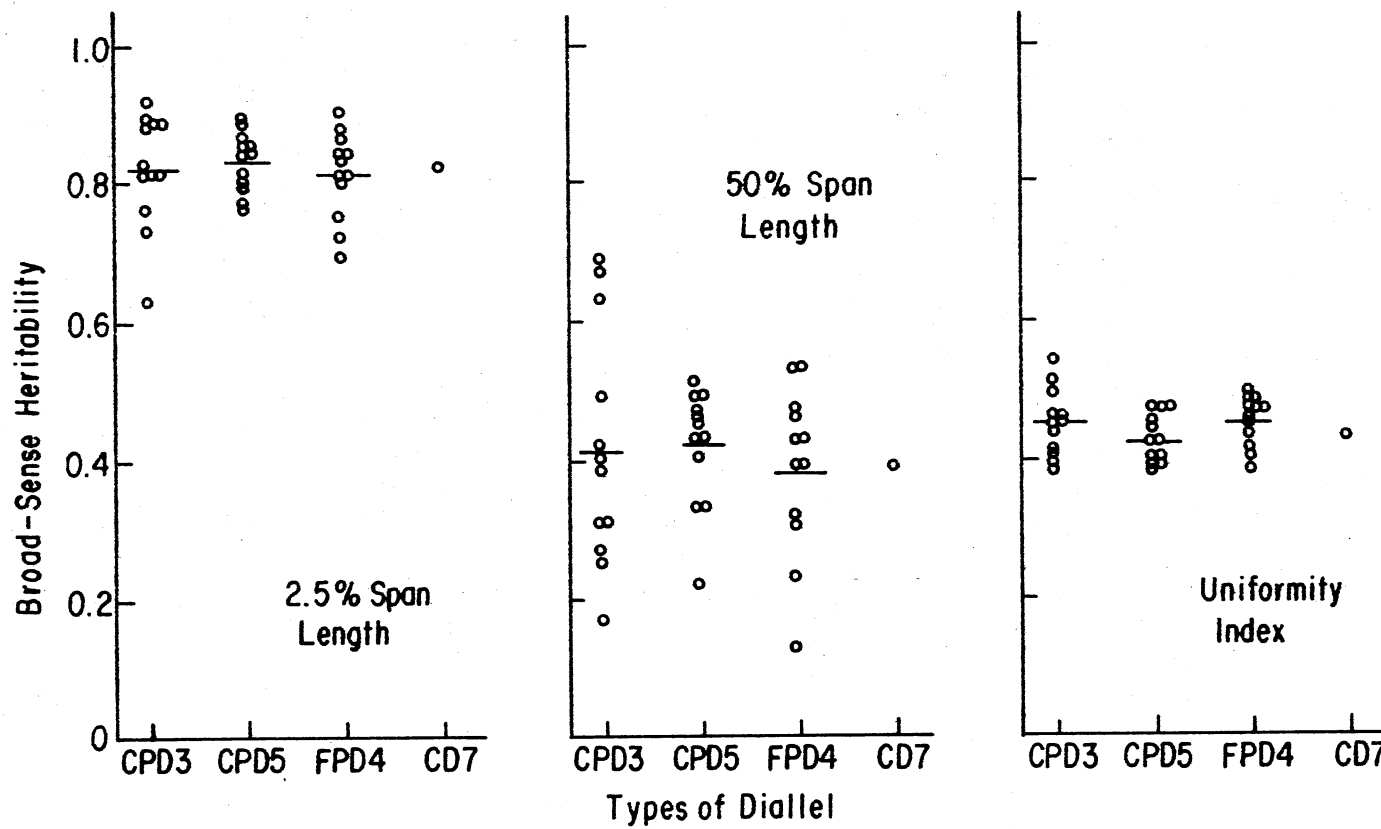


Fig. 5. Estimates of broad-sense heritability for three fiber characters in three partial diallels vs. the complete diallel (Bars indicate mean values).

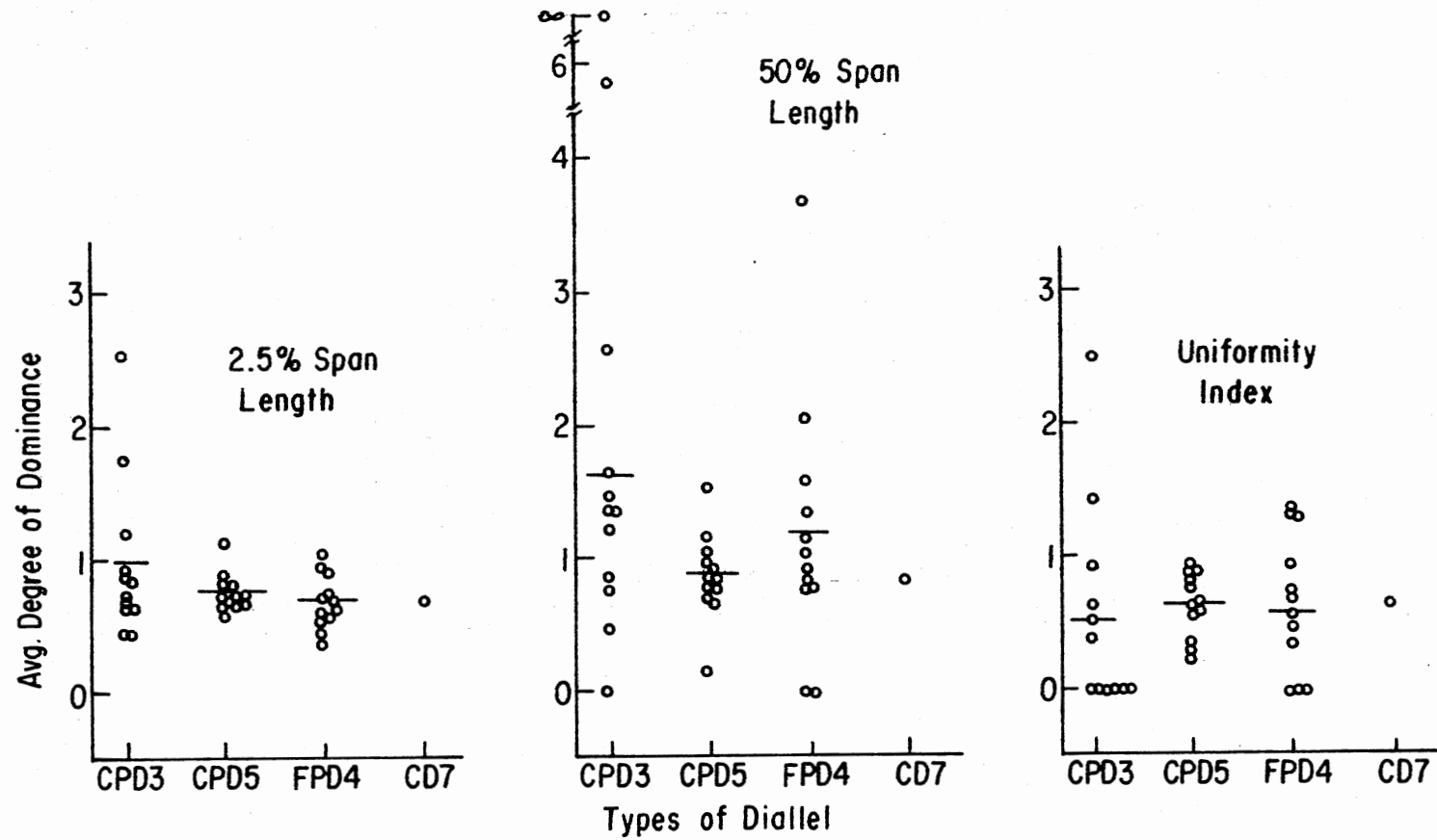
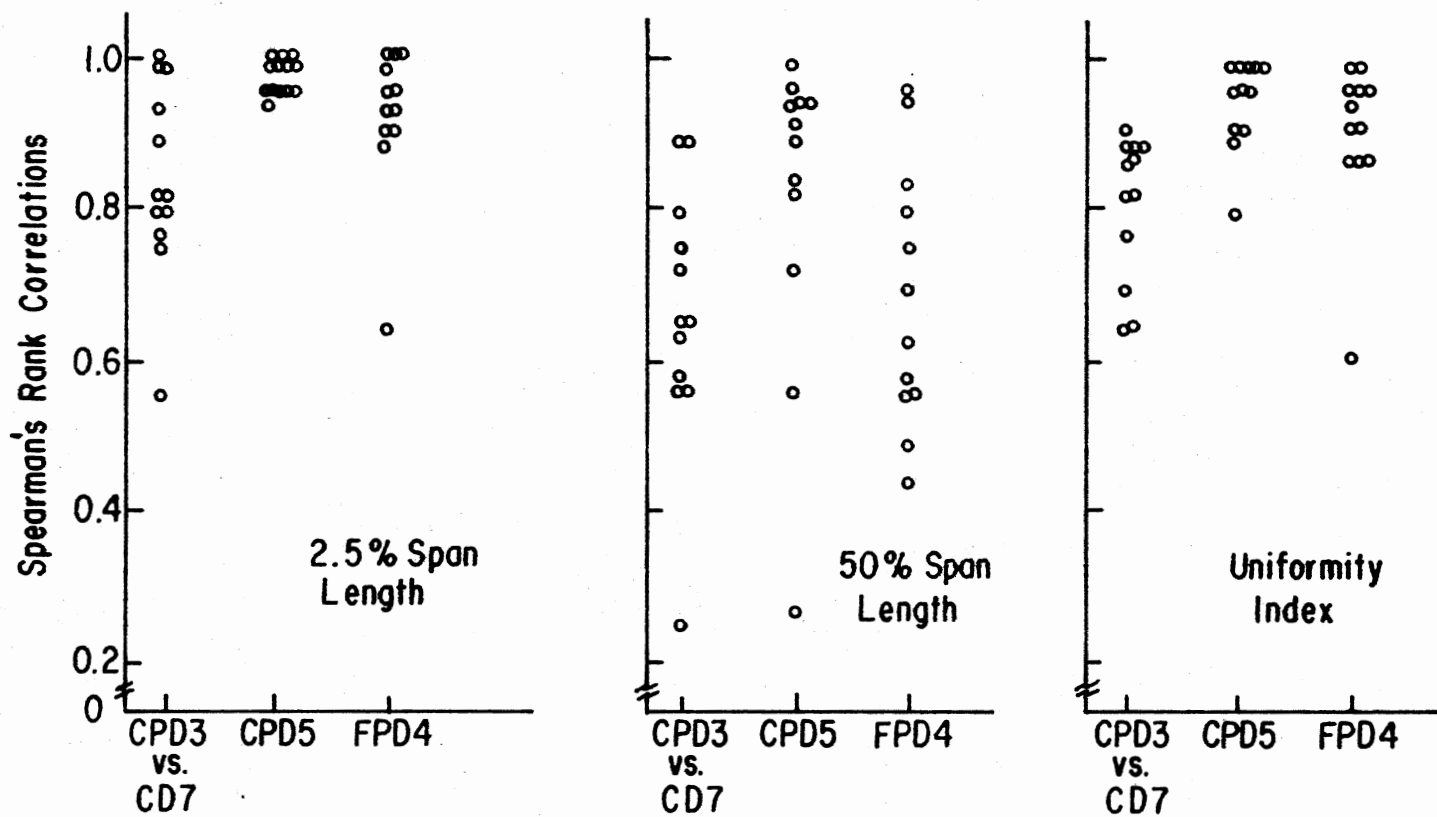


Fig. 6. Estimates of average degree of dominance for three fiber characters in three partial diallels vs. the complete diallel (Bars indicate mean values).



Complete vs. Partial Diallels

Fig. 8. Spearman's rank correlations between three partial diallels vs. the complete diallel.

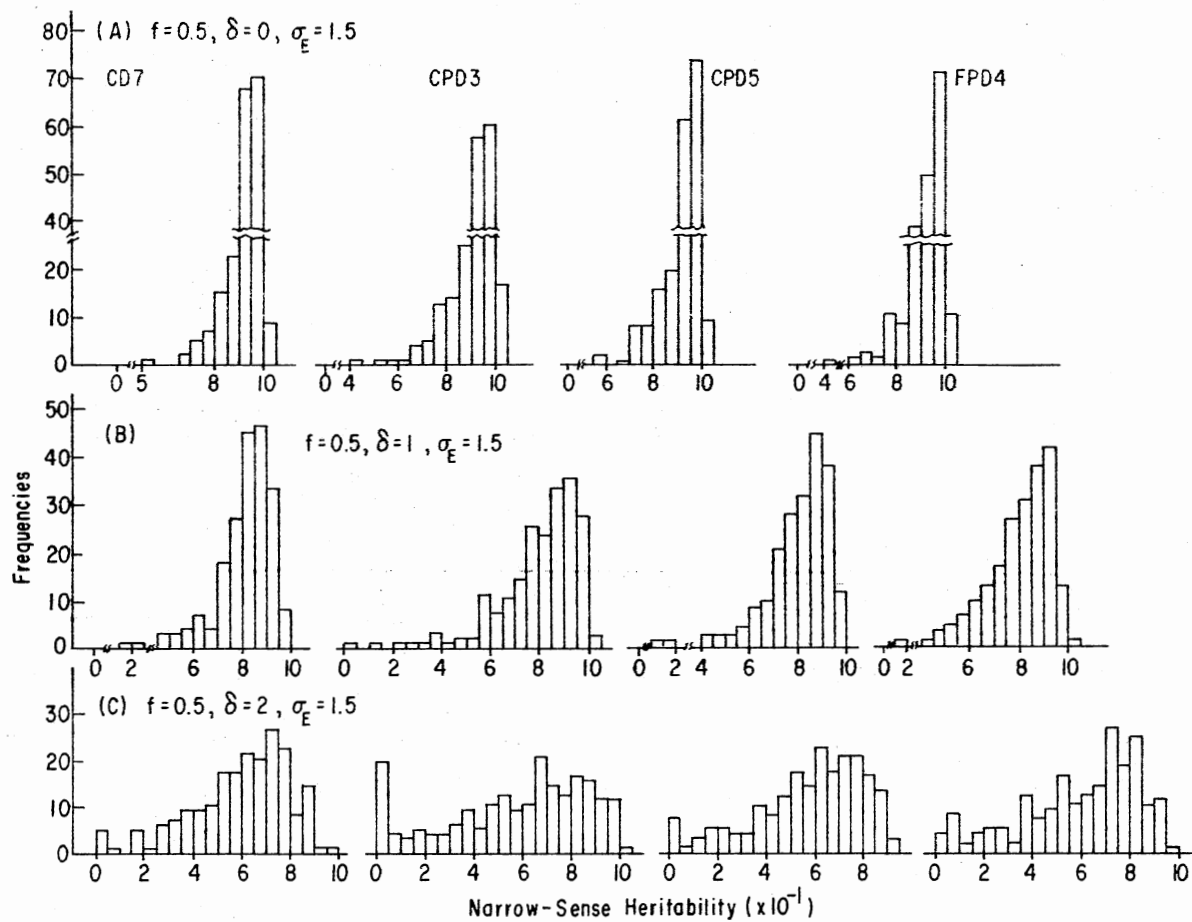


Fig. 9. Frequency distributions of heritability estimates for a simulated character in three partial diallels (200 samples apiece) vs. the complete diallel (f = gene freq., δ = dom. effects, σ_E = environ. SD).

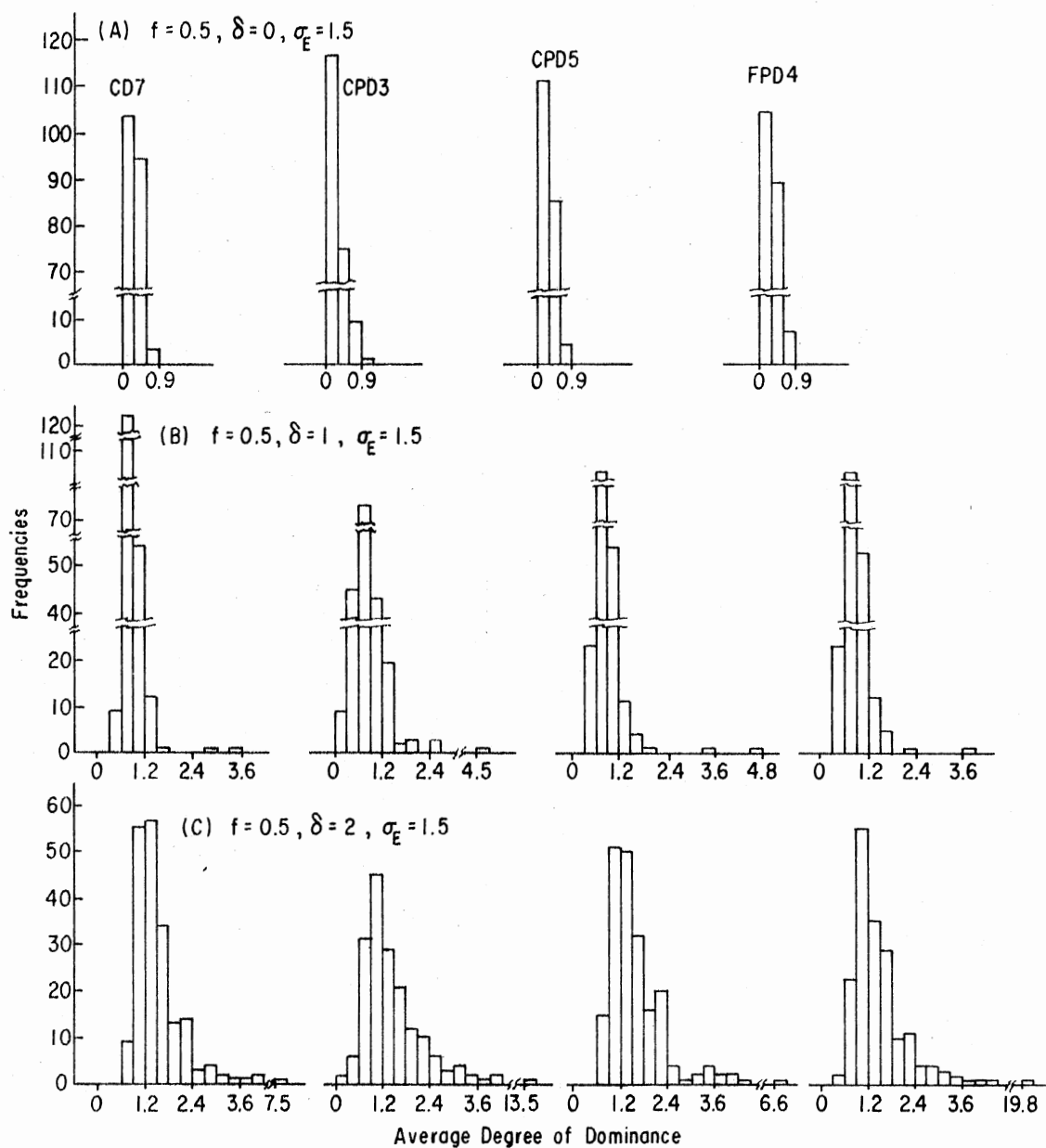


Fig. 10. Frequency distributions of average degree of dominance estimates for a simulated character in three partial diallels (200 samples apiece) vs. the complete diallel (f = gene freq., δ = dom. effects, σ_E = environ. SD).

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