(DOGGET and EBERHART, in press). In crops where no sterility factors are available, hand crossing may be necessary. The amount of crossing required in this systematic breeding system using heterogenous populations need be no greater than that required in many of the successful current breeding programs in which only paired variety crosses are made.

Zusammenfassung

Es wird über ein umfassendes Züchtungssystem berichtet, das von der Kenya Maize Research Section entwickelt und angewendet wurde. Es umfaßt folgende 4 Hauptphasen:

1. Beurteilung lokaler und fremder Sorten, um das beste Zuchtmaterial verfügbar zu haben.

2. Zusammenstellung des ausgewählten Zuchtmaterials in zwei oder mehr Populationen oder Sorten derart, daß jede Population bezüglich der zu verbessernden Merkmale eine erhebliche genetische Variation aufweist und die Kreuzungen dieser Populationen Heterosiseffekte ergeben.

3. Rekurrente Selektion in jeder Population, um die Häufigkeit brauchbarer Gene zu erhöhen und damit die Populationen und Populationskreuzungen mit jedem Selektionszyklus zu verbessern.

4. Entwicklung einer Handelssorte auf einem der folgenden Wege: a) Kreuzung von 2 Populationen als Sortenhybride, b) Hybriden aus Einzel-, Dreiweg- oder Doppelkreuzungen von Inzuchtlinien, die nach jedem Selektionszyklus aus Elitematerial entwickelt wurden, oder c) eine synthetische Sorte aus einer fortgeschrittenen Generation der Populationskreuzung in Gebieten, wo eine Hybriderzeugung noch nicht möglich ist.

Es werden vorläufige Ergebnisse mitgeteilt, die anzeigen, daß eine züchterische Verbesserung des Maises bei Anwendung dieses Systems möglich ist. Darüber hinaus wird die mögliche Anwendung dieses Systems auf andere Fruchtarten kurz besprochen.

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Diallel Cross Designs and their Relation to Fractional Replication*[1]

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Summary. Various diallel crossing plans or designs were studied as fractional replicates of a p^2 factorial for p any positive integer. The method of constructing the complete diallel crossing (CDC) design with $p(p-1)/2$ possible crosses among the p lines, as a fractional replicate was described. Then from this point of view it is immediately obvious that other fractions of the series $x = k/2p$, $k = 2, 3, \ldots, 2p$ are possible for p even and that fractions in the series k/p are possible for p odd and for $k = 1, 2, \ldots, p$. One of the interaction components $(AB^{p-1})_g$ for $g = 0, 1, \ldots, p-1$, of a p^2 factorial was utilized in constructing these fractional replicates because the selfs were those entries in $(AB^{p-1})_0$. A list of partial diallel crossing (PDC) treatment designs for various values of x and p was given. An algorithm for constructing PDC designs of the type described above was also presented.

Diallel crossing plans and related genetic concepts have direct and indirect applications in many subject matter areas other than genetics. A number of specific examples was discussed to illustrate the diversity of uses for CDC and PDC designs. Examples discussed included competition between strains of wheat, job classifications, communication between individual persons, drug applications, paired comparisons studies, teaching methods, cock fighting, and tournaments.

I. Introduction

A frequently used genetic treatment design is the one in which p lines (generally inbred) are crossed in all possible combinations to produce $p(p-1)/2$ crosses. If the individual organism possesses both male and female organs (e.g., most plants) each organism can be crossed with every other one as well

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as itself. If, on the other hand, there are male and female individuals then the crossing involves the males of one line with the females of the other line. These concepts were discussed by SCHMIDT (1919) under the "Method of Diallel Crossing". He also considered "test crossing" to be a form of diallel crossing; in test crossing a number of tester parents are crossed with a number of lines. Dr. George F. SPRAGUE used inbred lines as tester parents in several of his test cross experiments in the 1940's; this, in effect, could be considered as a sample or fraction of the total number of crosses in a complete diallel crossing (CDC) scheme. A subset or fraction of the total crosses in a CDC design has been defined to be a partial diallel cross (PDC) design by HINKELMANN and KEMPTHORNE (1963). Although the PDC probably has been in use for some time, its use was reported by KUDRJAWZEW (1934) over thirty years ago and if one considers a test cross as a PDC then SCHMIDT had described such a design as early as 1919. In any event, it is difficult to assign priority because of differences in definitions and concepts among various workers.

The development of the concepts of general and specific combining ability by SPRAGUE and TATUM (1942) and the emphasis on variance component analyses in quantitative genetics led to considerable research effort on concepts, construction of plans, and analyses of diallel crossing schemes. Various definitions of specific combining ability variance have appeared in the literature; FEDERER and HENDERSON (1962) discuss and formulate definitions leading to the various forms and suggest another definition which would make the specific combining ability variance component, σ^2_δ, and the non-additive genetic variance be in the same relation as the general combining ability variance component, σ^2_α, and the additive genetic variance in the absence of epistasis. The new definition would yield $2\,(\sigma^2_\alpha + \sigma^2_\delta)$ + error variance for the phenotypic variance instead of $2\,\sigma^2_\alpha + \sigma^2_\delta$ + error variance as given by GRIFFING (1956a, b), e.g.

In addition to the plan for the CDC design involving $p\,(p-1)/2$ crosses, GRIFFING (1956b) considers three other plans. The four plans for p lines he discussed are:

Plan 1: All crosses, selfs, and reciprocal crosses yielding p^2 entries.

Plan 2: All crosses and reciprocals yielding $p\,(p-1) = p^2 - p$ entries.

Plan 3: All crosses and selfs yielding $p\,(p+1)/2$ entries.

Plan 4: All crosses yielding $p\,(p-1)/2$ entries.

The work on construction of PDC plans evidently started with the unpublished work of Dr. George H. BROWN (see KEMPTHORNE, 1957, page 458) some time around 1948 in connection with questions raised by Dr. George F. SPRAGUE and his students. Several papers have appeared since 1957 on aspects of construction of PDC designs (e.g., CURNOW, 1963, FYFE and GILBERT, 1963, GILBERT, 1958, HINKELMANN and KEMPTHORNE, 1963, HINKELMANN and STERN, 1960, KEMPTHORNE and CURNOW, 1961, WALKER, 1957, and various unpublished results). JENSEN (1959) and Dr. George F. SPRAGUE (unpublished results) used PDC designs of the type suggested by Dr. George H. BROWN.

The purpose of this paper is to discuss the four plans listed above as fractional replicates, to present a method of constructing some PDC and other designs, and to discuss the usefulness of CDC and PDC designs in fields of inquiry other than genetics.

II. Diallel Crossing Plans as Fractional Replicates

Suppose that we set $p = 5$ and list the combination ij which is line i crossed with line j for $i, j = 1, 2, \ldots, p$, for each of the four plans listed above as follows:

Plan 1. *Crosses, reciprocals, and selfs* $= p^2$ *entries*

line	1	2	3	4	5
1	11	12	13	14	15
2	21	22	23	24	25
3	31	32	33	34	35
4	41	42	43	44	45
5	51	52	53	54	55

Plan 2. *Crosses and reciprocals* $= p^2 - p$ entries

line	1	2	3	4	5
1	—	12	13	14	15
2	21	—	23	24	25
3	31	32	—	34	35
4	41	42	43	—	45
5	51	52	53	54	—

Plan 3. *Crosses and selfs* $= p(p+1)/2$ *entries*

line	1	2	3	4	5
1	11	12	13	14	15
2	—	22	23	24	25
3	—	—	33	34	35
4	—	—	—	44	45
5	—	—	—	—	55

Plan 4. *Crosses* $= p\,(p-1)/2$ *entries*

line	1	2	3	4	5
1	—	12	13	14	15
2	—	—	23	24	25
3	—	—	—	34	35
4	—	—	—	—	45
5	—	—	—	—	—

We now set up the following relations between sets of entries and levels of an interaction effect in a p^2 factorial, *viz.* $(AB^{p-1})_{(i-1)+(p-1)(j-1)}$, modulo p (FEDERER, 1955, Chapter VII, or KEMPTHORNE, 1952, Chapter 17):

Interaction effect		Set of entries for $p = 5$
General p	$p = 5$	
$(AB^{p-1})_{(i-1)+(p-1)(j-1)=0}$	$(AB^4)_0$	11, 22, 33, 44, 55
$(AB^{p-1})_{(i-1)+(p-1)(j-1)=1}$	$(AB^4)_1$	21, 32, 43, 54, 15
$(AB^{p-1})_{(i-1)+(p-1)(j-1)=2}$	$(AB^4)_2$	31, 42, 53, 14, 25
$(AB^{p-1})_{(i-1)+(p-1)(j-1)=3}$	$(AB^4)_3$	41, 52, 13, 24, 35
⋮		
$(AB^{p-1})_{(i-1)+(p-1)(j-1)=p-1}$	$(AB^4)_4$	51, 12, 23, 34, 45

The various sets represent the entries in the various diagonals from left to right of plan 1. This procedure is general for p any positive integer.

In plan 2 the set $(AB^{p-1})_{(i-1)+(p-1)(j-1)=0} = (AB^4)_0$ is omitted. In plans 3 and 4 we note that cross ij = cross ji if there is no reciprocal effect. This allows us to rewrite the form of the plan and to use the above terminology for sets. Thus by rewriting plan 3 and by omitting the sets of entries in $(AB^4)_1$ and in $(AB^4)_2$ we obtain the following:

line	1	2	3	4	5
1	11	12	13	—	—
2	—	22	23	24	—
3	—	—	33	34	35
4	41	—	—	44	45
5	51	25	—	—	55

In plan 4 we omit the sets $(AB^4)_0$, $(AB^4)_1$, and $(AB^4)_2$ after rearranging the treatments as for plan 3 above and noting that cross ij = cross ji. In general for plan 4 we would omit sets $(AB^{p-1})_0$, $(AB^{p-1})_1$, ... $(AB^{p-1})_{(p-1)/2}$ for p odd. When p is even, the duplicates in the set $(AB^{p-1})_{p/2}$ are also omitted. For example, for $p = 6$ the treatments in $(AB^5)_3$ are 41, 52, 63, 14, 25, and 36; the pairs of duplicates are 41 and 14, 52 and 25, and 63 and 36, since $ij = ji$. The treatments retained in this set would be 14, 25, and 36. These entries plus those from sets $(AB^5)_4$ and $(AB^5)_5$ would make up the entries in plan 4. The entries in plan 4 plus those from $(AB^{p-1})_0$ would constitute the entries in plan 3.

Any of the above plans may be constructed by deleting sets of treatments from the complete factorial. It is obvious that other sets may be deleted or added to those in plan 4, say, to obtain additional diallel crossing plans. All such plans including those above would be fractional replicates of the p^2 factorial. Fractions, x, in the series $2/2\,p$, $3/2\,p$, ..., $(p-3)/2\,p$ would all result in fewer entries than $p\,(p-1)/2$ which is a $(p-1)/2\,p$ fraction of p^2. Fractions in the series $p/2\,p$, $(p+1)/2\,p$, $(p+2)/2\,p$, ..., $2\,p/2\,p = 1$ would result in more entries than given by plan 4. For small p the fraction x, say, might be greater than 1/2 and for large p the fraction x might be less than 1/2. For example, if $p = 50$ then $p\,(p-1)/2 = 50\,(49)/2 = 1225$ entries involves a large number of crosses. However, for $x = 4/2\,p$, $xp^2 = 100$ entries; for $x = 6/2\,p$, $xp^2 = 150$; etc. Table 4 was constructed to illustrate the various treatment designs for various values of p and x; treatment numbers for which xp^2 is an integer and for $0 < x \leq 1$ were included in the table.

The fractions for $x < 1/2$ may be constructed in a straightforward manner as was described above or from the design for plan 4 given above. We shall illustrate the procedure for $p = 6$ and 7. The $p\,(p-1)/2$ entries are:

$p = 6$

12	13	14	15	16
—	23	24	25	26
—	—	34	35	36
—	—	—	45	46
—	—	—	—	56

$p = 7$

12	13	14	15	16	17
—	23	24	25	26	27
—	—	34	35	36	37
—	—	—	45	46	47
—	—	—	—	56	57
—	—	—	—	—	67

For $p = 6$ and for nine crosses, use 12, 23, 34, 45, 56, 16, 14, 25, 36, and for 12 crosses use 12, 23, 34, 45, 56, 16, 13, 24, 35, 46, 15, 26. When $p = 7$ and $x = 2/p$ the 14 crosses used are the set 12, 23, 34, 45, 56, 67, 17, 14, 25, 36, 47, 15, 26, 37 or the set 12, 23, 34, 45, 56, 67, 17, 13, 24, 35, 46, 57, 16, 27. In the 9 treatment design for $p = 6$ each number 1 to 6 appears 3 times and in the 12 treatment design each number appears 4 times. For the 14 treatment design when $p = 7$, each number 1 to 7 appears 4 times. This type of balance leads to ease of analysis and equality of variances on estimated effects.

The construction algorithm for obtaining $xp^2 \leq p\,(p-1)/2$ entries may be stated as follows. For p odd and for p even but for $x =$ (even number)$/2\,p$ use the following crosses to obtain $x^2p^2 = sp$ entries: $ij = i, i+1;\ i, i+2;\ i, i+3; \ldots,\ i, i+s$ (for $i = 1, 2, \ldots, p$, for $i + s \leq p$ use $i + s$, and for $i + s > p$ use $i + s - p$) where $s \leq (p-1)/2$ for p odd and $s \leq p/2$ for p even but omitting duplicates when $s = p/2$. If xp^2 (minus duplicates) crosses are desired for p even, and for $x =$ (odd number)$/2\,p$, then use the sequence $ij = i, i+1; i, i+p/2; i, i+2; \ldots, \ldots, i, i+s$ omitting duplicates to obtain the xp^2 entries.

Table 1. *Number of entries for various fractional replicates. Number of entries* $= xp^2$ *for* $0 < x \leq 1$

p	Fraction x[1] 3/2 p	4/2 p	5/2 p	6/2 p	7/2 p	8/2 p	9/2 p	10/2 p	11/2 p	12/2 p	$p\,(p-1)/2$
3	—	6	—	9	—	—	—	—	—	—	3
4	6	8	10	12	14	16	—	—	—	—	6
5	—	10	—	15	—	20	—	25	—	—	10
6	9	12	15	18	21	24	27	30	33	36	15
7	—	14	—	21	—	28	—	35	—	42	21
8	12	16	20	24	28	32	36	40	44	48	28
9	—	18	—	27	—	36	—	45	—	54	36
10	15	20	25	30	35	40	45	50	55	60	45
11	—	22	—	33	—	44	—	55	—	66	55
12	18	24	30	36	42	48	54	60	66	72	66
13	—	26	—	39	—	52	—	65	—	78	78
14	21	28	35	42	49	56	63	70	77	84	91
15	—	30	—	45	—	60	—	75	—	90	105
20	30	40	50	60	70	80	90	100	110	120	190
30	45	60	75	90	105	120	135	150	165	180	435
40	60	80	100	120	140	160	180	200	220	240	780
50	75	100	125	150	175	200	225	250	275	300	1225
100	150	200	250	300	350	400	450	500	550	600	4950

[1] — means that an integer number of crosses was not possible or that $x > 1$.

Treatment designs with $x > 1/2$ or $x > 1$ may also be constructed by the above methods simply by adding the above to plan 4. Also, it should be pointed out that the fraction need not be of the type $x = k/2\,p$ for $k = 2, 3, \ldots$ but may be of the type $x = k/p^2$ to yield the desired fraction. Fractions of this type will not generally be balanced and will generally be more difficult to analyze.

III. Diallel Cross Plans from the Point of View of Experimental Design

GILBERT (1958), HINKELMANN and STERN (1960), KEMPTHORNE and CURNOW (1961), CURNOW (1963), FYFE and GILBERT (1963), and HINKELMANN and KEMPTHORNE (1963) have considered the use of partially balanced incomplete block (PBIB) designs in the construction of PDC designs. Such classes of designs as circulant designs, group divisible designs, and m-associate class PBIB designs have been used to construct PDC designs. The paper by HINKELMANN and KEMPTHORNE (1963) is particularly instructive in precisely defining a PDC design and showing the correspondence of these designs with m-associate class PBIB designs.

Estimation of specific and general combining ability effects, of the specific combining ability and general combining ability variance components, and of the efficiency of PDC designs were considered by KEMPTHORNE and CURNOW (1961), CURNOW (1963), and FYFE and GILBERT (1963). Discussion of other topics such as g. c. a. PDC designs, relative number of degrees of freedom associated the s. c. a. and g. c. a. mean squares in the analysis of variance, etc. has also been presented by these authors. Analyses for the designs in the previous section would follow the form given by KEMPTHORNE and CURNOW (1961), e.g.

IV. Use of PDC and CDC Designs in Other Fields

Diallel crossing plans have considerable importance outside the field of genetics and breeding. Therefore, the designs, the analyses, the genetic theory, etc. developed in connection with CDC and PDC designs will be useful to many subject matter research areas other than genetics. A number of examples are listed below to illustrate the diversity of uses encountered by the author.

Drs. Urie BRONFENBRENNER and John HARDING, Cornell University, were studying the communication between p individuals. Plan 2 was used because individuals cannot be measured communicating (talking) to themselves in a group of p individuals. In this psychological research problem many of the concepts used in genetic experiments were usable directly in psychology. Dr. Charles R. HENDERSON, Cornell University, in working with these individuals, found that concepts such as "general communicability", "specific communicability", reciprocal effect, and communication effect were exactly analogous, statistically, to g. c. a., s. c. a., reciprocal effects, and maternal effects, respectively, in genetics.

RUSHFORTH (1961) used job classifications such as salesman, clerk, stenographer, supervisor, executive, etc., and obtained expressions from an individual concerning all types of jobs including his own. He found that individuals thought very highly, in general, of their own positions in relation to others. Thus, these opinions, the selfs, had to be removed from the p^2 entries resulting in a plan 2 diallel cross design. He utilized the results of GRIFFING (1956b) for his analyses.

JENSEN and FEDERER (1965) presented the concepts of general competing ability, specific competing ability, and reciprocal competing effect for strains of wheat (or other plants) bordered by various other lines including the variety itself (the selfs). General and reciprocal competitive effects were large for the strains of wheat studied, but there was no evidence of specific competitive effects.

Other research areas wherein diallel crossing plans have been or could be utilized are:

i) **Cock fighting.** In order to determine "general fighting ability" and "specific fighting ability", p fighting cocks would fight each of the other $p - 1$ cocks to yield $p\,(p - 1)/2$ fights. Reciprocal fights and selfs are impossible, necessitating the use of the CDC or a PDC design with $x < 1/2$.

ii) **Paired comparisons.** All possible paired comparisons among p items results in a BIB design with $p\,(p - 1)/2$ blocks of a pair ($k = 2$). The PDC designs would be useful here when p is large.

iii) **Successive doses of drugs.** Suppose that two doses of the same drug (selfs) or of diiferent drugs (crosses and reciprocals) are to be given a patient. This would result in plan 1. If successive doses of the same drug are not to be used, or give a different result, then plan 2 might be adopted. If there is no reciprocal effect then plans 3 or 4 might be useful. For p large, one of the PDC designs might be appropriate. Also, a PDC design might be appropriate if the researcher eliminates certain combinations (crosses) because of deleterious effects.

iv) **Teaching methods.** Suppose that a teacher, topic, or method is to be followed by another teacher, topic, or method, that there are p such categories, and that achievement by a student is the measure used. This situation would be analogous to the drug situation in iii) above.

v) **Bridge and other tournaments.** If each player must play with every other player then the design would be plan 4. However, if the number of players is large then some PDC design might be useful and such effects as "general playability" and "specific playability" might be useful in determining the winner.

Presumably, one could conjure up other examples wherein CDC and PDC designs and associated genetic theory were useful. As has been amply demonstrated by the references listed herein, the statisticians have found this a fruitful area for research in statistical theory. Undoubtedly they have not finished writing papers on the subject as is evidenced by the present paper. Additional designs and additional statistical analyses will be developed and published.

Zusammenfassung

Es werden verschiedene diallele Kreuzungspläne oder -anlagen mit partiellen Wiederholungen eines p^2 faktoriellen Versuches für eine beliebige ganze, positive Grundzahl p untersucht. Die Methode, die vollständige diallele Kreuzungsanlage (CDC) mit $p\,(p - 1)/2$ möglichen Kreuzungen zwischen p Linien mit partiellen Wiederholungen aufzubauen, wird beschrieben. Aus diesem Blickpunkt wird unmittelbar klar, daß noch andere Fraktionen, und zwar der Reihe $x = k/2\,p$, wobei $k = 2, 3, \ldots, 2\,p$ ist, für ein geradzahliges p und der Reihe k/p für ein ungeradzahliges p,

wobei $k = 1, 2, \ldots, p$ ist, möglich sind. Eine bestimmte Interaktionskomponente eines p^2 faktoriellen Versuchs, $(A\ B^{p-1})_g$, wobei $g = 0, 1, \ldots, p-1$ ist, wurde benutzt, um diese partiellen Wiederholungen aufzubauen, weil die Selbstungen die Elemente von $(A\ B^{p-1})_0$ sind. Eine Liste unvollständig dialleler Kreuzungsversuche (PDC) wird für verschiedene Werte von x und p gegeben. Zugleich wird ein Algorithmus für den Aufbau von PDC-Anlagen des obigen Typs mitgeteilt.

Diallele Kreuzungspläne und verwandte genetische Verfahren finden auch auf vielen Gebieten außerhalb der Genetik direkte und indirekte Anwendung. Es wird eine Anzahl spezifischer Beispiele diskutiert, um die Mannigfaltigkeit der Anwendung von CDC- und PDC-Verfahren darzulegen. Die besprochenen Beispiele umfassen die Konkurrenz zwischen Weizensorten, Berufsklassifizierungen, Mitteilungen zwischen Einzelpersonen, Drogenanwendung, Lehrmethoden, Hahnenkämpfe und Turniere.

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Genetic Variances in the Open-Pollinated Variety of Maize, Iowa Ideal*[1]

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Summary. Iowa Ideal is a white, open-pollinated variety of corn that has been under mass selection (or individual plant selection) for the improvement of grain yield. In order to make a comparison between the observed and predicted response to selection for increased grain yield, a mating design was imposed on the original Iowa Ideal variety. Ninety-six half-sib families containing 384 full-sib families were developed and evaluated in three environments. Estimates of additive and total genetic variances were obtained for grain yield and eight other traits.

For all traits, the estimates indicated that the greatest proportion of the total genetic variance was due to additive effects; this was under the assumption of no epistasis. The estimates for yield indicated that approximate 80% of the total genetic variance was additive. This would indicate that some form of intra-population selection should be effective, initially, for increasing the frequency of favorable factors determining yield. Additive genetic, genotypic, and phenotypic correlations showed that ear length was the most important component of yield in the Iowa Ideal variety.

The initial evaluation of the original and three reconstituted populations, formed by compositing equal quantities of seed from individually selected ears, was made in 1965. The observed progress for increased grain yield was less than the predicted on the basis of the variance component estimates. For a selection intensity of 7.5% in each cycle of selection, observed progress for increased grain yield was 1.5% per cycle or year. Either the estimates of additive genetic variance were over-estimated, or the individual plant selection techniques were not precise enough to properly identify the higher-yielding genotypes in the selection program.

* Dedicated to Dr. GEORGE F. SPRAGUE on the occasion of his 65th birthday.

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Introduction

The determination of genetic variability of a quantitative trait is based upon the division of the phenotypic value into genetic and environmental effects. If the observed phenotype (P) of a quantitatively inherited character is determined additively by genetic (G) and environmental (E) effects (*i.e.*, $P = G + E$), it is important to the plant breeder to know how much of the variation in the phenotypic values can be attributed to genetic and environmental forces. A knowledge of the relative contributions of the various types of genetic effects present for quantitative traits in the populations undergoing selection is also basic to all plant-breeding programs. Estimates of heritability, prediction of response to selection, and the designing of the most effective breeding sche-