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Computer Applications in Plant Breeding
and Genetics

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to Mandy

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SUMMARY

Various aspects of the application of computer science to plant breeding have been investigated.

A crossing system based upon a diallel model was tested, both by computer simulation and by field experimentation. The simulations, using the genetic system of a self-pollinating crop, showed that only a small subset of the diallel was necessary to provide the plant breeder with selection criteria for deciding which crosses should be used in a breeding programme.

When a character has a large additive genetic component of its variance, general combining ability (gca) may be used for predicting values of unavailable progeny. Further, if emphasis is placed on the ranks of the gca's in a diallel, rather than on their actual numerical values, the incomplete partial diallel is a powerful tool for the selection of parental material. In a self-pollinating species, the simulation studies showed that when gca effects are greater than or equal to specific combining ability (sca) effects, only 20% of the partial diallel is necessary to rank the parental gca's very precisely.

A twelve parent diallel of triticale yielded results similar to the simulation studies. The F_1 and the F_4 generations of the triticale diallel were subjected to measurement and both were valuable in obtaining accurate gca rank information.

Correlations between the F_1 and the F_4 generations were also analysed. F_1 harvest index and the number of seed in the tallest tiller both correlated significantly with F_4 yield. This indicates that it may be possible to choose F_1 plants that have a high probability of producing high yielding progeny.

By investigating the means and variances of the F_4 diallel (thirty plots of each F_4 family were measured), it was found that the (homozygous) parental lines were as variable as the (less homozygous) F_4 plots. It is suggested that selection for a low variance F_4 family may be a successful approach to plant improvement.

Environmental effects were found to be significant both within and between sites. Methods of reducing field heterogeneity without the use of major replication within sites were investigated. Covariates were calculated, based both upon the proximal control plots and the nearby experimental plots ("moving mean"). It was found that by inversely weighting by a power of the distance between plots, larger variance reductions could be obtained from the covariate regression analysis.

In general, it was found that many plant breeding decisions could be simplified and made more effective by the use of computer science in both presentation and analysis of data.

Statement of Originality

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university, and to the best of my knowledge and belief, contains no material previously published or written by another person, except when due reference is made in the text.

Geoffrey H. Gordon

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1. LITERATURE REVIEW AND GENERAL INTRODUCTION

1.1 Introduction

Computers have been used extensively by plant breeders as calculators and filing cabinets. Their use as either dynamic organisational devices or as heuristic devices has been less explored. However, large modern digital computers are capable of performing many of the organisational tasks of the plant breeder and, with correct programming, are also able to make some simpler plant breeding decisions.

The use of computers for genetic research can be divided into four main categories (Scheinberg, 1968). They are:

(a) "the design of efficient field and laboratory experiments" - this involves supplying the optimum number of observations, treatment conditions and any other factor which may help investigators fulfill their objectives;

(b) "the statistical analysis of data" i.e. the statistical interpretation of experimental results;

(c) "the numerical solution of mathematically formulated problems that cannot be solved analytically";

(d) "the simulation of real and model biological systems".

A fifth category (e) "the storage and retrieval of information", may also be added.

Scheinberg (loc. cit.) states that the field of designing and optimising genetic experiments is one in which surprisingly little work has been done. This thesis primarily deals with this category, i.e. (a) above. Problems are looked at from a plant breeder's perspective, and design and prediction of outcomes of breeding methods and experimental techniques are investigated.

Three specific areas are dealt with, viz., methods of selecting parents, methods of distinguishing between genotypic and environmental effects in yield trials and methods of evaluating the potential of hybrid families.

Before parents can be confidently incorporated into a breeding programme, they should pass through some form of crossing system for evaluation. Once entered into such a system the hybrids, and their families must be evaluated, and such results related back to the original set of parents. The time and place for such evaluation is, however, subject to much conjecture. Leaving that argument aside for the time being, before evaluation of any type can be made the breeder must be satisfied that an accurate measurement of the hybrid has been made; such measurement must exclude as far as possible local environmental effects. Once this has been done the problems of determining the correct generation in which to make the evaluation, and how to actually make this evaluation, can be reasonably investigated.

1.2 Incomplete Diallels - A Generalised Crossing System

1.2.1 Introduction

Before any selection procedures can be initiated, the plant breeder must be satisfied that the best parents available have been used and that the most promising crosses have been made. The job of finding the optimum genotypic combination from a hybrid family is difficult enough; if the best parents are not used the task may also be fruitless.

1.2.2 Diallels

A diallel is the set of all possible crosses between a given number of parental lines. It can best be represented by a two dimensional $N \times N$ matrix where N is the number of parents (see, ~~for~~ *example*, Figure 1.1). The ij th element in the matrix represents the hybrid between parent i and parent j , the leading diagonal (ii th) elements represent the product of self-fertilization, that is, the parents.

The full diallel (F.D.) may conveniently be divided into three groupings: the parental lines; one set of hybrid lines, where for each ij th element $i < j$; and the reciprocal set of hybrids where $i > j$.

A partial diallel (P.D.) differs from a full diallel by way of exclusion of the reciprocal crosses or the reciprocal crosses and the parental lines.

	T28	T31	T33	T34	T58
T28	A	B	B	B	B
T31	C	A	B	B	B
T33	C	C	A	B	B
T34	C	C	C	A	B
T58	C	C	C	C	A

Figure 1.1: The complete diallel includes crosses A, B and C.

The partial diallel can be either

(a) crosses A and B (or A and C), or

(b) crosses B (or C) only.

The incomplete diallel is represented by any

subset of the partial diallel.

In this thesis, the term "incomplete partial diallel" (I.P.D.) refers to any subset of the partial diallel.

1.2.3 Use of Diallels

Diallels have traditionally been used both to measure the mode of inheritance of quantitative genetic characters within a population and to isolate individual variations between parents in the diallel. That is it may be used to describe the mode of inheritance of a character within a species (e.g. Chaudhary, Katar and Singh, 1977), or it may be used to make comparisons between varieties of the same species (e.g. Dhillon and Singh, 1977). A diallel experiment would normally take the observations of all the possible hybrid, and parental, phenotypes within a relatively uniform environment. This provides the mechanism for optimising the measurement of genetically controlled characters whilst helping to minimise environmental effects.

The genetic component of a quantitative character may be divided into three effects: the additive genetic effect of each of the parents involved in the cross [called general combining ability (gca)]; a specific effect caused by the interaction of the two parental haploid genotypes [called specific combining ability (sca)]; and a reciprocal effect (r) due to the reversal of the male and female parental haploid genotypes.

Thus, the model of a quantitative character (G) becomes:

$$G_{ij} = \text{mean effect} + \text{gca}(\text{parent } i) + \text{gca}(\text{parent } j) + \text{sca}(\text{hybrid}) \\ + r_{ij} \quad (i.i)$$

The model for the phenotype of a quantitative character has the extra term e_{ij} which is used here to represent all environmental effects, as well as any error factors involved in the measurement of the character trait.

Various methods have been described to estimate these effects from observed values of a diallel (Schmidt, 1919; Griffing, 1956a,b; Dickinson & Jinks, 1956; Hayman, 1954a; Yates, 1947; Keuls & Garretsen, 1977; Garretsen & Keuls, 1977). Such analyses are of use to the geneticist and breeder for evaluating the mode of inheritance of a given character within a population.

With P parents used in a diallel, $P(P-1)$ hybrids have to be made, and this rapidly becomes a very large number as P increases. For this reason, diallels with more than a few parents are rare and methods to reduce the number of crosses in a diallel have been developed. The simplest reduction is achieved by assuming a negligible reciprocal effect and thus eliminating all reciprocal crosses. This reduces the number of hybrids to $P(P-1)/2$ and the model for the phenotype in the partial diallel becomes:

$$P_{ij} = \mu + gca_i + gca_j + sca_{ij} + e_{ij} \quad (i.ii)$$

One may predict the phenotype of a particular hybrid with the use of diallel-type analysis: once a full analysis of a diallel experiment has been made, the right hand side of equation (i.ii) may be used to estimate the left-hand side. While this may yield interesting information about the fit of the linear model, its practical applicability is questionable as the left-hand side values have already been observed. However, if all the hybrids

are not observed, the missing ones may be estimated as follows:

$$\hat{P}_{ij} = \bar{X} + g\hat{c}a_i + g\hat{c}a_j \quad (\text{i.iii})$$

where \bar{X} = the sample population mean

A number of assumptions are made before such an estimate may be expected to have a reasonable range of accuracy. The first group of assumptions are the genetic assumptions of diallel analysis proposed by Hayman (1954b):

- (a) diploid segregation
- (b) no differences between reciprocal crosses;
- (c) independent action of non allelic genes;
- (d) no multiple alleles;
- (e) homozygous parents;
- (f) genes independently distributed between the parents.

As Hayman showed, assumption (d) is only important for generations after the F_1 . Gilbert (1958), Dickinson and Jinks (1956) and Kempthorne (1956) give a full discussion on the implications of these assumptions and suggest methods of adjusting diallel analysis when some of them do not apply. As these assumptions, and subsequent discussions of them, are tangential to the use made of the diallel design in this thesis, and as it is the design and not the methods of analysis that will be introduced, the above assumptions will not be further elaborated.

Two further assumptions put forward at this time are:

- (g) environmental effects within an experiment are small -
- Use of a homozygous genotype as a control at a predesigned

placement in an experimental block allows environmental effects to be evaluated, subsequent correction for this variation allows acceptance of this assumption [this hypothesis is dealt with in Section 1.3].

(h) accurate estimates of the general combining ability can be made. The rest of this section deals with this assumption.

Within the partial diallel model are two distinct options for the estimation of general combining ability. They are:

- i. the use of a partial diallel;
- ii. the use of an incomplete partial diallel.

Use of a partial diallel is of little value, as the objective is to predict hybrid performance and the partial diallel contains all possible hybrids. The partial diallel could, however, be used for estimating hybrids which are outside and/or between sets of diallels.

Clearly it is not possible to estimate the result of a cross between a parent in a diallel and a parent which is not included in this diallel, as only the gca estimate of the parent in the diallel is available. If two diallels exist, and if one parent is in each diallel, then an estimate of both gca's is possible and hence an estimate of the hybrid may be calculated. However, diallel analysis with regard to gca estimation is an "averaging" and "fitting" process, involving all the hybrids and estimating their non-interactive genetic effect; this estimate is thus extremely sensitive to the set of genotypes used in the fitting

process.

Within a diallel the gca estimates are fitted relative to other parents in the diallel. No information is necessarily obtained about parental varieties not included in the diallel, nor about the effects other parents may have on the diallel. For interdiallel hybrids to be estimated with such gca's, it would be necessary to assume that the addition and/or deletion of parents to either diallel would not affect the gca estimates of the remaining parental gca's. As Kempthorne (1956) shows, such extrapolation from results within a diallel subset of a population, to the population itself, form a weakness in the diallel method.

This leaves the incomplete partial diallels as a source of gca estimation. Here, all the gca's are estimated within the same set of genotypes. However, a similar question still remains, as to whether the addition (towards a partial diallel) or deletion (towards a more sparse incomplete partial diallel) of elements from the diallel affects the gca estimates of the parents. As there will be a gca estimate for every parent that could be used in the predicted hybrid, here the problem is more one of precision than of relativity.

One form of incomplete partial diallel is the "tester cross" method. "Tester crosses", "top crosses" and the "North Carolina I & II" are all similar examples of an extreme case of the incomplete diallel. Here some parents in the diallel (the "testers") are crossed with all the remaining parents. No hybrids are made between the tester parents, nor between the remaining

Kempthorne and Curnow (1961) suggest a systematic method for dividing the diallel into a smaller number of crosses which will allow a larger number of parent lines to be assessed. Curnow (1963) and Fyfe and Gilbert (1963) elaborated upon this theme by presenting slightly more restrictive ways of sampling the diallel (introducing more symmetry and hence orthogonality), but which give more accurate estimates of the combining abilities. Curnow (1963) also introduced the idea of the circulant sampling method, which was further investigated by Bray (1971). In general, these authors all conclude that sampling only a subset of the diallel entails risk. This risk is quantified by the increased standard errors that are associated with the combining ability estimates. As Bray (1971) points out, errors in the estimation of specific combining ability are particularly exaggerated when the diallel is sampled. However, he showed that by using at least 6-8 crosses per parent, one can reduce much of this error.

parents. Lupton (1965) discussed the value of estimates of gca from the tester cross method. Although he concluded that this method had advantages over other methods he examined, he spent little time discussing the error inherent in the gca estimation by using an incomplete partial diallel (tester cross method) compared to the partial diallel.

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However, these arguments regarding the accuracy of estimating combining ability are more critical when the objective of the diallel is to describe precisely the mode of inheritance - both of the population sampled and for individual members within that sample. As Gilbert (1958) pointed out, most breeders are only interested in the parental lines and crosses themselves, and not with their representativeness, or otherwise, of the population as a whole.

1.2.4 Ranking

Consider the breeders' main problem: they initially have only two sets of information:

- i. the characteristics of the existing genotypes,
- ii. the desired characteristics of the genotypes he/she wishes to produce.

Hence the evaluation of existing and new parental material, for hybridisation, is an essential part of the breeder's task.

As shown earlier, before any prediction of unknown hybrids can

Chaudhary, Katar and Singh (1977) obtained gca ranks for an eight parent partial diallel. They compared the gca ranks of the partial diallel to the gca ranks from a set of incomplete partial diallels from the original diallel, but they concluded that the IPD ranks could not be used to predict the partial diallel gca ranks. However as the gca estimates for the IPD in Chaudhary, Katar and Singh's work (ibid) were calculated from the unadjusted method for the partial diallel, these results must be viewed with caution. This is, however, the only direct example found where gca ranks in the IPD are compared to those of the partial diallel.

be used, the additive genetic effects (gca) must be estimated. These gca's have two estimative qualities: first, there is the gca value itself, usually expressed in the same units as the quantitative genetic character it represents; and secondly there is the relative positioning, or ranking, of parental gca's as compared to each other. Of the two, the latter is clearly more important to the plant breeder, who must work with the assumption that two high-ranking gca individuals have more hybrid (and hence breeding) potential than two low-ranking gca individuals. [Although interactive genetic effects (sca) will also be important, they can only be associated with each separate hybrid and not with the parents individually. Thus they are not useful as a predictive tool.] Although the sca values themselves are not useful in prediction they are, nevertheless, critical for the effective use of gca values as predictors. If the sca values are large in comparison to the gca values, then prediction will be poor.

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For this reason, the standard errors of the gca estimates will be largely ignored, for the remainder of this thesis, in favour of the accuracy of gca ranking. Comparisons will be made between gca ranks in the incomplete partial diallel, as compared to those in the partial diallel. If the ranking of gca values is seen as the critical statistic, then methods of diallel analysis can be reassessed according to this different criterion.

Statistical treatment of rank correlations is most conveniently done by using Spearman's Rank Correlation Coefficient (Snedecor, 1946). The chief advantage of Spearman's Rank Correlation Coefficient, as compared to other methods (e.g. Kendall's Coefficient of Rank Correlation), is that it can be more easily computed directly from the ranks of paired variables (Sokal and Rohlf, 1969). According to Sokal and Rohlf (ibid), both methods give good results and they are highly correlated.

1.3 Experimental Design and Environmental Variation

1.3.1 Introduction

In cereal breeding experiments large numbers of genotypically diverse varieties and their hybrid families are grown in an attempt to make an objective classification of their yielding abilities. Environmentally induced similarities between adjacent plots create a potential for misclassification of lines - this has been illustrated by Shebeski (1967), who calculated serial correlations between plots in a wheat uniformity trial.

Fisher (1918) introduced the statistical analysis known as "analysis of variance", which is now used almost exclusively for the statistical analysis of breeding experiments. Provided that observations are independent and that any errors in observation are normally distributed, significance tests can be performed on the observed data. Such tests are used to determine whether or not classifications of the data into subgroups significantly deviate from the case in which there are no subgroups. Fisher (eg. 1932) also introduced the concept of randomisation so that inference between the sample and the population statistics (eg. mean, variance) was possible. For observations to be independent, serial correlations between plot positions have to be nullified; randomisation of the position of replicates within an experiment randomises observational errors that are due to plots being closely positioned.

Systematic designs have also been suggested, and tested, as an

alternative to randomisation (Wiebe, 1935; Barbacki & Fisher, 1936; and Gosset, 1937). In summary, Yates (1938) concluded that randomisation is required if the values are to be analysed by a method that assumes independence of the observations and that the advantage of systematic arrangements is likely to be offset by the possibility of a biased estimate or experimental error.

1.3.2 Heterogeneity in Field Experiments

In the early part of the twentieth century, the existence of environmentally induced variation within the same experimental site was recognised, and uniformity trials, in which a single genotype was planted in a field and harvested as small plots, were conducted (Mercer & Hall, 1911; Smith, 1938). It was observed that the larger the plot the smaller the between-plot variance (Smith, 1938; Whittle, 1956). Smith showed that adjacent plots were correlated inversely with the square of the plot size, and that the further apart plots were, the smaller their serial correlation. Significantly, he also showed that the plot size needed to reduce between-plot variation differed between sites and crops. A ten season uniformity trial of barley (Baker, Huberty and Veihmeyer, 1952) showed that changes occurred in the ranks of different varieties between years, and that high and low yielding regions in their trial sites varied from one year to another.

1.3.3 Control Plots

Control plots were used by Summerby (1925) and McClelland (1926) so that comparisons could be made between experimental "treatment" plots and their neighbouring homozygous "control" plots.

As mentioned earlier, one of the fundamental assumptions of using an analysis of variance is that the errors associated with the measurement of each plot are normally distributed. However, if control plots are used in the measurement of their neighbouring experimental plots, then clearly independence of measurements is removed. An analysis of covariance, using the control plots to calculate the covariate, largely removes this problem. This idea was postulated by Yates (1936). However, Outhwaite & Rutherford (1955) and Federer & Schlottfeldt (1954) stated that this method may not be as efficient as the use of a "latin square" design. The interpretations of the regression coefficient calculated by the analysis of variance and the subsequently adjusted experimental observations are further discussed by Smith (1957). Smith (ibid) states that such statistics seem to become relevant only when the variance within treatments can be regarded as a random variable.

If heterogeneity in a field is continuous and if the control plots are systematically placed so as to be close enough to echo this heterogeneity, then the use of control plots should be helpful (Lamacraft, 1974). Shebeski (1967), Briggs & Shebeski (1968) and Briggs, Bushuk & Shebeski (1969) investigated the correlation between control plots placed at differing distances from each other. They found highly significant correlations at small distances (2.7 metres) decreasing to non-significance at larger distances (20 metres). Both Baker & McKenzie (1967) and Seif et al. (1974) are critical of the use of control plots as a method of directly adjusting experimental plots. However, Baker & McKenzie (loc. cit.) stated that it would be more appropriate to use control plots to calculate a covariate, and this idea was successfully used by Pesek (1973).

Papadakis (1937) suggested using adjacent experimental plots to create a covariate. Detailed discussion of this design is made by Bartlett (1938), Atkinson (1969), Whittle (1962) and Pearce & Moore (1976). These and other views are drawn together by Bartlett (1978). Although this method suggests a large improvement in the accuracy of experimental plot comparisons, it demands a replication factor of at least three (Bartlett, 1978). This creates problems for the breeder as physical limitations, both of the number of plots sown and the amount of seed available, usually make such a replication factor undesirable.

Pesek (1974) found difficulty in comparing control plot designs with other designs. His problem was that unlike most other designs, those with control plots do not rely on a high replication factor for the adjustment for environmentally induced variation within an experiment. By the same token, this is the chief argument for the use of control plots in plant breeding experiments. Even though bulking early generations may give enough seed to the breeder to allow replication in field trials, the subsequent mixture of genotypes may also shield the value of genotypes from the breeder.

1.4 Breeding Methods in Self Pollinating Cereals

Restrictions on the numbers of plants and plots that can be observed in a breeding programme ensure that early generation selection must be made. Whether this selection should be random [eg. take only fifty seed from an F_2 population] or by some other form of breeder selection, is debatable. Shebeski (1967) argues that the breeder should make the selection so that valuable genotypes are not lost by chance. Van der Kley (1955), Lupton & Whitehouse (1957) and Allard (1960) argue that no selection should be made by the breeder in the early generations as the phenotype of the heterozygous plant may not be indicative of its homozygous descendants.

With a large number of loci controlling a quantitative trait, a genotype with all the desirable alleles is expected to be extremely rare (Shebeski, 1967) and only by grouping enormous numbers could one feel confident that the genotype sought is present (assuming of course that it is clearly identifiable). Happily, however, as Palmer (1953) points out, genotypes which fall short of this "perfection" will do. The bulk of cereal breeding uses one of the following six methodologies (or a combination of two or more):

A. Pedigree or Line Method

References: Heyne & Smith (1967); Shebeski (1967); Hayes, Immer & Smith (1955); Poehlmen (1959); Love (1927); Harrington (1952); Elliot (1958).

Summary: Plants are selected for desirable characters in the F_2

generation; further selection is made on the progeny of these selected plants until phenotypic homogeneity is reached in about the F_6 generation.

Advantages: Source of final selected material is known exactly by its pedigree. Unselected earlier generation lines may be reappraised for other criteria (e.g. disease resistance). All material is genetically distinct and its relatedness to other lines is known.

Disadvantages: Relies on potentially superior genotypes to be identified in very early generations. Genetic diversity is limited very early. Extremely time-consuming in the recording and storage of detailed pedigree information and plant statistics.

B. Bulk or Population Method

References: Hayes, Immer & Smith (1955); Ackermen & MacKay (1948); Love (1927); Florrell (1929).

Summary: Material is bulked from F_2 plots until about F_6 , where plant or single head selection is made.

Advantages: Ease of recording and growing make large numbers of crosses easy to handle. Plants are (nearly) homozygous before breeder selection is made. Environmental restrictions (artificial or natural) may be placed on the bulked generations to select against obvious disadvantages (eg. drought or disease resistance, early or late maturity etc.).

Disadvantages: Many advantageous genotypes may be lost because only a certain percentage of the bulked population can be grown in the ensuing generations (because of physical space restrictions) - these bulked progenies are effectively a random selection. For complete segregation in F_6 to be

observed an impossibly large number of plants would need to be grown, e.g. in wheat with one relevant gene per chromosome, two million plants would need to be grown (Allard 1960; Whan 1978). (This, however, is not likely to be important in practice.) The genetic relatedness between two F_6 selections is unknown.

C. Mass Pedigree Method

Reference: Harrington (1937).

Summary: Similar to bulk method except that single plants and/or heads may be taken at any generation to start off new bulks.

Advantages and Disadvantages: When compared to methods A and B this hybrid method appears to be an example of having one's cake and eating it. The main advantage is the flexibility to channel off superior genotypes virtually at any time. The problem of course is that it can't be done too often, or numbers become excessive. Other advantages and disadvantages are similar to methods A and B.

D. Composite Crosses or Complex Bulk Method

References: Harlan & Martini (1929); Suneson (1956); Suneson & Stevens (1953); Suneson & Wiebe (1962); Harlan, Martini & Stevens (1940); Suneson (1964); Tee & Qualset (1975); Hamblin & Morton (1977).

Summary: A heterogeneous population is created by a mixture of many initial crosses. A male sterility mutant may also be incorporated to further mix the population gene pool. Bulked populations are grown for many generations, allowing natural selection to take place. As many as fifteen to twenty generations of bulking may take place before conventional breeder selection takes place. This essentially involves

evolutionary breeding. A major variation of this method involves management of male-sterility in composite crosses. For example if seed is harvested only from male-sterile plants in each generation, then quite different results emanate than for those expected on the basis of bulk harvesting the entire population (Driscoll, per. comm.).

Advantages: Because of the number of generations involved, natural selection will tend to develop a population adapted to the environment in which the bulks are grown. Thus the ensuing breeder selections will be amongst already adapted material. The large gene pool of the parental material and the subsequent heterogeneity of the population, gives the potential for large variety in the adapting lines.

Disadvantages: The most obvious disadvantage is time. As each generation represents a year (summer generations are not possible as natural selection in the environment where the cereal is to be grown is often wanted), this method may be three to four times as slow as previously mentioned methods. The natural selection takes place in only one environment and thus selected lines may not be well adapted to other environments. Natural selection may encourage highly competitive lines which may not do as well as a pure stand commercial crop. The method of Driscoll (loc. cit.) involves only three or four generations of outcrossing (some of which can be grown out of season), before selection commences. If this method is used the time disadvantage is lost whilst still creating a high level of heterogeneity within the composite population. The pedigree of the bred line is unknown.

E. Mass Selection Method

References: Romero & Frey (1966); Derera & Bhatt (1972), (1973); Bhatt & Derera (1973); Derera, Bhatt & Ellison (1974); Frey (1967); Chandhanamutta & Frey (1973); Gadelmann & Frey (1975).

Summary: Similar to bulk method except that each generation is screened for easily discernible phenotypic traits (e.g. seed type, maturity time). These selections are then grown in the next generation.

Advantages and Disadvantages: This method is only effective for simply inherited traits. Multifactorial traits could well be masked by heterozygous genotypes in early generations and thus escape selection. It may, however, be very effective where a high correlation occurs between a neutral but simply inherited trait, and a highly desirable but non-simply inherited trait.

F. Single Seed Descent or Modified Pedigree Method

References: Goulden (1941); Grafius (1965); Brim (1966); Kaufman (1971); Knott & Kunar (1975); Baker (1971); Snape & Riggs (1975).

Summary: This method consists of growing many generations as fast as possible before selection is made. This is done by growing a large number of plants in an extremely small space with minimal nutritional requirements, and then taking one or two seeds from each plant for the next generation. In a glasshouse, three generations a year may be grown this way. After six generations (two years) the (nearly) homozygous progeny are grown conventionally for selection procedures to be initiated.

Advantages and Disadvantages: The main advantage is speed, the main disadvantage is the large amount of variation lost by only taking one or two seeds from each plant. Selection amongst (nearly) homozygous lines with an exact pedigree has its advantages.....provided the desirable genotypes are still present. Other advantages and disadvantages are similar to the Bulk Method (B).

In general, breeding methodologies strive to have the major breeder selection processes performed in a generation approaching homozygosity. The major problem is to make sure that the genotypes sought have not already been eliminated (either consciously - by breeder selection, or inadvertently - because of the inability to grow all possible genotypes).

Review Summary

Plant breeding techniques, for quantitative traits, can be divided into the three major categories described in this chapter, that is: the genetic evaluation of the parental material; the separation of genetic effects from environmental effects; and the subsequent evaluation and selection within the breeding programme.

Although a great deal of work has been done on these topics, there seems to be a gap between the needs of the pragmatic plant breeder and the theoretical geneticist. The rigorous experimental designs that are available to genetically describe a small group of varieties within a species are far too resource consuming, and cannot encompass a large enough range of varieties to be practical to the plant breeder.

Thus a quick assessment technique for the most important genetic parameters is necessary. Together with the necessity for speed is the need to be able to process a large number of potential parents. It will be suggested, later in this thesis, that the measurement of additive genetic effects (general combining ability) should fulfill the dual criteria of obtaining the most essential genetic information whilst minimising the number of evaluative crosses needed.

To be of relevance to a breeding programme other than those which do not require a homozygous product (e.g. F_1 hybrids), evaluation should be carried out in a generation approaching homozygosity. For these reasons the applicability of incomplete partial diallels, evaluated in both the F_1 and F_4 generations will be investigated. Also, as such material would not be able to be replicated, methods of measuring soil fertility differences within an experiment will be subjected to further investigation.

2. Diallels - A Simulation Study.

2.1 Introduction

Evaluating forms of crossing designs is a difficult problem as it is extremely time-consuming to obtain direct biological results. Also, if a design is tested biologically for a given set of parents, then the question must arise as to whether the results of such an experiment are representative for all parents that might have been used, or only for the parents that were actually used.

The obvious way to answer this question is to perform these crossing design trials for a number of sets of parents and to see whether the results are similar or different for each set. The problem with this, of course, is that it is too time- and resource-consuming to be done in practice.

A computer simulation enables the modelling of a large number of sets of parents, with different characteristics given to each parent and has the considerable advantage of being extremely fast in performance.

2.2 The Simulation Program

A computer program was written to simulate observations from a diallel of a self-pollinating species. The program was written in the PASCAL general purpose programming language (Jensen and Wirth,

1975) for a Control Data Corporation Cyber 173 computer. The phenotypic observations of the diallel were generated with the following specifications:

- (i) The variances of the general and specific combining abilities of the diallel were represented by the two variables GCAR and SCAR, respectively.
- (ii) P values were chosen at random from a normal distribution of mean zero and variance GCAR, $[N(0,GCAR)]$. These values were then assigned to represent the gca values of the P parents in the diallel.
- (iii) $P(P + 1)/2$ values were then chosen at random from a normal distribution with mean zero and variance SCAR, $[N(0,SCAR)]$. These values were then assigned to represent the specific combining ability values plus the environmental effects of all the hybrids and selfs in the diallel.
- (iv) Individual observations were then generated using equation 1.ii [Section 1.2.3], where the last two terms were combined:

$$\text{i.e. } P_{ij} = \text{mean} + gca_i + gca_j + \underbrace{sca_{ij}}_{sca_{ij}} + e_{ij}$$

It should be noted that the values generated in steps (ii) and

(iii) above do not conform exactly to the standard definitions $\sum gca_i = 0$ and $\sum sca_{ij} = 0$. As they are taken at random from the normal distribution they will only approximate this restriction.

This simulated diallel can now be analysed as a complete or an incomplete partial diallel. It was systematically reduced to incomplete partial diallels representing 2, 4, 6, 8 and 10 crosses per parent (see Figure 2.1). Each of these reduced diallels was then analysed for the parental gca estimates which were compared to those of the partial diallel. The analysis took the form of a least square analysis to minimize $\sum E_{ij}^2$ where:

$$E_{ij} = P_{ij} - gca_i - gca_j - \mu \quad (\text{See Appendices V \& VI})$$

where μ is the overall mean.

The simulation was carried out for diallels of sizes $P=15, 20, 30$ and 50 . The number of trials for each diallel size was $100, 50, 30$ and 14 respectively. (eg. 100 diallels of size $P=15$ were simulated, etc.). The number of diallels simulated for the different numbers of parents was pragmatically allocated as a function of the amount of computer time needed to complete a set of simulations (approx. 300 seconds). Each simulation replicate was independent of the others and thus represented a completely new set of parents. This independence was maintained by using a random number generator with a unique starting point each time. The random number generator used was the IMSL program library's GGNOF (IMSL, 1977). Its starting point seed was obtained as follows:

$$\text{SEED} = (\text{Time of day}) \times (\text{date}).$$

		PARENT NUMBER									
		1	2	3	4	5	6	7	8	9	10
PARENT NUMBER	1	P	A	B	C	D	E	D	C	B	A
	2		P	A	B	C	D	E	D	C	B
	3			P	A	B	C	D	E	D	C
	4				P	A	B	C	D	E	D
	5					P	A	B	C	D	E
	6						P	A	B	C	D
	7							P	A	B	C
	8								P	A	B
	9									P	A
	10										P

Figure 2.1: This figure illustrates how the incomplete partial diallels were systematically sampled. The partial diallel consists of the parents (P) and all of the crosses (A, B, C, D & E). The two crosses per parent incomplete partial diallel consists of P + A. Similarly, the 4, 6 and 8 crosses per parent incomplete partial diallel consist of P+A+B, P+A+B+C, and P+A+B+C+D respectively.

As the accuracy of the cross prediction using this method is clearly dependent on the proportional contribution of gca/sca, wide ranges of GCAR and SCAR values were used for the diallel generation. The values used were 1024, 256, 64, 16, 4 and 1. All permutations (36) of these values of GCAR and SCAR values were used for each diallel size. In all, 27,936 diallels were simulated.

The gca values generated in step (i) above were not used, as the idea of the simulation was to mimic an experimental situation in which only the gca's calculated from the diallel analysis are known. Therefore gca's calculated from the partial diallel were used as the true gca values. Their separate processing also gives a higher degree of independence between the simulation of observed values and their subsequent analysis and evaluation.

Thus the rank differences were obtained by subtracting the rank obtained for a parental gca in the incomplete partial diallel from the rank of the same parent's gca in the partial diallel. This was done for all parents and the absolute values of these rank differences were stored as ten values representing the number of parents in the diallel which varied in rank by zero, the number that varied in rank by one, and so on up to the number of parents which varied in rank by nine or more.

2.3 Simulation Results

2.3.1 Ranks

After each diallel was simulated and analysed, a tally was taken of the number of parents in the incomplete partial diallels which differed in rank from those in the partial diallel.

Of the thirty-six combinations of gca to sca variance ratios used, eleven were unique; for example, the ratio of the variance of gca's from the distribution $N(0,1024)$ to the variance of sca's from the $N(0,256)$ distribution is the same as for the two distributions $N(0,256)$ and $N(0,64)$ [i.e. $1024/256 = 256/64 = 4.0$]. The eleven distinct ratios were 1024, 256, 64, 16, 4, 1, 0.25, 0.0625, 0.0156, 0.0039 and 0.0010 with replications 1, 2, 3, 4, 5, 6, 5, 4, 3, 2 and 1 respectively.

Duncan's Multiple *Range* Test (Duncan, 1955) was performed on the components of the eleven groupings of variance ratios to see whether scaling differences were present. No significant differences were found. This meant that the groups with the same variance ratios could be averaged to give a single mean value without significant loss of information. Thus, the original thirtysix gca/sca ratios were reduced to eleven.

Of these eleven remaining groups, five had a larger gca component than sca component (i.e. ratio greater than one), one had equal components (i.e. ratio equal to one) and five had

smaller gca components than sca components (i.e. ratio less than one). As would be expected, the latter five yielded many rank changes between the partial diallel and incomplete partial diallel. Table 2.1 shows Spearman's rank correlation coefficients for all the diallels simulated that had a variance ratio of 1 or greater. The range and scatter of this coefficient did not differ appreciably for these ratios, so only the range from the 256/1 ratio down to the 1/1 ratio is shown.

Similarly, Table 2.2 shows the range of Spearman's rank correlation coefficient for the variance ratios less than one (i.e. 0.5 down to 0.0010). This table is included to illustrate the instability of the gca ranks as the gca/sca variance ratio decreases below unity. Table 2.1, however, shows the stability of the ranks for the various incomplete partial diallels. If none or only a few rank changes occur then the ranks may be considered to be stable. However, if there are many rank changes, or if there are rank changes of more than, say, three, then the ranks may be considered to be unstable. This stability is reflected by a high Spearman's rank correlation coefficient (i.e. approaching 1.0), a low coefficient showing instability in the rankings.

It is difficult to visualise, from this information alone, the significance of these rank changes for the plant breeder. For this reason, tables were also drawn up to show the percentage of gca estimates whose rank did not change at all for the incomplete partial diallels. Similarly, tables showing rank changes of one or less, two or less and up to nine or less changes in rank were compiled. As these tables are cumbersome, a subset of them appears here as Tables 2.3.1 to 2.3.4. These show the percentages

TABLE 2.1

Range of Spearman's rank correlation coefficients for gca:sca variance ratios of 256:1 to 1:1. The ranks of the gca estimates from the partial diallel are compared to those from the incomplete partial diallel. The bracketed numbers represent the percentage of the crosses from the partial diallel used in the incomplete partial diallel.

	15 Parent Diallel	20 Parent Diallel	30 Parent Diallel	50 Parent Diallel
10 crosses per parent I.P.D.	0.999-0.979 (71.4%)	0.999-0.968 (52.6%)	0.999-0.964 (34.5%)	0.999-0.966 (20.4%)
8 crosses per parent I.P.D.	0.999-0.969 (57.1%)	0.999-0.957 (41.2%)	0.999-0.955 (27.6%)	0.999-0.959 (16.2%)
6 crosses per parent I.P.D.	0.999-0.955 (42.9%)	0.999-0.950 (31.6%)	0.999-0.948 (20.7%)	0.999-0.952 (12.2%)
4 crosses per parent I.P.D.	0.999-0.940 (28.6%)	0.999-0.936 (21.1%)	0.999-0.935 (13.8%)	0.999-0.938 (8.2%)
2 crosses per parent I.P.D.	0.999-0.918 (14.3%)	0.999-0.896 (10.5%)	0.999-0.918 (6.9%)	0.999-0.912 (4.1%)

TABLE 2.2

Range of Spearman's rank correlation coefficients for gca:sca variance ratios of 256:1 to 1:1. The ranks of the gca estimates from the partial diallel are compared to those from the incomplete partial diallel. The bracketed numbers represent the percentage of the crosses from the partial diallel used in the incomplete partial diallel.

	15 Parent Diallel	20 Parent Diallel	30 Parent Diallel	50 Parent Diallel
10 crosses per parent I.P.D.	0.94-0.84 (71.4%)	0.93-0.73 (52.6%)	0.90-0.61 (34.5%)	0.91-0.50 (20.4%)
8 crosses per parent I.P.D.	0.92-0.75 (57.1%)	0.90-0.68 (41.2%)	0.88-0.55 (27.6%)	0.90-0.44 (16.2%)
6 crosses per parent I.P.D.	0.89-0.67 (42.9%)	0.89-0.62 (31.6%)	0.85-0.50 (20.7%)	0.88-0.39 (12.2%)
4 crosses per parent I.P.D.	0.84-0.59 (28.6%)	0.84-0.53 (21.1%)	0.82-0.44 (13.8%)	0.83-0.35 (8.2%)
2 crosses per parent I.P.D.	0.79-0.49 (14.3%)	0.79-0.46 (10.5%)	0.78-0.37 (6.9%)	0.78-0.29 (4.1%)

TABLE 2.3.1

Means and Standard Errors of the percentage of parents in 20 x 20 Diallel whose GCA estimates do not change in rank when the incomplete partial diallel analysis is compared to the partial diallel analysis.

GCA/SCR Variance Ratio	2 crosses per parent (20/190=10.5% of possible crosses)	4 crosses per parent (40/190=21.1% of possible crosses)	6 crosses per parent (60/190=31.6% of possible crosses)
1024.0	91.00 ± 1.12	93.40 ± 1.05	94.00 ± 1.03
256.0	87.30 ± 0.99	88.60 ± 1.03	90.90 ± 0.97
64.0	77.87 ± 1.03	81.27 ± 0.99	85.23 ± 0.90
16.0	62.82 ± 0.91	68.45 ± 0.99	72.30 ± 0.87
4.0	43.54 ± 0.81	49.48 ± 0.87	55.56 ± 0.93
1.0	25.67 ± 0.64	29.95 ± 0.69	36.22 ± 0.70
0.2500	15.78 ± 0.58	19.62 ± 0.57	22.24 ± 0.66
0.0625	11.95 ± 0.52	13.87 ± 0.55	15.20 ± 0.63
0.0156	9.00 ± 0.53	10.33 ± 0.55	11.80 ± 0.68
0.0039	8.95 ± 0.64	9.90 ± 0.72	12.10 ± 0.80
0.0010	9.60 ± 0.99	10.90 ± 1.00	10.30 ± 0.84

TABLE 2.3.2

Means and Standard Errors of the percentage of parents in a 20 x 20 Diallel whose GCA estimates do not change in rank more than one when the incomplete partial diallel analysis is compared to the partial diallel analysis.

GCA/SCR Variance Ratio	2 crosses per parent (20/190=10.5% of possible crosses)	4 crosses per parent (40/190=21.2% of possible crosses)	6 crosses per parent (60/190=31.6% of possible crosses)
1024.0	100.00 ± 0.00	100.00 ± 0.00	100.00 ± 0.00
256.0	99.10 ± 0.26	99.20 ± 0.24	99.50 ± 0.19
64.0	97.30 ± 0.37	97.70 ± 0.35	98.23 ± 0.33
16.0	90.78 ± 0.59	93.15 ± 0.51	94.97 ± 0.43
4.0	77.84 ± 0.71	83.00 ± 0.69	86.94 ± 0.59
1.0	56.67 ± 0.75	63.02 ± 0.75	69.00 ± 0.66
0.2500	38.82 ± 0.81	45.16 ± 0.75	49.04 ± 0.77
0.0625	29.00 ± 0.73	34.55 ± 0.78	36.82 ± 0.82
0.0156	25.53 ± 0.76	26.37 ± 0.82	29.40 ± 0.88
0.0039	24.40 ± 1.13	25.30 ± 0.97	31.80 ± 1.13
0.0010	25.10 ± 1.52	24.60 ± 1.55	28.30 ± 1.49

TABLE 2.3.3

Means and Standard Errors of the percentage of parents in a 20 x 20 diallel whose GCA estimates do not change in rank more than two when the incomplete partial diallel analysis is compared to the partial diallel analysis.

GCA/SCR Variance Ratio	2 crosses per parent (20/190=10.5% of possible crosses)	4 crosses per parent (40/190=21.2% of possible crosses)	6 crosses per parent (60/190=31.6% of possible crosses)
1024.0	100.00 ± 0.00	100.00 ± 0.00	100.00 ± 0.00
256.0	100.00 ± 0.00	100.00 ± 0.00	100.00 ± 0.00
64.0	99.67 ± 0.15	99.80 ± 0.09	99.83 ± 0.09
16.0	97.82 ± 0.29	98.73 ± 0.20	99.25 ± 0.17
4.0	92.58 ± 0.41	94.92 ± 0.39	96.38 ± 0.34
1.0	74.38 ± 0.70	80.52 ± 0.60	85.18 ± 0.55
0.2500	55.24 ± 0.80	62.42 ± 0.74	68.10 ± 0.79
0.0625	43.97 ± 0.85	49.40 ± 0.81	53.40 ± 0.85
0.0156	38.70 ± 0.91	40.83 ± 0.95	44.77 ± 1.00
0.0039	35.50 ± 1.22	38.60 ± 0.99	45.05 ± 1.13
0.0010	36.90 ± 1.50	38.40 ± 1.62	42.50 ± 1.38

TABLE 2.3.4

Means and Standard Errors of the percentage of parents in a 20 x 20 diallel whose GCA estimates do not change in rank more than three when the incomplete partial diallel analysis is compared to the partial diallel analysis.

GCA/SCR Variance Ratio	2 crosses per parent (20/190=10.5% of possible crosses)	4 crosses per parent (40/190=21.2% of possible crosses)	6 crosses per parent (60/190=31.6% of possible crosses)
1024.0	100.00 ± 0.00	100.00 ± 0.00	100.00 ± 0.00
256.0	100.00 ± 0.00	100.00 ± 0.00	100.00 ± 0.00
64.0	100.00 ± 0.00	100.00 ± 0.00	100.00 ± 0.00
16.0	99.88 ± 0.06	99.92 ± 0.06	99.98 ± 0.03
4.0	99.12 ± 0.15	99.66 ± 0.10	99.78 ± 0.10
1.0	92.62 ± 0.42	95.67 ± 0.33	99.47 ± 0.25
0.2500	78.36 ± 0.65	83.58 ± 0.63	87.12 ± 0.60
0.0625	64.88 ± 0.85	70.67 ± 0.80	76.44 ± 0.81
0.0156	59.03 ± 0.97	64.50 ± 0.92	68.10 ± 1.05
0.0039	57.55 ± 1.31	61.55 ± 1.28	66.75 ± 1.23
0.0010	55.50 ± 1.49	58.50 ± 1.40	63.50 ± 1.52

Rank change is only critical in one direction, that is, in the direction where material which should be included is not included. Once such a misclassification has occurred, the lost lines may never be exploited. On the other hand, material that is misclassified as being better than it actually is will ultimately be discovered and discarded with no loss to the breeding programme (other than wasted resources). Thus, as the

of observed changes in the estimated gca ranks for a twenty parent diallel. The complete set of such tables is presented in appendix I. In Tables 2.3.1 to 2.3.4 the full range of variance ratios is shown in order to indicate the rapid loss of information which occurs once the gca/sca ratio drops below one.

From these tables it is possible to estimate the probability of the breeder making an incorrect decision based on an incomplete partial diallel. The breeder may, for example, be looking at 20 possible parental lines and wish to choose those with the top five gca values to incorporate into a breeding programme. If a parent is ranked fifth in the partial diallel then any change towards an increased rank in the incomplete partial diallel will cause it to be incorrectly excluded from the top five. From Table 2.3.1 in a twenty parent diallel with two crosses per parent and a variance ratio of sixty-four to one, $(100-77.87)\%=22.13\%$ of the diallel would be expected to change rank. ^{Insert} _{opposite page} _{here} rank change is only important in one direction, this statistic can be halved to encompass only changes towards the lower ranks. Thus the approximate chance of the fifth ranked parent not being ranked in the top five becomes:

$$\begin{aligned} \frac{1}{2} (100 - 77.87)\% &= \frac{1}{2} (22.13)\% \\ &= 11.07\% \end{aligned}$$

Similarly from Tables 2.3.2 and 2.3.3 the estimates for the fourth and third ranked parents become:

$$\begin{aligned} \frac{1}{2} (100 - 97.30)\% &= 1.35\% && \text{(Table 2.3.2)} \\ \frac{1}{2} (100 - 99.67)\% &= 0.165\% && \text{(Table 2.3.3)} \end{aligned}$$

The probabilities of the first and second ranked parents being incorrectly ranked outside of the top five parents are obtained from the rank difference tables of four or less and three or less respectively (the table for four or less is not presented here).

Table 2.4 summarises these results for the 15, 20, 30 and 50 parent diallels, in which the incomplete diallel contains approximately 20% of all possible crosses. The 20% (or its closest approximate) incomplete partial diallel was chosen, as this was observed to be a reasonable cut-off point between having an excessively large number of crosses and having too little information. Similarly, the selection of five parents only is used, as this would be a practical number for a plant breeder to use in more extensive experimentation. It is, however, only an example and plant breeders may in fact wish to choose more (or less) parents from their original set of varieties.

As the probabilities shown in these tables are associated with any parent in the diallel and not just the first five ranked parents, these estimates can be considered upper limits and accordingly it would be expected that the exact probabilities (which are not calculable) should be lower. For this reason and for the sake of brevity, standard errors associated with these estimates were not included in Table 2.4.

2.3.2 Predictions

The values of the gca estimates obtained from the partial and incomplete partial diallels were used to predict the partial

TABLE 2.4

Probability of the Top Five Ranked Parents being Incorrectly Ranked Outside of the Top Five when the Incomplete Partial Diallel is Compared to the Partial Diallel.

	Ranking	Variance Ratio					
		1024	256	64	16	4	1
15 Parent Diallel	1	0.0000	0.0000	0.0000	0.0001	0.0005	0.0062
4 Crosses/parent	2	0.0000	0.0000	0.0000	0.0005	0.0023	0.0191
(30/105=28% of	3	0.0000	0.0000	0.0003	0.0027	0.0127	0.0501
possibl crosses)	4	0.0000	0.0017	0.0060	0.0224	0.0495	0.1274
	5	0.0207	0.0330	0.0721	0.1248	0.2013	0.3063
10 Parent Diallel	1	0.0000	0.0000	0.0000	0.0004	0.0017	0.0217
4 Crosses/parent	2	0.0000	0.0000	0.0002	0.0021	0.0069	0.0488
(40/190=21.1% of	3	0.0000	0.0000	0.0010	0.0064	0.0254	0.0974
possible crosses)	4	0.0000	0.0040	0.0115	0.0342	0.0850	0.1849
	5	0.0030	0.0570	0.0937	0.1577	0.2526	0.3502
30 Parent Diallel	1	0.0000	0.0000	0.0002	0.0004	0.0064	0.0419
6 Crosses/parent	2	0.0000	0.0000	0.0002	0.0026	0.0207	0.0790
(90/435=20.7% of	3	0.0000	0.0006	0.0020	0.0138	0.0530	0.1424
possible crosses)	4	0.0000	0.0061	0.0135	0.0589	0.1329	0.2414
	5	0.0444	0.0678	0.1259	0.2244	0.3167	0.3906
50 Parent Diallel	1	0.0000	0.0000	0.0000	0.0021	0.0214	0.0973
10 Crosses/parent	2	0.0000	0.0000	0.0010	0.0082	0.0520	0.1487
(250/1225=20.4% of	3	0.0000	0.0011	0.0031	0.0325	0.1026	0.2196
possible crosses)	4	0.0029	0.0064	0.0329	0.0991	0.2011	0.3096
	5	0.0414	0.0996	0.1707	0.2771	0.3693	0.4230

diallel using equation (i.ii) [Section 1.2.3]. Each of these estimated crosses, and estimated selfs (parental lines) was then compared to the observed values (in this case, the original simulated values). This yielded a value:

$$E = \text{observed value} - \text{predicted value.}$$

The absolute value of E for each component of the diallel was then calculated and a mean determined for the entire partial diallel:

$$\text{i.e. mean deviation} = \frac{\sum |E_{ij}|}{N} \quad \text{where } i = 1 \dots n, i < j \quad (\text{ii.i})$$

Similarly, variances associated with the statistics were calculated for all the diallels simulated. The replication of each diallel* simulation was then used to obtain the mean deviation, and its associated standard error, for each diallel size with a given gca/sca variance ratio. These results are summarised in Table 2.5. The absolute value was used, as it was felt that the magnitude rather than the direction of the deviation from the observed value was the important statistic.

As the mean deviation is directly related to the sca variance, only the gca/sca variance ratios of 256/64 are shown in Table 2.5. To obtain the new mean deviation the old mean deviation is multiplied by the square root of the ratio of the new sca variance to the old sca variance. Thus the complete range of variance ratios may be approximated by the formula:

$$\text{new mean deviation} = \text{old mean deviation} \times \sqrt{\frac{\text{new sca variance}}{64}} \quad (\text{ii.ii})$$

TABLE 2.5

Means and standard errors of the mean deviation of the predicted partial diallel and the incomplete partial diallel. All values are based on a *gca:sca* variance ratio of 1024:64. The bracketed numbers represent the percentage of the crosses from the partial diallel used in the incomplete partial diallel.

	15 Parent Diallel	20 Parent Diallel	30 Parent Diallel	50 Parent Diallel
Partial Diallel	6.04 ± 0.45 (100.0%)	6.03 ± 0.65 (100.0%)	1.91 ± 0.21 (100.0%)	1.94 ± 0.31 (100.0%)
10 crosses per parent I.P.D.	6.14 ± 0.46 (71.4%)	6.19 ± 0.67 (52.6%)	1.98 ± 0.23 (34.5%)	2.01 ± 0.34 (20.4%)
8 crosses per parent I.P.D.	6.22 ± 0.47 (57.1%)	6.28 ± 0.68 (42.1%)	2.00 ± 0.23 (27.6%)	2.03 ± 0.35 (16.2%)
6 crosses per parent I.P.D.	6.33 ± 0.48 (42.9%)	6.37 ± 0.70 (31.6%)	2.02 ± 0.24 (20.7%)	2.06 ± 0.36 (12.2%)
4 crosses per parent I.P.D.	6.50 ± 0.50 (28.6%)	6.51 ± 0.72 (21.2%)	2.05 ± 0.25 (13.8%)	2.19 ± 0.37 (8.2%)
2 crosses per parent I.P.D.	6.71 ± 0.52 (14.3%)	6.77 ± 0.76 (10.5%)	2.11 ± 0.27 (6.9%)	2.16 ± 0.40 (4.1%)

For example, if a gca/sca variance ratio of 256/16 in a 15 parent partial diallel occurs, then the expected mean deviation would be:

$$6.04 \times \sqrt{\frac{16}{64}} = 3.02$$

This relationship is further illustrated in Table 2.6, which will be introduced later in this Chapter.

Variance of the gca estimates and the mean deviation can be obtained from the incomplete partial diallel. Thus, equation ii.ii may be used to estimate the sca variance of the diallel. For example, using equation ii.ii, in a 15 parent diallel with a gca variance of 64 and a mean deviation of 1.5, the expected sca variance would be:

$$\begin{aligned} \sqrt{\text{SCA variance}} &= \frac{\text{new mean deviation}}{\text{old mean deviation}} \times \sqrt{64} = \frac{1.5}{6.04} \times \sqrt{64} \\ &= 1.98 \\ \text{SCA variance} &\doteq 4 \end{aligned}$$

Hence the gca/sca variance ratio of approximately $4/4=1.0$ may be expected.

Table 2.5 shows a drop in the mean deviation from approximately six down to two when the number of parents in the diallel goes from twenty to thirty. It seems that the larger number of parents, and thus observations, in the bigger diallels acts as a "buffer" which smooths out the variation. Similarly, in the larger diallel simulations the random sampling from the normal distribution (Section 2.2) should echo the complete density

My simulation study is essentially with the identification of the "best" parent in a diallel for its F₁ combining ability rather than its value in selection from advanced generations. Thus, it assists in elimination of certain parents from further use in diallel or related crosses, rather than in further selection within selected crosses. This is because the approach used does not treat the genetic basis for general and specific combining ability.

distribution more accurately. Hence extremes in the random sampling procedure would be buffered (i.e. concealed) more when many parents were used than when a small sample was taken.

2.4 Discussion

It can be seen from Tables 2.3.1 to 2.3.4 that very little change occurs in the ranking of the gca estimates when the partial diallel is reduced. Thus the plant breeder loses very little information when the number of crosses made is reduced.

Insert opposite page here

As would be expected, the gca/sca variance ratios which have a higher sca component than gca component lead to inaccuracies in the incomplete partial diallel ranking. This suggests that it would be unwise to place a great deal of emphasis on the incomplete partial diallel analysis of characters which have a gca/sca variance ratio of less than one. Whilst this restriction excludes some traits, many agronomic characters do conform to this restriction and have a gca/sca ratio of one or greater (cf. Griffing, 1956b; Reddy, 1976; Chaudhary et al. , 1977; Dhillon & Singh, 1977; and Lupton, 1965).

The simulations indicate that any added accuracy in the estimation of gca gained by using the partial diallel rather than the incomplete partial diallel would not outweigh the extra work involved. As an example, instead of making a partial diallel with twenty parents (190 crosses) twenty percent (approximately) of a forty parent partial diallel could be made (160 crosses). Here, fewer crosses are made but twice the number of parents are evaluated. In terms of finding the best parents to use in a

breeding programme very little information is lost by using only a fraction of the partial diallel. Table 2.4 shows the estimated upper probabilities for parents being incorrectly ranked outside of the top five; for most gca/sca variances the probability of not finding the top three parents is minimal. If more than five parents are to be chosen, the probabilities of an incorrect ranking assignment outside of those chosen become increasingly attractive for the plant breeder.

A critical part of this analysis was the inclusion of the parental lines themselves. Simulations were run excluding the parents and it was found that for similar accuracies to be attained, the number of observations (parent or cross) had to be maintained. That is, if observations of the twenty parents were not used in the incomplete partial diallel then a further twenty crosses would have to replace them in the analysis to give results of approximately the same accuracy. As it is usually disadvantageous to increase the number of crosses performed, the parents were used in the diallel analysis instead.

The case where only the parent means are used to evaluate their potential is investigated in Chapters 3 and 5.

Theoretically, this can be justified on the grounds that the breeder is fundamentally only interested in comparing the breeding material (parent lines). Including the parental observations in the diallel might well introduce a bias if the diallel were to be used to extrapolate to the population genetic parameters of the species. However, here this is not the case. As the breeder is mainly concerned with bias affecting the parental lines from which selection is made, any bias that affects information on parents outside the diallel is tolerable.

In outcrossing species, where selfed parental material cannot be obtained (or where it would suffer infertility and/or inbreeding depression), a larger number of crosses would, of necessity, be made to replace the parental lines in the diallel.

The simulated diallels were in the form of mean values of each genotype observation; in the field, the observations would of course be in the form of replicates of some convenient number. As replicated trials are the more usual use of least squares analysis, the method is easily adapted to multiple replicate input rather than input in the form of means. Because of the way in which the mean values were simulated, input in the form of replicated trials was not necessary for the simulation testing of the method: as the diallel consists only of parental lines and F_1 's, all of which do not genetically segregate, replication is only needed to minimise the environmental differences, which are not relevant to this particular type of computer simulation.

Rather than only the best parental gca's, all possible crosses between parents may be predicted [equation (i.iii)] and then the best of the predicted crosses chosen. With diallels appraised for a number of characters, the use of hybrid prediction may give a simpler selection procedure to the breeder than the individual use of gca estimates for each character. The accuracy of these predicted crosses may be appraised by Table 2.5, in which the closeness of fit between the predictions based on the partial diallel and those based on the 20% incomplete partial diallel is striking.

Tables 2.4 and 2.5 will be referred to at a later stage, when a

breeding plan using incomplete partial diallels will be suggested.

2.5 A Random Crossing System

2.5.1 Method and Results

In all the simulations previously mentioned the partial diallel was reduced by the systematic method illustrated by Figure 2.1. In practice, however, not all plant breeders would be able to obtain the incomplete diallel in this systematic way. This may be due to a variety of reasons ranging from F_1 seeds not germinating to a wish by the plant breeder to include some crosses which are not systematically required (and not to include others).

For this reason diallels were also simulated by randomly sampling the incomplete partial diallel. So as to have a basis of comparison with the previous set of simulation results, whilst at the same time simplifying the procedures, the following specifications were used:

- A thirty parent diallel was simulated.
- Only the eleven unique gca/sca variance ratios were simulated. These were 1024, 256, 64, 16, 4, 1, 0.25, 0.0625, 0.0156, 0.0039 and 0.0010.
- Five incomplete partial diallels were sampled by taking crosses from within the diallel at random. The number of crosses sampled corresponded to the number of crosses that would have been used in the 2, 4, 6, 8

and 10 crosses per parent incomplete partial diallels.

- Fifty diallels for each variance ratio were sampled in this way.

The results of these simulations are summarised in Tables 2.6 to 2.9. Table 2.6 shows the complete range of results obtained for the mean deviation statistics (cf. Table 2.5). The entire range is shown in this table in order to illustrate the relationship produced by equation ii.ii. As can be seen, equation ii.ii could be used to reduce Table 2.6 to a one line table. Table 2.7 and 2.8 compare the randomly sampled incomplete partial diallel to the systematically sampled incomplete partial diallel. They compare the mean deviations and the Spearman's rank correlation coefficients, respectively. Table 2.9, shows the probabilities of incorrectly ranking a parent in the 30 parent randomly selected incomplete partial diallel outside of the top five ranked parents. This table can be directly compared to Table 2.4.

2.5.2 Discussion

Table 2.6 demonstrates that even the randomly selected diallel is very stable when the number of crosses used is greatly reduced. The magnitude of the mean deviation is, however, three-fold that observed in the systematically reduced diallel (Table 2.7). This contrasts sharply with the gca rank change results (Tables 2.8 and 2.9) which indicate very little change between the two sampling methods; the probabilities given in Table 2.9 are almost identical with those in Table 2.4.

TABLE 2.6

Means and standard errors of the mean deviation of the predicted partial diallel and the incomplete partial diallel. A Thirty parent diallel was used and all gca:sca variance ratios are shown, for all incomplete partial diallels simulated. The incomplete diallel was obtained by taking a random set of crosses from the partial diallel.

RATIO	P.D.	10 C/P	8 C/P	6 C/P	4 C/P	2 C/P
1024	0.78±0.08	0.81±0.09	0.82±0.09	0.84±0.09	0.86±0.09	0.88±0.10
256	0.78±0.08	0.81±0.09	0.82±0.09	0.84±0.09	0.86±0.09	0.88±0.10
64	1.55±0.17	1.62±0.17	1.64±0.18	1.67±0.18	1.71±0.19	1.77±0.20
16	3.09±0.33	3.29±0.35	3.27±0.35	3.34±0.36	3.41±0.37	3.51±0.39
4	6.25±0.67	6.53±0.71	6.63±0.72	6.75±0.73	6.93±0.75	7.13±0.79
1	12.54±1.35	13.12±1.41	13.26±1.43	13.55±1.46	13.85±1.50	14.21±1.56
0.2500	12.41±1.34	13.01±1.41	13.17±1.43	13.37±1.46	13.74±1.50	14.15±1.57
0.0625	12.35±1.32	12.94±1.39	13.12±1.41	13.38±1.44	13.67±1.49	14.03±1.55
0.0156	12.58±1.35	13.13±1.42	13.29±1.44	13.52±1.47	13.83±1.50	14.26±1.57
0.0039	12.46±1.34	13.07±1.41	13.24±1.43	13.45±1.67	13.79±1.50	14.17±1.56
0.0010	25.00±2.68	26.15±2.82	26.57±2.86	27.05±2.92	27.58±3.00	28.45±3.11

TABLE 2.7

A comparison of the mean deviation from the systematically reduced incomplete partial diallel and the randomly reduced incomplete partial diallel. The gca:sca variance ratio of 256:16 is illustrated.

	P.D.	10 C/P	8 C/P	6 C/P	4 C/P	2 C/P
Systematically selected	0.96	0.99	1.00	1.01	1.03	1.06
Randomly selected	3.09	3.23	3.27	3.34	3.42	3.52

TABLE 2.8

A comparison of Spearman's rank correlation coefficients from the systematically reduced 30 parent incomplete partial diallel and the randomly reduced 30 parent incomplete partial diallel. The two variance ranges given for each case are 1024 to 1 and 0.25 to 0.0010 respectively.

	10 C/P	8 C/P	6 C/P	4 C/P	2 C/P
Systematically selected	0.99-0.96 0.90-0.61	0.99-0.95 0.88-0.55	0.99-0.94 0.85-0.50	0.99-0.93 0.82-0.44	0.99-0.91 0.78-0.37
Randomly selected	0.99-0.96 0.89-0.59	0.99-0.96 0.86-0.52	0.99-0.94 0.83-0.46	0.99-0.94 0.79-0.41	0.99-0.92 0.75-0.37

TABLE 2.9

Probability of the top five ranked parents being incorrectly ranked outside of the top five when the randomly reduced 30 parent incomplete partial diallel is compared to the 30 parent partial diallel. An incomplete partial diallel with 90 crosses is illustrated ($90/435 = 20.7\%$ of possible crosses).

Ranking	Variance Ratio					
	1024	256	64	16	4	1
1	0.0000	0.0000	0.0000	0.0016	0.0083	0.0450
2	0.0000	0.0000	0.0000	0.0033	0.0233	0.0817
3	0.0000	0.0000	0.0016	0.0150	0.0600	0.1466
4	0.0016	0.0066	0.0216	0.0550	0.1366	0.2433
5	0.0450	0.0733	0.1300	0.2050	0.3083	0.3800

This further exemplifies the advantages in calculating ranks of gca estimates rather than their numerical values. The random sampling of crosses in diallels markedly affects the precision of the gca estimate, as shown by Table 2.7, but it only marginally affects the gca ranks (Tables 2.4 and 2.9). As discussed in Chapter One, it is the ranking rather than the actual value of the gca estimates which is of primary importance to the plant breeder. Thus it is possible for the breeder to use randomly selected crosses from within a diallel instead of a systematic reduction of this diallel.

As a breeder is unlikely to choose crosses at random, and as information is lost when this is done, this would at first seem an unlikely method. However, as the definition of an incomplete partial diallel is so broad, previous sets of crosses made by a plant breeder may now be re-analysed, and treated as an incomplete partial diallel. If equation ii.ii is used to estimate the sca variance in a randomly sampled crossing system, then the increased mean deviation would yield a disproportionately large sca variance value. Although this is by no means desirable it at least deviates in the direction which makes the breeder more cautious rather than less cautious. That is, the deviation influences the breeder to use more parents and crosses rather than use less and risk everything on those few crosses.

The random case simulated is the worst case for the non-systematic sampling of the diallel. Other systematic designs, such as top-cross methods, would be expected to yield intermediate results between the systematic incomplete diallels presented here and the randomly reduced diallels. Systematic crossing designs

such as top cross methods would be expected to be extremely similar to the non-random method simulated here. However, it is hard to overlook the bias introduced when there are no crosses between the tester lines and between the lines to be tested. As the systematic design simulated here gives a large amount of accurate information, with the same number of crosses as would have to be used in other designs, and as bias within the parents tested is greatly (if not entirely) reduced, the use of such a design would seem appropriate for plant breeders.

3. A Twelve Parent Diallel of Triticale

3.1 Introduction

As discussed previously, diallels of various sizes and gca/sca variance ratios were simulated in order to measure their use as both a predictive and an evaluative tool of the plant breeder. Although this large range of diallels simulated is impossible to repeat in a biological experiment, it is possible to make a sample diallel in order to evaluate the advantages and disadvantages of the analysis suggested in Chapter Two.

Thus an experimental diallel was made, primarily in order that the stability or instability of the gca ranks and the F_1 predictions could be observed as the diallel was reduced. The results of this F_1 diallel will again be referred to in later chapters, in which breeding programmes will be discussed in the light of further analysis of generations beyond the F_1 .

3.2 Triticale

The plant materials used in the diallel were twelve hexaploid triticales (x Triticosecale Wittmak). Triticales are man-made hybrids of wheat (Triticum L.) and rye (Secale L.), initially formed by pollinating the wheat parent with rye pollen. For the production of hexaploid triticale a tetraploid (Durum, $n=14$) wheat is used. The hybrid plant has the A and B genome chromosomes from the tetraploid wheat and the R genome from the rye ($n=7$). this

haploid plant (ABR), having no homologues, is sterile. The chromosome number of this hybrid can be doubled by means of a chemical called colchicine; this gives a hexaploid plant (AABBRR, $n=21$) which is fertile.

Certain agronomic improvements may be made by backcrossing triticale to hexaploid wheat (AABBDD) to "mix" the alleles of the A and B genomes and the chromosomes the third genome. Some of these mixtures will become stabilised, i.e. have 21 pairs of homologues enabling regular meiosis. The effect of this backcrossing is that rye chromosome pairs are replaced by D genome chromosome pairs from the hexaploid wheat (e.g. 3D may replace 3R). The twelve triticales used, their origin and their chromosome complement (if known), are listed in Table 3.1. The main observable phenotypic differences between the twelve parental lines are also shown in this table. (Sterility in the F_1 's between these lines was low enough to be most unlikely to influence g.c.a.)

The choice of triticale as the test crop was a subjective one. The only criterion set down by the simulations was that the crop should be self-pollinating. As triticale is a new crop it has not been subjected to large selection pressures and thus its genetic base is potentially extremely broad. In a study such as this, it was considered advantageous to have as wide a range of genetic material amongst the parental lines as possible. Also, as triticale has many of the agronomic features of other cereal crops, it does not have to be managed in a markedly different way to wheat (for example). Most importantly, however, as a new crop it is one in which parental evaluation by the plant breeder is very important, as no history of the effectiveness of different triticale parental lines is available. (To a limited extent this

Table 3.1

The Twelve parents used in the triticales diallel described in Chapter Three.

Number	Name	Origin (Parentage)	Rye Chromosomes Missing	Distinguishing Traits
T28		Mexico (Armadillo PM-105)	2R	
T31	Camel	Mexico (Inia-Arm"S")	2R,7/4R	
T33	Drira	Mexico (D-R44/Inia-Rye x Arm "S")	None	Long droopy head
T34	Cinnamon	Mexico (Tcl Maya*II-Arm"S")	2R,7/4R	
T58	Badger	Mexico (Outcross Blk Sel.)	Unknown	
T106	Cachirulo	Spain (Unknown)	Unknown	Very tall late maturing
T246		Mexico ² (AUS 15898)	Unknown	
T686		Mexico ² (MayaII Arm"S")	2R	Awnless
T702		Mexico ² (Koala x MayaII - Arm"S")	Unknown	Short, slightly compact head
T710		Mexico ² (D ² 28-Velegas Prot.Alts. x Arm "S"/Koala)	Unknown	
T896		Aust.Selection ³ (Unknown)	Unknown	Waxless
T937	Beagle	Mexico (UM-"S"-Tcl Bulk)	None	Long droopy head

1 Merker, 1975.

2 Further selection at Tamworth, N.S.W.

3 Further selection at Perth, W.A.

information is available to breeders of other cereals.)

It was also felt that the use of triticale in this breeding experiment might permit the evaluation of the sensitivity of diallel analysis to chromosomal abnormalities (meiotic irregularities) caused by the mixture of R and D genome chromosomes. This mixture of the R and D genome chromosomes would be different for each F_1 involved in the diallel and thus this mixture would mainly affect the sca values for the crosses. If the analysis is still effective despite probable chromosomal abnormalities, then meiotically regular material would be expected to be at least as informative.

This "sensitivity" of the diallel analysis will also be tested by the fact that triticale is not 100% self-pollinating. The degree of outcrossing in triticale may vary between lines and could range from 1 or 2% to as much as 20% (Driscoll, pers. comm.).

3.3 Production of the Diallel

All crosses were made in 1976. The twelve parents were grown under glasshouse conditions, as well as in an irrigated birdproofed field site. Three planting times were used in both the glasshouse and the field, in order that crosses could be made between the early and late maturing genotypes.

As the partial diallel analysis method ^{which was} used assumes that there are no reciprocal effects, male and female parents were used according to the availability of pollen and spikes for emasculation.

Table 3.2 shows the crosses made with their assigned numbers. These numbers are not consecutive as in order to ensure that enough seed was produced more than one cross with the same parents was often made.

Table 3.2

Table of crosses used for the partial diallel. Notation is in the form of:

Cross Number (female parent x male parent).

X76-700	(T31	x	T28)	X76-761	(T702	x	T34)
X76-702	(T33	x	T28)	X76-763	(T34	x	T710)
X76-705	(T34	x	T28)	X76-765	(T896	x	T34)
X76-707	(T58	x	T28)	X76-766	(T34	x	T937)
X76-708	(T106	x	T28)	X76-767	(T58	x	T106)
X76-709	(T246	x	T28)	X76-768	(T58	x	T246)
X76-711	(T686	x	T28)	X76-770	(T58	x	T686)
X76-713	(T702	x	T28)	X76-771	(T58	x	T702)
X76-714	(T710	x	T28)	X76-773	(T710	x	T58)
X76-715	(T896	x	T28)	X76-775	(T896	x	T58)
X76-717	(T28	x	T937)	X76-776	(T58	x	T937)
X76-718	(T33	x	T31)	X76-778	(T246	x	T106)
X76-721	(T31	x	T34)	X76-779	(T686	x	T106)
X76-722	(T58	x	T31)	X76-780	(T106	x	T702)
X76-725	(T31	x	T106)	X76-781	(T106	x	T710)
X76-727	(T31	x	T246)	X76-784	(T896	x	T106)
X76-729	(T686	x	T31)	X76-785	(T106	x	T937)
X76-730	(T702	x	T31)	X76-786	(T246	x	T686)
X76-733	(T896	x	T31)	X76-787	(T246	x	T702)
X76-734	(T31	x	T937)	X76-789	(T710	x	T246)
X76-735	(T34	x	T33)	X76-790	(T896	x	T246)
X76-737	(T33	x	T58)	X76-791	(T246	x	T937)
X76-742	(T33	x	T106)	X76-793	(T702	x	T686)
X76-744	(T33	x	T246)	X76-795	(T686	x	T710)
X76-745	(T686	x	T33)	X76-797	(T896	x	T686)
X76-747	(T702	x	T33)	X76-798	(T686	x	T937)
X76-748	(T710	x	T33)	X76-801	(T710	x	T702)
X76-750	(T896	x	T33)	X76-802	(T702	x	T896)
X76-751	(T33	x	T937)	X76-804	(T702	x	T937)
X76-752	(T58	x	T34)	X76-805	(T896	x	T710)
X76-754	(T34	x	T106)	X76-806	(T710	x	T937)
X76-755	(T34	x	T246)	X76-808	(T896	x	T937)
X76-758	(T34	x	T686)	X76-810	(T710	x	T31)

The F_1 diallel referred to in this chapter was grown from residual seed in 1978, in the same season in which the F_4 generation was grown. This was done in order that comparisons between the results of the F_1 diallel and the later generation families could be made, with no seasonal interaction. Such comparisons will be drawn in later chapters. The 1977 season was only used to advance the generations, and no data were collected in the F_2 and F_3 plants.

The F_1 diallel was grown in a birdproofed enclosure with no supplementary irrigation. The sixty-six F_1 's and the twelve parent lines were replicated five times. They were split into five blocks with a single replicate in each block, and each block was separately randomised. Eight seeds from each of the seventy-eight genotypes were placed in peat pellets and germinated in a glasshouse. The five most vigorous plants of each genotype were then planted in the field (vigour was subjectively assessed). Three crosses had less than five germinations even when more germinations were attempted; in the field layout their numbers were made up to five by supplementing them with a parental variety. This was done in order to regulate competitive effects which may occur between plants simply as a result of plant numbers. These supplementary plants were not harvested. The plants were placed on a 4.2 x 8.4 metre grid with a 30cm square spacing between plants. This spacing ensured that competitive effects would be minimised, and allowed each plant to obtain the nutrients, water and space it required.

Unfortunately, a disease struck this experiment, badly damaging

some plants and affecting about 30% of the total. These diseased plants were recorded and later discarded when it was realised that yield and other observed traits were affected. This had the effect of severely limiting the degree of replication. Instead of five replicates of each genotype many were reduced to three and some to only one or two. Because of this and the ensuing statistical difficulties in analysing such small and varied replication factors, the data were analysed in the form of means for each genotype rather than as individual replicates.

As the diseased plants occurred in clusters through the experiment and were randomly distributed throughout the genotypes present, it appeared that there was no interaction between the disease and the various genotypes.

3.4 Observed Characteristics

The following measurements were taken on all the F_1 and parental plants:-

1. Days to Heading: the time taken from germination to the complete emergence of the first head. Measured to the nearest week.
2. Days to Anthesis: the time taken from germination to the emergence of the first anthers from the florets. This character was also measured to the nearest week. Both this character and one above are indications of the maturation potential for the plant. However, they can be measured exactly rather than by the more subjective decision of determining when the plant is ready for harvesting. Also, as all the the plants were sown at the same time and grown under the same conditions these two characters act as indicators of daylength sensitivity and/or vernalization requirements.

3. Height: the distance (cm.) from the soil to the top of the tallest tiller. This character is important because of the large range of heights amongst triticales; some are extremely short, whilst others are so tall that that lodging is a problem. It is worth noting that although lodging of tall varieties is observed in triticales, it seems to be less serious in this crop than in wheat and other cereals because of the greater straw strength.

4. Number of Productive Heads: this is a component of yield of the plant; a greater potential for yield is obtained when there is a large number of productive heads. Only mature heads with seed were counted; this prevented secondary flushes of tillers from affecting the results.

5. Total Biological Weight: the weight of the entire plant, excluding the root system, measured to the nearest gram. This is used in conjunction with the grain yield of the plant to determine an efficiency factor - (harvest index).

6. Head Length (TT): this character was measured by observing the length of the tallest tiller's (TT) spike. It was measured to the nearest centimetre. Like character four, this character may influence the capability of the plant to produce more seed. The tallest tiller was used for this character, and others to follow, as

this tiller is usually the most vigorous and thus can be used by the plant breeder to approximate the optimum potential for the plant.

7. Number of Spikelets (TT): measured on tallest tiller (TT) only. Used with characters six, eight and nine, this gives an indication of the efficiency with which the plant utilizes its resources. A plant with thirty spikelets but only twenty seeds is no better than, and perhaps worse than, one with ten spikelets and twenty seed.
8. Number of Seed (TT): the number of seeds on the tallest tiller.
9. Weight of Seed (TT): the weight (gm) of seed on the primary tiller. This helps to show the capability of a plant more clearly than would an averaging of the seed from all the spikes of a plant. However, if the plant has many other tillers which produce little or no seed, this potential may be biased upward.
10. Grain Yield: the weight (gm) of all the seed on the plant. Increase in yield is probably the chief objective of most plant breeders - thus this character is commercially the most important.
11. Harvest Index: as well as the ten observed characters above, harvest index was also calculated from characters ten and five above:

Harvest Index (H.I.) = Yield/Total Biological Weight

This character is often cited by plant breeders as a powerful indicator of a plant genotype's potential for high yielding in later generations (see Chapter Six).

As stated earlier, the above measurements were made on all the replicates and then a mean value was obtained. These mean values are presented in Appendix II.

3.5 Results

The partial diallel was analysed in the same way as were the simulated diallels in the previous chapter. The ranks of the gca's were calculated for the partial diallel and then compared to the various incomplete partial diallels. Also, the gca estimates were used to calculate an estimate for each observation (equation i.iii). This estimated value was used to calculate a mean absolute residual value for the diallel, again in the same way as described in Chapter Two. The results of these analyses for each of the measured characters are tabulated in Tables 3.3.1 to 3.3.11. The ranks of the parental lines for each character are also included in these tables.

3.6 Discussion

In presenting the results of the F_1 diallel in this Chapter, discussion will be largely limited to the appraisal of the F_1 analysis techniques simulated in Chapter Two. Wider applications of the F_1 diallel analysis as well as the correlation results of the F_1 characteristics will be presented and discussed in Chapter

Table 3.3.1

F1. Character 1 Days to Heading

Mean 116.77 gca variance 21.6 gca/sca variance ratio 2.13
S.D. 7.32 sca variance 10.17

Parent	gca Ranks						Rank of Parent
	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p	
T28	10	10	10	10	10	8(2)	9
T31	9	9	9	9	9	10(1)	10(1)
T33	5	5	5	5	4(1)	3(2)	3(2)
T34	12	12	12	12	12	12	12
T58	8	8	8	8	8	9(1)	8
T106	1	1	1	1	1	1	1
T246	3	4(1)	3	2(1)	2(1)	2(1)	2(1)
T686	11	11	11	11	11	11	11
T702	6	6	6	6	6	7(1)	4=6
T710	2	2	2	3(1)	5(3)	4(2)	4=6(3)
T896	7	7	7	7	7	6(1)	4=6(2)
T937	4	3(1)	4	4	3(1)	5(1)	7(3)
Mean of Abs. Residuals	2.62	2.67	2.69	2.72	2.73	2.97	
S.D. of Abs. Residuals	1.84	1.84	1.81	1.86	1.82	2.25	

Table 3.3.2

F1. Character 2 Days to Anthesis

Mean 130.57 gca variance 12.60 gca/sca variance ratio 1.81
S.D. 5.67 sca variance 6.97

Parent	gca Ranks						Rank of Parent
	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p	
T28	11	10(1)	10(1)	10(1)	10(1)	8(3)	9 (2)
T31	8	8	8	8	8	10	10(2)
T33	2	3(1)	3(1)	2	2	2	2
T34	12	12	12	12	12	12	12
T58	9	9	9	9	9	9	7=8(1)
T106	1	1	1	1	1	1	1
T246	5	5	5	4(1)	4(1)	4(1)	4(1)
T686	10	11(1)	11(1)	11(1)	11(1)	11(1)	11(1)
T702	6	6	6	6	7(1)	7(1)	7=8(1)
T710	3	2(1)	2(1)	3	3	3	3
T896	7	7	7	7	6(1)	5(2)	5(2)
T937	4	4	4	5(1)	5(1)	6(2)	6(2)
Mean of Abs. Residuals	2.15	2.16	2.18	2.26	2.33	2.43	
S.D. of Abs. Residuals	1.54	1.56	1.57	1.57	1.57	2.00	

Table 3.3.3

F1	Character 3	<u>Height</u>					
Mean	125.35	gca variance		80.60	gca/sca variance ratio		1.75
S.D.	14.40	sca variance		46.04			
Parent		gca Ranks					Rank of
	(Bracketed numbers indicate deviation from P.D.ranks)						Parent
	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p	
T28	8	7(1)	8	8	8	8	8
T31	7	8(1)	7	6(1)	7	5(2)	6(1)
T33	3	4(1)	3	5(2)	4(1)	6(3)	7(4)
T34	9	9	9	9	9	10(1)	9
T58	4	5(1)	5(1)	4	5(1)	3(1)	2(2)
T106	1	1	1	1	1	1	1
T246	10	10	10	10	10	9(1)	10
T686	11	11	11	12(1)	12(1)	12(1)	12(1)
T702	12	12	12	11(1)	11(1)	11(1)	11(1)
T710	5	3(2)	4(1)	3(2)	3(2)	4(1)	3(2)
T896	2	2	2	2	2	2	4(2)
T937	6	6	6	7(1)	6	7(1)	5(1)
Mean of Abs. Residuals	5.16	5.25	5.33	5.63	5.63	6.62	
S.D. of Abs. Residuals	4.45	4.42	4.43	4.59	4.60	5.05	

Table 3.3.4

F1	Character 4	<u>Number of Productive Heads</u>					
Mean	10.48	gca variance		0.76	gca/sca variance ratio		0.38
S.D.	1.88	sca variance		2.00			
Parent		gca Ranks					Rank of
	(Bracketed numbers indicate deviation from P.D.ranks)						Parent
	P.D.	10/c/p	8c/p	6c/p	4c/p	2c/p	
T28	12	12	12	12	12	9(3)	7=8(4)
T31	7	8(1)	7	5(2)	7	7	10(3)
T33	2	2	2	2	1(1)	2	5=6(3)
T34	8	7(1)	10(2)	11(3)	10(2)	8	12(4)
T58	11	11	11	9(2)	6(5)	10(1)	7=8(3)
T106	1	1	1	1	2(1)	1	1
T246	5	5	4(1)	4(1)	4(1)	4(1)	4(1)
T686	10	10	8(2)	10	9(1)	11(1)	11(1)
T702	3	3	3	3	3	3	2(1)
T710	6	6	6	6	8(2)	12(6)	3(3)
T896	9	9	9	7(2)	11(2)	5(4)	5=6(3)
T937	4	4	5(1)	8(4)	5(1)	6(2)	9(5)
Mean of Abs. Residuals	1.14	1.14	1.17	1.19	1.18	1.19	
S.D. of Abs. Residuals	0.84	0.86	0.84	0.89	0.90	0.96	

Table 3.3.5

F1	Character 5		<u>Total Biological Weight</u>				
Mean	104.37	gca variance	331.38	gca/sca variance ratio 0.80			
S.D.	32.79	sca variance	412.51				
Parent	gca Ranks						Rank of Parent
(Bracketed numbers indicate deviation from P.D.ranks)							
	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p	
T28	12	12	12	12	12	11(1)	9(3)
T31	11	11	11	8(3)	7(4)	8(3)	10(1)
T33	2	2	2	2	2	3(1)	3(1)
T34	10	10	9(1)	10	10	9(1)	12(2)
T58	7	6(1)	7	5(2)	6(1)	6(1)	6(1)
T106	1	1	1	1	1	1	1
T246	5	5	5	7(2)	5	5	5
T686	8	9(1)	10(2)	11(3)	11(3)	12(4)	11(3)
T702	6	7(1)	6	6	8(2)	7(1)	8(2)
T710	9	8(1)	8(1)	9	9	10(1)	4(5)
T896	4	3(1)	3(1)	3(1)	3(1)	2(2)	2(2)
T937	3	4(1)	4(1)	4(1)	4(1)	4(1)	7(4)
Mean of Abs.							
Residuals	16.19	16.32	11.37	16.92	17.03	18.00	
S.D. of Abs.							
Residuals	12.22	12.38	12.33	13.32	12.93	13.69	

Table 3.3.6

F1	Character 6		<u>Head Length (TT)</u>				
Mean	13.80	gca variance	2.08	gca/sca variance ratio 1.72			
S.D.	2.32	sca variance	1.21				
Parent	gca Ranks						Rank of Parent
(Bracketed numbers indicate deviation from P.D.ranks)							
	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p	
T28	12	12	12	12	12	12	11(1)
T31	11	11	11	11	10(1)	11	12(1)
T33	1	1	2(1)	2(1)	2(1)	2(1)	2(1)
T34	6	6	6	6	6	7(1)	7(1)
T58	10	10	10	9(1)	11(1)	10	10
T106	3	4(1)	4(1)	4(1)	4(1)	3	3=4
T246	7	7	7	7	7	6(1)	6(1)
T686	5	5	5	5	5	5	5
T702	8	8	8	8	8	8	9(1)
T710	9	9	9	10(1)	9	9	8(1)
T896	4	3(1)	3(1)	3(1)	3(1)	4	3=4
T937	2	2	1(1)	1(1)	1(1)	1(1)	1(1)
Mean of Abs.							
Residuals	0.80	0.81	0.82	0.83	0.81	0.90	
S.D. of Abs.							
Residuals	0.76	0.77	0.78	0.79	0.80	0.90	

Table 3.3.7

F1	Character 7		<u>No. of Spikelets (TT)</u>				
Mean	27.76	gca variance	5.48	gca/sca variance ratio 2.20			
S.D.	3.67	sca variance	2.49				
Parent	gca Ranks						Rank of Parent
	(Bracketed numbers indicate deviation from P.D.ranks)						
	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p	
T28	12	12	12	12	12	12	11=12
T31	11	11	11	11	11	11	11=12
T33	3	3	3	3	3	3	5(2)
T34	8	8	8	9(1)	8	8	8=9
T58	9	9	9	8(1)	9	9	8=9
T106	1	1	1	1	1	1	1
T246	5	5	5	5	5	5	3=4(1)
T686	10	10	10	10	10	10	10
T702	7	7	7	7	7	7	7
T710	6	6	6	6	6	6	6
T896	4	4	4	4	4	4	3=4
T937	2	2	2	2	2	2	2
Mean of Abs. Residuals	1.20	1.21	1.22	1.24	1.25	1.33	
S.D. of Abs. Residuals	1.06	1.10	1.12	1.11	1.15	1.23	

Table 3.3.8

F1	Character 8		<u>Number of Seed (TT)</u>				
Mean	72.83	gca variance	64.53	gca/sca variance ratio 0.28			
S.D.	19.04	sca variance	233.35				
Parent	gca Ranks						Rank of Parent
	(Bracketed numbers indicate deviation from P.D.ranks)						
	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p	
T28	10	10	10	10	10	10	10
T31	7	8(1)	8(1)	9(2)	7	8(1)	9(2)
T33	3	3	3	3	4(1)	4(1)	4=5(1)
T34	5	5	4(1)	6(1)	6(1)	6(1)	6(1)
T58	8	6(2)	6(2)	5(3)	5(3)	5(3)	8
T106	11	12(1)	12(1)	12(1)	12(1)	12(1)	12(1)
T246	4	4	5(1)	4	3(1)	3(1)	1(3)
T686	6	7(1)	7(1)	7(1)	8(2)	11(5)	11(5)
T702	2	2	2	2	2	1(1)	2
T710	9	9	9	8(1)	9	9	7(2)
T896	12	11(1)	11(1)	11(1)	11(1)	7(5)	4=5(7)
T937	1	1	1	1	1	2(1)	3(2)
Mean of Abs. Residuals	12.55	12.50	12.63	12.68	13.14	14.19	
S.D. of Abs. Residuals	8.74	9.00	9.09	9.74	9.52	11.63	

Table 3.3.9

F1	Character 9	<u>Wt. of Seed (TT)</u>					
Mean	23.4	gca variance	13.32	gca/sca variance ratio 0.21			
S.D.	9.45	sca variance	62.74				
Parent	P.C.	gca Ranks (Bracketed numbers indicate deviation from P.D.ranks)					Rank of Parent
		10c/p	8c/p	6c/p	4c/p	2c/p	
T26	10	10	10	11(1)	12(2)	9(3)	10
T31	8	9(1)	8	7(1)	6(2)	7(1)	7(1)
T33	2	1(1)	1(1)	1(1)	1(1)	1(1)	1(1)
T34	9	8(1)	7(2)	8(1)	9	8(1)	12(3)
T58	7	3(4)	6(1)	5(2)	3(4)	2(5)	5(2)
T106	4	7(3)	9(5)	6(2)	7(3)	11(7)	4
T246	6	5(1)	4(2)	4(2)	4(2)	6	3(3)
T686	5	6(1)	5	9(4)	8(3)	10(5)	11(6)
T702	3	4(1)	3	3	5(2)	5(2)	9(6)
T710	11	12(1)	11	10(1)	11	12(1)	8(3)
T896	12	11(1)	12	12	10(2)	4(8)	2(10)
T937	1	2(1)	2(1)	2(1)	2(1)	3(2)	6(5)
Mean of Abs. Residuals	6.44	6.48	6.49	6.56	6.67	7.37	
S.D. of Abs. Residuals	4.61	4.69	4.79	4.91	4.80	5.55	

Table 3.3.10

F1	Character 10	<u>Yield</u>					
Mean	27.32	gca variance	16.08	gca/sca variance ratio 0.21			
S.D.	10.36	sca variance	75.21				
Parent	P.D.	gca Ranks (Bracketed numbers indicate deviation from P.D.ranks)					Rank of Parent
		10c/p	8c/p	6c/p	4c/p	2c/p	
T28	10	10	10	11(1)	12(2)	9(3)	10
T31	9	9	8(1)	6(3)	6(3)	7(2)	8(1)
T33	2	1(1)	1(1)	1(1)	1(1)	1(1)	1(1)
T34	8	7(1)	7(1)	8	9(1)	8	12(4)
T58	7	3(4)	5(2)	5(2)	3(4)	2(5)	5(2)
T106	5	8(3)	9(4)	7(2)	8(3)	11(6)	4(1)
T246	6	5(1)	4(2)	4(2)	4(2)	6	3(3)
T686	4	6(2)	6(2)	9(5)	7(3)	10(6)	11(7)
T702	3	4(1)	3	3	5(2)	5(2)	9(6)
T710	11	12(1)	11	10(1)	11	12(1)	7(4)
T896	12	11(1)	12	12	10(2)	4(8)	2(10)
T937	1	2(1)	2(1)	2(1)	2(1)	3(2)	6(5)
Mean of Abs. Residuals	7.11	7.16	7.16	7.23	7.36	8.09	
S.D. of Abs. Residuals	4.97	5.07	5.19	5.31	5.19	6.15	

Table 3.3.11

F1	Character	11	Harvest Index				
Mean	0.269	gca variance	0.0018	gca/sca variance ratio			0.54
S.D.	0.084	sca variance	0.0034				
Parent			gca Ranks				Rank of
	(Bracketed	numbers	indicate deviation from P.D.ranks)				Parent
	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p	
T28	7	9(2)	9(2)	9(2)	9(2)	5(2)	5(2)
T31	5	6(1)	5	8(3)	6(1)	6(1)	2(3)
T33	9	8(1)	8(1)	7(2)	7(2)	4(5)	1(8)
T34	4	5(1)	3(1)	4	8(4)	9(5)	9(5)
T58	8	4(4)	6(2)	6(2)	3(5)	1(7)	8
T106	11	12(1)	12(1)	12(1)	12(1)	12(1)	12(1)
T246	6	7(1)	7(1)	3(3)	5(1)	8(2)	4(2)
T686	3	2(1)	4(1)	5(2)	4(1)	7(4)	7(4)
T702	2	1(1)	1(1)	1(1)	1(1)	2	6(4)
T710	10	10	10	10	10	10	11(1)
T896	12	11(1)	11(1)	11(1)	11(1)	11(1)	10(2)
T937	1	3(2)	2(1)	2(1)	2(1)	3(2)	3(2)
Mean of Abs.							
Residuals	0.046	0.047	0.047	0.047	0.049	0.051	
S.D.of Abs.							
Residuals	0.034	0.035	0.036	0.036	0.036	0.043	

Six.

3.6.1 Observed Variance Ratios

The eleven characters measured can be divided into three main groups - five with a variance ratio greater than one (range 2.20 to 1.7), one with a variance ratio near one (0.80) and five with a variance ratio of less than one (range 0.52 to 0.21). As this variance ratio should dictate the stability of the incomplete partial diallel analysis, the eleven characters will be ranked according to this statistic in order to simplify their presentation in further tables.

Table 3.4 shows the order of the eleven characters with their corresponding variance ratios.

3.6.2 Rank Changes

In observing the rank changes from Tables 3.3.1 to 3.3.11 it is clear that the ranks do become less stable as the gca/sca variance ratio decreases. Table 3.5 shows the percentage of gca estimates that change in rank by 0, 1, 2 and 3. As these cannot be directly compared to the 20 parent diallel illustrated in Tables 2.3.1 to 2.3.4, the values obtained for the fifteen parent simulated diallels, which should be a closer approximation, are also shown in this table. As the eight and ten crosses per parent incomplete diallels require too many crosses for most plant breeding purposes, and for the sake of brevity, only the partial diallel and the two, four and six crosses per parent diallels have been included in this table. The remaining data may be obtained in

Table 3.4

The gca/sca variance ratios of the eleven characters observed in the twelve parent triticales diallel.

No.	Character Name	gca/sca variance ratio
7	Number of Spikelets	2.20
1	Days to heading	2.13
2	Days to Anthesis	1.81
3	Height	1.75
6	Head Length	1.72
5	Total Biological Wt.	0.83
11	Harvest Index	0.54
4	Number of Prod. Heads	0.38
8	Number of Seed	0.28
10	Yield	0.21
9	Weight of Seed	0.21

Table 3.5

The percentage of parents in the 12 parent triticale diallel which did not change in rank by more than four when the partial diallel was reduced. Bracketed numbers represent the results from the 15 parent simulated diallel.

Chr.	I.P.D.	Var.	Rank Changes				
			0	≤1	≤2	≤3	≤4
7	6c/p	2.20	83.0(65.6)	100(93.0)	100(98.9)	100(99.9)	100(100)
	4c/p	(4.0)	100(59.7)	100(90.1)	100(97.5)	100(99.5)	100(99.9)
	2c/p		100(54.3)	100(85.6)	100(96.3)	100(99.1)	100(99.8)
1	6c/p	2.13	83.3	100	100	100	100
	4c/p		66.6	91.6	91.6	100	100
	2c/p		25.0	75.0	100	100	100
2	6c/p	1.81	66.6	100	100	100	100
	4c/p		50.8	100	100	100	100
	2c/p		50.0	75.0	91.6	100	100
3	6c/p	7.75	50.0	83.3	100	100	100
	4c/p		58.3	83.3	100	100	100
	2c/p		25	83.3	91.6	100	100
6	6c/p	1.72	50.0	100	100	100	100
	4c/p		50.0	100	100	100	100
	2c/p		66.6	100	100	100	100
5	6c/p	0.80	50.0(45.2)	66.6(80.3)	83.3(93.4)	100(97.9)	100(99.3)
	4c/p	(1.0)	50.0(38.7)	75.0(74.5)	83.3(90.0)	91.6(96.2)	100(98.8)
	2c/p		16.6(33.7)	75.0(68.4)	83.3(84.9)	91.6(93.2)	100(97.2)
11	6c/p	0.54)	16.6(31.8)	50.0(63.8)	83.3(82.1)	100(91.3)	100(96.1)
	4c/p	(0.25)	8.3(25.9)	66.6(56.7)	83.3(75.8)	83.3(87.3)	91.6(93.3)
	2c/p		16.6(22.6)	41.6(51.0)	66.6(69.4)	66.6(82.0)	75.0(89.7)
4	6c/p	0.38	50.0	58.3	83.3	91.6	100
	4c/p		25.0	66.6	91.6	91.6	91.6
	2c/p		41.6	66.6	75.0	83.3	91.6
8	6c/p	0.28	41.6	83.3	91.6	100	100
	4c/p		41.6	83.3	91.6	100	100
	2c/p		16.6	75.0	75.0	83.3	83.3
10	6c/p	0.21	25.0	58.3	83.3	91.6	91.6
	4c/p		8.3	33.3	66.6	91.6	100
	2c/p		16.6	33.3	58.3	66.6	66.6
9	6c/p	0.21	16.6	66.6	91.6	91.6	100
	4c/p		16.6	33.6	75.0	91.6	100
	2c/p		8.3	41.6	58.3	66.6	66.6

this form from Tables 3.3.1 to 3.3.11. Table 3.5 shows that the observed diallel conforms to the simulated diallels illustrated in Chapter Two. As the gca/sca variance ratio decreases the stability of the ranks also decreases; however, even the gca/sca variance ratios of less than one are comparatively stable. This is especially true for the six and four crosses per parent cases.

the higher stability of ranks in the observed diallel as compared to the simulated diallel may be accounted for by the differences in diallel sizes: the observed diallel having only twelve parents, it has a higher percentage of crosses when the incomplete partial diallel is compared to the partial diallel than does the simulated fifteen parent diallel (when the same number of crosses per parent are used).

In the previous chapter it was shown that there was a low probability of incorrectly ranking a parental gca outside of the top five. These results were echoed in the observed diallel. Tables 3.3.1 to 3.3.11 can be used to show exactly how many parents were incorrectly ranked out of the top five. For all the characters with a gca/sca variance ratios of greater than one, none of the top five parents was ranked outside of the top five when more than two crosses per parent were used. Even when the two crosses per parent case is observed, only two cases occur when a parent is incorrectly ranked outside of the top five (a ranking of 3 went to 6 and one of 5 went to 6). When the gca/sca variance ratio drops below unity the frequency of these occurrences increases. The implications of this and ways in which a plant breeder could compensate for it will be discussed in the conclusion of this chapter.

If one considers the best ranked parents, then in fact the highest ranked gca value parent has also the highest ranked parental mean for most of the characters measured. However, as at least two or three parents would be needed for a breeding program, it becomes apparent that apart from the top ranking parent the ranks change markedly when the gca ranks are compared to the parent mean ranks.

3.6.2.1 Ranking by Parental Means

One of the arguments against the use of incomplete partial diallels is that if the incomplete partial diallel analysis relies solely on a high general combining ability value, then the ranks of the parental lines themselves, for the characters measured, may be just as informative as the ranks of their gca values.

This raises a number of issues. The main one is the assumption inherent in the argument that the ranking of the parental means will be the same as the ranking of the parental gca values. If this is not true, and Tables 3.3.1 to 3.3.11 show that it is in fact not true, then it would be hoped that the ranking of the parental means is at least as accurate as the ranking of the gca estimates in the incomplete partial diallels when they are compared to the partial diallel. Table 3.6 summarises the percentages of parents in the diallel whose rank (based on the parental mean only) does not change as compared to the gca ranks for the same characters in the partial diallel, and those which change in rank by up to four. A comparison of this Table with Table 3.5 shows that the incomplete partial diallels are more stable in terms of rank changes than are the parental means.

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This drawback is compounded by the lack of information on the inheritance of characters from each of the parents that results if a crossing system is not used for evaluation of the parents. Without making crosses with the parental lines, specific combining ability effects of the parental lines may be falsely interpreted by the plant breeder as general combining ability effects. For

Table 3.6

The percentage of parents in the observed 12 parent triticales diallel which did not change rank by more than four when the ranks of the parental means are compared to the gca ranks from the partial diallel analysis.

Char.	gca/sca Var. Ratio	Rank Changes				
		0	≤1	≤2	≤3	≤4
7	2.20	83.3	91.6	100.0	100.0	100.0
1	2.13	50.0	66.6	83.3	100.0	100.0
2	1.81	33.3	66.6	100.0	100.0	100.0
3	1.75	33.3	66.6	91.6	91.6	100.0
6	1.72	33.3	100.0	100.0	100.0	100.0
5	0.80	16.6	41.6	66.6	83.3	91.6
11	0.54	8.3	25.0	58.3	66.6	83.3
4	0.38	8.3	33.3	33.3	75.0	91.6
8	0.28	25.0	50.0	75.0	83.3	83.3
10	0.21	8.3	33.3	41.6	50.0	66.6
9	0.21	16.6	33.3	41.6	66.6	66.6

example, a parent's yield is different from its ability to pass its yielding ability on to its offspring, either in all crosses (GCA) or in a specific one (SCA). This is clearly shown in Table 3.3.10 where the top-ranked parent for GCA (T937) was only ranked sixth when the parents were ranked according to their mean yields.

3.6.3 Estimation of Specific Combining Abilities

Using equation ii.ii and Table 2.5 from the previous chapter the mean of the absolute value of the deviations in the observed diallels may be used to estimate the specific combining ability variances for the characters measured. Once the sca variance has been estimated, the observed variance of the gca estimates may be used to obtain an estimated gca/sca variance.

Table 3.7 shows the results of these estimations for the eleven characters measured. The observed gca/sca variance ratios were obtained by analysing the partial diallel in order to obtain sca estimates and hence an sca variance. This analysis was carried out according to the method given by Griffing (1956a). The values given in the 15 parent diallel of Table 2.5 were then used to calculate the gca/sca variance ratios. The first line of numbers for each character is the gca/sca value derived when the mean of the absolute values of the deviation is calculated for all the crosses in the diallel. The bracketed numbers represent the gca/sca ratio when only the crosses sampled in the incomplete partial diallel are used to calculate a mean of the absolute values of the deviations.

As can be seen from this table, the variance ratios are

Table 3.7

The gca/sca variance ratios predicted from the mean of the absolute values of deviations (Observed - Predicted) of the twelve parent triticales diallel. The bracketed numbers indicate the calculation of the mean of the absolute deviations were from the crosses sampled.

Character	Observed gca/sca var.ratio	Estimated gca/sca variance ratio		
		P.D.	6 crosses / parent	4 crosses /parent
7	2.20	2.23	2.15 (2.82)	2.15 (3.80)
1	2.13	1.76	2.10 (2.24)	2.10 (2.14)
2	1.81	1.57	1.71 (1.73)	1.51 (1.71)
3	1.75	1.91	1.83 (2.12)	1.97 (1.69)
6	1.72	1.81	1.67 (1.90)	1.86 (1.73)
5	0.80	0.72	0.74 (0.77)	0.89 (0.72)
11	0.54	0.52	0.61 (0.65)	0.60 (0.56)
4	0.38	0.33	0.26 (0.38)	0.24 (0.29)
8	0.28	0.27	0.31 (0.34)	0.32 (0.30)
10	0.21	0.19	0.13 (0.13)	0.15 (0.12)
9	0.21	0.19	0.12 (0.12)	0.18 (0.19)

accurately predicted from the two incomplete partial diallel sizes illustrated. The four and six crosses per parent diallels were used as these gave accurate results to the plant breeder without the necessity of a comparatively large number of crosses per parent. Thus, because fewer crosses are needed, more parents could be included in the diallel.

The bracketed numbers (that is, the estimates when only the crosses made are used in the calculations) accurately emulate the information which would be obtained by a plant breeder (the whole idea of using the incomplete partial diallel would be defeated if the mean of the absolute values of the deviations needed to be calculated from the partial diallel). However, Table 2.5 was made up by comparing the observed values calculated from the gca estimates of the incomplete partial diallel to the observed estimates from the partial diallel. For this reason the bracketed estimates are not quite as accurate as the other estimates. Unfortunately a table such as Table 2.5 could not be drawn up to simulate the estimate when only the sampled crosses were used (bracketed) as this information was not stored during the simulations. Presumably Table 2.5 would vary slightly had this criterion been used for the estimations of the mean of the absolute value of the deviations. This may have made the bracketed estimates in Table 3.7 more accurate than the other estimates. However the differences between these two estimates are marginal and this slight loss of accuracy to the plant breeder should not change any decisions made using these estimates. As a result of the above factors it is apparent that a repetition of the simulations in the future could be used to obtain this missing information, which should give slightly more accurate results than

those in Table 3.7. Although this may not be a necessary repetition, it is nevertheless desirable.

It should be noted that, in the simulations, the sca variance component was in fact the total of the combined sca, environmental and error variance. Thus the variance ratios simulated are perhaps more precisely described as the ratio of the variance of the additive genetic components to the variance of the remaining components (environmental variance was essentially absent, sampling effects replacing it).

In the twelve parent diallel described in this chapter the sca variance also includes environmental and error variance. The environmental and error variance are small in this case as the analysis was done using mean values rather than using individual replicates. Thus here the partitioning of variance could only be obtained between the variance of the gca's and all other non-additive genetic effects.

The results of the simulations in Chapter Two are verified by the diallel results given in this Chapter. Some of the F_1 plants were cytologically investigated in 1977. Pollen mother cells were examined to see whether univalents were present at metaphase. Although univalents were observed in these cells problems arising from these meiotic irregularities did not seem to effect the diallel analysis in any discernable way. Thus, it would appear that the simulations were general enough to be directly and accurately related to a self pollinating crop such as triticale.

3.7 Conclusions

The results show that a plant breeder using an incomplete partial diallel can obtain accurate estimates of the gca/sca variance ratio for the various observed characters in the diallel. They also show that, providing this ratio is not too far below unity, the gca ranks can be accurately estimated from the incomplete partial diallel.

Using these two items of information the plant breeder would be able to assess a large number of parents for their breeding potential. Should the gca/sca variance ratio be greater than one, it is also possible for the breeder to estimate accurately the phenotype of crosses which were not included in the original incomplete partial diallel.

If the gca/sca variance ratio drops below one, then the plant breeder would have to enlarge the number of higher ranking gca parents used in a breeding programme to ensure that the better parents were being used (and thus he would have to include some mediocre parents rather than risk losing the best ones).

It is not possible to assess whether all the simulated results given in Chapter Two would be as accurately verified by diallels of other sizes, crops and observable traits. However, within the scope of this dissertation the results are clearly encouraging.

Other authors have suggested using incomplete partial diallels to estimate values for parental combining abilities. Bray (1971) showed how errors occur in such estimates; however, he did not use the ranks of the gca's - instead, he used their actual values. Chaudhary, Katar and Singh (1977) did compare gca ranks, but they incorrectly used Griffing's analysis method, without adjustment, to calculate the gca values from both the partial diallels and the incomplete partial diallels. This explains the discrepancy between the results of Chaudhary et al. (ibid) and those presented in this thesis.

4. Control Plots

4.1 Introduction

The heterogeneity of field sites is a vexing problem for the plant breeder. Depending on the size of the experiment, the problem may be overcome in various ways. In small scale experiments environmental variation can be minimised by topsoil treatment, irrigation, birdproofing, hand weeding and many other treatments to standardise the environment in which the plants are grown.

Many of the above treatments were used when conducting the F_1 diallel experiment described in the previous chapter. The small area used in the experiment had had a uniform treatment during many previous seasons, and thus was not considered to have large soil fertility differences. Although this was encouraging, it was felt that a single genotype planted at regular intervals throughout the F_1 experiment would have indicated the extent of the homogeneity. Thus a wheat check plot was planted in every eighth position to measure soil fertility differences. The wheat plants, being a commercial homozygous stock, should only differ due to local environmental effects, and hence they should reflect differences in soil fertility factors.

Unfortunately, although only 30% of the triticales were affected by disease, approximately 80% of the wheat check plots were affected. Hence the possibility of using the wheat plants to

Experiments have been specifically designed without the above deficiencies, and are now being grown at the Waite Institute by other workers. However, as these results will not be available for some time, the wheat experiments mentioned above - grown in similar environments to those of the triticale experiment - were used to evaluate methods of measuring soil homogeneity.

measure soil homogeneity in this trial did not eventuate.

In larger plant breeding experiments, where experimental sites cover hectares rather than just a few square metres, there is reason to expect variation in soil heterogeneity, and hence it is essential to try to measure and compensate for these factors in some way.

4.2 Experimental Design and Materials

Experiments involving nearly three thousand field plots will be described in the next chapter. In an effort to determine an efficient way to compensate for soil heterogeneity a group of wheat trials were examined to determine the amount of environmentally induced variance which could be isolated.

The experiments were grown in three years over a number of sites. The experiments did not contain the same genotypes from one year to the next. Experiments grown at the same sites in different years were not grown in the same paddock more than once.
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Table 4.1 summarises the main features of the experimental trials examined. These experiments were grown under the direction of Dr. A.J. Rathjen as part of his wheat breeding programme at the Waite Agricultural Research Institute.

The plots in each experiment were randomised with no replication within a site. Because of limited seed and resources several different sites were used for growing each genotype in preference to replicating genotypes at only one site. Also, because of the possibility of an experimental site failing completely due to

Table 4.1

The variances associated with the ^{field means of the} four wheat field trials evaluated in Chapter Four.

Year	Site	Total Var.	Exp. Var.	Control Var.
1975	1 Windsor	4687	4697	2495
	2 Clinton	11843	10912	4527
	3 Mortlock	22188	23020	14424
1976	1 Waite	30924	32289	13859
	2 Palmer	4140	4132	4047
	3 Gulnare	12071	12298	10019
1977	1 Clinton	3007	3104	2328
	2 Mortlock	33709	33833	32398
	3 Dublin	723	716	493
	4 Waite	11920	11750	6341

environmental factors (e.g. drought, disease etc.), this strategy is pragmatically more reliable than the use of a single site with replicated plots within that site. In South Australia, site failures (for the purposes of genotype evaluation) as high as one in three occur, so caution is recommended.

To measure soil heterogeneity factors, control plots of a commercially released South Australian wheat variety were placed at regular intervals within the experimental layout. Control plots were placed in every sixth, ninth and eighth grid position for the 1975, 1976 and 1977 experiments respectively.

4.3 Covariate Analysis

A computer programme was written to undertake covariate regression analysis on the results in order to remove, as far as possible, environmental variations occurring within an experimental site (refer Section 1.3). The variance removed by this covariance analysis may be tabulated in the form:

$$[(\text{regression SS}/\text{total SS}) \times 100]\%$$

This part of the procedure is quite straightforward, indeed standard. The sums of squares are used for the comparison rather than the variances (mean squares), as the different degrees of freedom used to calculate the variances would make comparisons between experiments difficult. However the question arises of how the covariate should be calculated in the first place. Before the regression analyses can be carried out a matrix of covariates has to be created so that for every experimental plot there is a corresponding covariate value. This covariate value is based on the environmental differences expressed by the nearby control

plots. The formula used to calculate this covariate was:

$$\text{Cov}_i = \frac{\sum \left[\frac{\text{Obs}_i \times \text{CP}_j}{\text{DW}_j} \right]}{\sum \text{DW}_j}$$

where:

i = 1 to N , N being the number of experimental plots.

Cov_i = the covariate value for plot i

Obs_i = the observed value for plot i

j = 1 to M where M is the number of "relevant" control plots to be used

CP_j = the observed value for control plot j

DW_j = the distance weighting for control plot j and experimental plot i .

The two variable components in this equation are the number of "relevant" control plots (M) and the distance weighting (DW).

As the size of the plots remains constant, and as the number of rows and columns in an experiment is known, Pythagoras's theorem can be used to calculate the distance between any two plots. The plots were all four row plots which are 3.5 metres in length and 0.45 metres in width. A one and a half metre pathway between rows and a 30cm spacing between columns gives a centre to centre spacing of the plots of 5.0 metres in length and 0.75 metres in width (see Figure 4.1). Using these factors the two variable components M and DW can both be defined as follows:

M = the number of control plots within a given distance of the experimental plot.

DW = the value of the distance between the control plot and the experimental plot, raised to a given power.

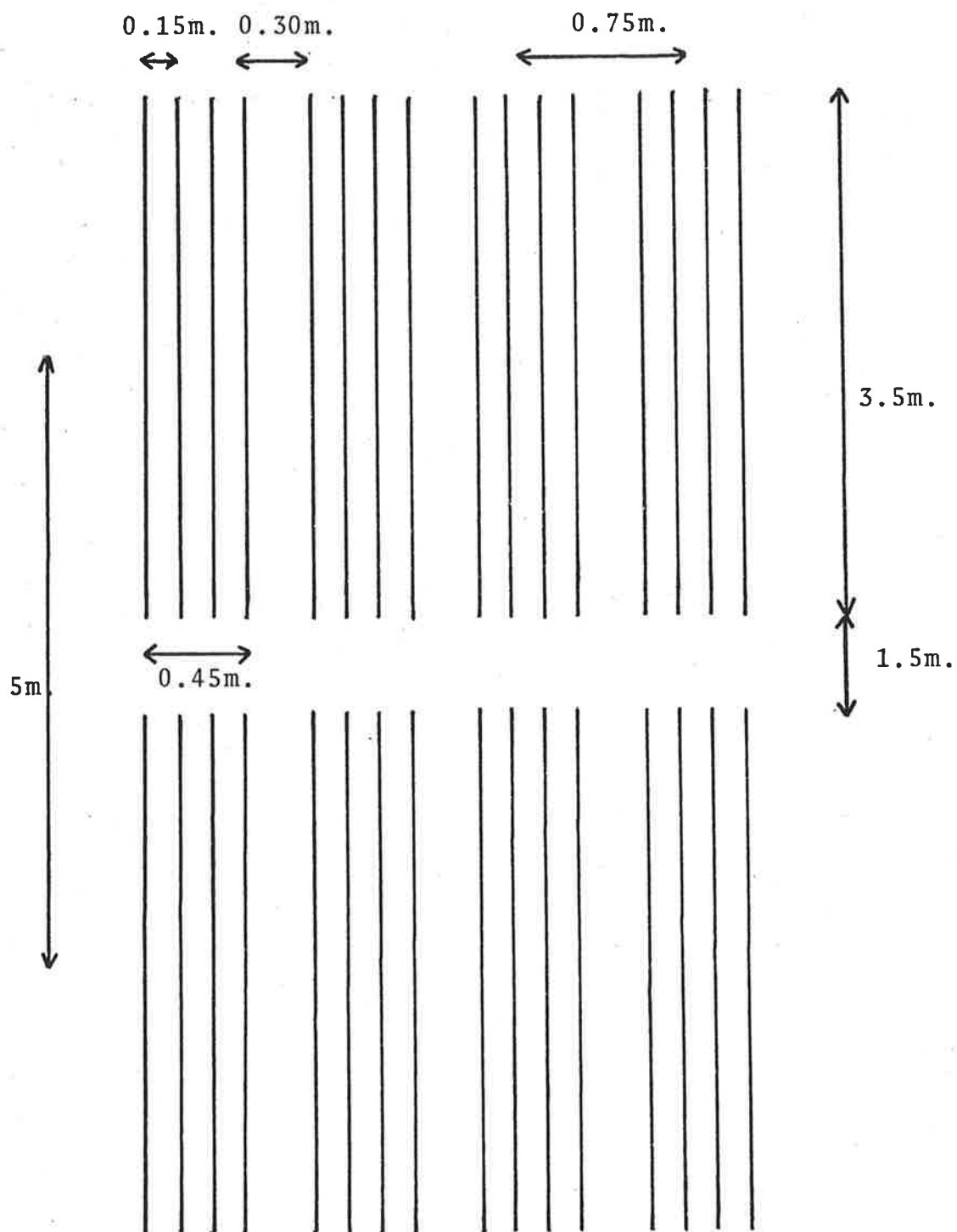


Figure 4.1

The dimensions of the wheat field plots described in Chapter Four (not drawn to scale).

The distances used to encompass the "relevant" number of plots (M) were 10, 20 and 30 metres. The powers used for DW were 0, 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 4.0 and 5.0.

A covariate analysis for all experiments was carried out using all the permutations of the above values of M and DW. Thus each experimental site was analysed $9 \times 3 = 27$ times.

4.3.1 Inclusion and Exclusion of Control Plots

Tables 4.2 shows the results of these analyses, for each of the distances 10, 20 and 30 metres. The power functions which yielded the minimum and maximum amounts of variance due to the regression are shown, i.e. the minimum and maximum regression SS/total SS (expressed as a percentage). The additional column in these tables is the inclusion of the regression percentage when a power of two is used for DW (i.e. the distance is squared). This is included because it is a usually acceptable method of weighting distance. [Its further implications to this study will be discussed in a later section of this chapter].

One of the problems with interpreting these results is that it is difficult to prove that the covariate analysis is removing the soil heterogeneity factors. [Other factors, such as competitive effects, genotype-environmental interactions etc., could also be influencing this analysis.] For this reason (that is, to help interpret the results more easily), a further set of analyses were done. These analyses were the same as those summarised in Table 4.2 except that the covariate analysis was performed on all plots, not just the experimental plots. Hence each control plot in this

Table 4.2

The minimum and maximum regression SS/total SS with their associated distance power weighting function when the experimental plots are adjusted with a covariate analysis using the control plots. The regression ss/total ss for the distance power weighting of two is also given.

Year	Site	Dist.	Min		Max		Power 2
			%	Power	%	Power	%
1975	1 Windsor	10	2.72	0.0	6.33	2.5	6.26
		20	0.50	0.0	6.29	3.0	6.10
		30	0.01	0.0	6.29	3.0	6.10
1975	2 Clinton	10	13.27	0.0	16.92	2.5	16.89
		20	6.11	0.0	16.89	3.0	16.67
		30	0.0	0.0	16.89	4.0	16.49
1975	3 Mortlock	10	8.63	0.0	9.32	0.5	7.40
		20	5.42	5.0	9.44	0.5	7.41
		30	5.42	5.0	8.68	0.5	7.28
1976	1 Waite	10	37.93	5.0	44.66	0.5	41.56
		20	37.95	5.0	45.53	1.0	42.54
		30	32.61	0.0	43.71	1.0	42.15
1976	2 Palmer	10	9.25	0.0	16.76	1.5	16.64
		20	7.56	0.0	15.87	2.0	15.87
		30	3.79	0.0	15.59	2.5	15.55
1976	3 Gulnare	10	16.39	0.0	21.85	1.0	20.33
		20	10.57	0.0	20.29	1.5	20.10
		30	8.72	0.0	20.04	1.5	19.93
1977	1 Clinton	10	48.44	0.0	57.53	2.5	57.37
		20	38.73	0.0	57.34	3.0	56.90
		30	33.15	0.0	57.58	3.0	56.74
1977	2 Mortlock	10	13.17	0.0	19.79	2.0	19.79
		20	12.49	0.0	19.80	2.0	19.80
		30	4.83	0.0	19.80	2.0	19.80
1977	3 Dublin	10	9.11	5.0	14.20	1.0	11.84
		20	1.41	0.0	11.56	1.0	10.99
		30	0.12	0.0	12.57	1.0	10.83
1977	4 Waite	10	15.39	0.0	26.30	2.5	26.26
		20	3.16	0.0	26.17	3.0	25.48
		30	0.30	0.0	26.24	3.0	25.63

This method differs in two significant aspects from previously published methods of using a moving mean (cf. Townley-Smith and Hurd, 1973; Lawrence and Townley-Smith, 1975). Firstly, the moving mean is used to calculate a covariate rather than directly adjusting the experimental plot; and secondly, because the type of experiment which uses a moving mean usually requires replication of genotypes.

set of analyses also had a covariate representing the effect of its neighbouring control plots.

The results of these analyses are presented in Table 4.3. If there is no experimental error and if the frequency and distribution of the control plots was optimum, then it would be expected that the variance of the control plots would approach zero, after they had been adjusted according to this second set of analyses. This concept will be examined later in this chapter.

4.4 Moving Means

The idea of moving means in experimental analysis is that the field heterogeneity is measured by the mean values of the experimental plots themselves. Here, rather than using control plots which are proximal to an experimental plot, all the nearby plots are used.

The computer programme used for the previous sets of analyses was easily adapted to this different strategy. The only change necessary was to ensure that the programme made no distinction between experimental plots and control plots. The covariates are now calculated by using all the surrounding plots (up to a given distance) and not just the surrounding control plots.

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Because this means that many more plots have to be used in the calculations of the covariate, additional and smaller distance increments were used. These were 0.75, 2.25 and 5.00 metres. The first two distances allow for one and three plots, respectively, on each side of the experimental plot to be included. The 5.00

Table 4.3

The minimum and maximum regression SS/total SS with their associated distance power weighting function when the experimental and control plots are adjusted with a covariate analysis using the control plots. The regression SS/total SS for the distance power weighting of two is also given.

Year	Site	Dist.	Min		Max		Power α %
			%	Power	%	Power	
1975	1 Windsor	10	3.54	0	8.46	3	8.24
		20	1.33	0	8.41	4	8.05
		30	0.19	0	8.41	4	7.98
1975	2 Clinton	10	15.30	0	19.13	2	19.13
		20	7.34	0	19.09	3	18.92
		30	0.08	0	19.09	3	18.82
1975	3 Mortlock	10	5.95	5	9.86	0.5	7.94
		20	5.96	5	10.39	0.5	8.00
		30	5.96	5	9.07	0.5	7.88
1976	1 Waite	10	34.6	5	42.25	0.5	38.56
		20	34.7	5	43.24	1.0	39.93
		30	34.7	5	41.94	1.0	39.84
1976	2 Palmer	10	10.13	0	16.85	1.5	16.62
		20	8.34	0	15.86	2.0	15.86
		30	4.39	0	15.47	2.0	15.47
1976	3 Gulnare	10	17.45	5	23.14	1.0	22.52
		20	11.41	0	21.32	1.5	21.15
		30	9.17	0	20.90	1.5	20.87
1977	1 Clinton	10	51.65	0	60.25	2.5	60.09
		20	41.15	0	59.89	3.0	58.94
		30	34.90	0	59.80	3.0	58.49
1977	2 Mortlock	10	15.62	0	21.27	1.5	21.22
		20	15.31	0	21.23	1.5	21.08
		30	5.67	0	20.79	1.5	20.72
1977	3 Dublin	10	8.46	0	12.74	1.0	10.87
		20	1.21	0	10.54	1.5	10.24
		30	0.00	0	11.19	1.0	10.10
1977	4 Waite	10	15.66	0	25.47	2.0	25.47
		20	3.63	0	25.04	3.0	24.36
		30	0.38	0	25.03	3.0	24.32

Lawrence and Townley-Smith (1975) do not recommend a covariate analysis for the adjustment of experimental plots by the moving mean method as they claim that there is no significant difference between directly adjusting control plots and using a covariate analysis - and thus as the covariate analysis is more cumbersome, it was not recommended. However, in this thesis, the moving mean method is to be compared to a control plot method which uses a covariate analysis and hence it was felt that the covariate approach to the moving mean method would make a valid comparison.

metre distance allows for the use of six plots on either side of the experimental plot, as well as the use of the two adjacent plots in the same column. The results of these analyses are tabulated in Table 4.4. The 30 metre distances are not presented in the 1977 experimental results shown in Table 4.4. This was due to the amount of computer resources needed to run the test programme when so many plots were used to calculate each covariate. When the experiment is large (eg. 750 plots in 1977), the thirty metre radius of "relevant" plots in the moving mean analysis created too large a demand on the computer resources available. Although the programme could have been run using these resources, in view of the small change in the earlier analyses between the twenty and thirty metre distances, it was felt that the use of such large computer resources was not warranted.

As Table 4.4 uses all the plots and not just the experimental ones, it should be compared to Table 4.3, but not to Table 4.2.

The use of the term "moving mean" may be a little misleading in this context, as it usually implies that the mean of the nearby plots is used to adjust the observed values. In the present analysis the means of the surrounding plots were obtained in the usual sense, but in addition a distance power weighting was used in the calculation of this moving mean. When the distance power weighting of zero is used, the distance between every plot is then equal to one (i.e. $d^0 = 1$). The usual moving means are in fact only a subset of the variations in which these covariates were calculated.

Table 4.4

The minimum and maximum regression SS/total SS with their associated distance power weighting function when the experimental and control polts are adjusted with a covariate analysis using the "moving mean" method described in Chapter Four. The regression ss/total ss for the distance power weighting of two is also given.

Year	Site	Dist.	Min		Max		Power 2 %
			%	Power	%	Power	
1975	1 Windsor	0.75	3.08	All	3.08	All	3.08
		2.25	3.08	7.0	11.58	0.0	4.47
		5.00	3.08	7.0	26.32	0.0	5.42
		10.00	3.08	7.0	9.67	0.5	5.40
		20.00	3.08	7.0	8.79	1.0	5.44
		30.00	3.08	7.0	8.25	1.0	5.43
1975	2 Clinton	0.75	13.06	All	13.06	All	13.06
		2.25	13.08	10.0	17.65	1.0	16.46
		5.00	13.08	10.0	20.50	0.5	17.29
		10.00	13.08	10.0	22.93	0.5	18.32
		20.00	13.08	10.0	20.70	1.0	18.11
		30.00	13.08	10.0	19.35	1.5	17.93
1975	3 Mortlock	0.75	5.51	All	5.51	All	5.51
		2.25	5.52	10.0	10.93	0	8.15
		5.00	5.52	10.0	13.56	0.5	8.79
		10.00	5.52	10.0	14.45	0.5	9.55
		20.00	5.52	10.0	12.97	1.0	9.57
		30.00	5.52	10.0	12.46	1.0	9.52
1976	1 Waite	0.75	53.55	All	53.55	All	53.55
		2.25	54.08	5.0	57.19	1.0	56.67
		5.00	54.10	5.0	59.53	1.0	57.81
		10.00	52.38	0.0	59.00	1.5	58.66
		20.00	44.67	0.0	58.65	2.0	58.65
		30.00	32.58	0.0	58.56	2.0	58.56
1976	2 Palmer	0.75	42.92	All	42.92	All	42.92
		2.25	40.63	0.0	44.49	2.0	44.49
		5.00	38.06	0.0	45.03	1.5	45.01
		10.00	12.34	0.0	44.79	2.0	44.79
		20.00	9.81	0.0	44.78	2.5	44.70
		30.00	1,72	0.0	44.78	2.5	44.73
1976	3 Gulnare	0.75	45.88	0.0	45.88	All	45.88
		2.25	44.09	0.0	47.53	1.5	47.52
		5.00	43.10	0.0	48.15	1.5	47.93
		10.00	29.54	0.0	47.84	2.0	47.84
		20.00	12.36	0.0	47.68	2.5	47.47
		30.00	8.21	0.0	47.70	2.5	47.52

.....cont..

Table 4.4 continued.

1977	1	Clinton	0.75	76.20	All	76.20	All	76.20
			2.25	76.44	0.0	78.16	1.5	78.00
			5.00	72.60	0.0	78.11	2.0	78.11
			10.00	56.02	0.0	77.95	2.5	77.66
			20.00	43.90	0.0	77.92	2.5	76.99
1977	2	Mortlock	0.75	46.54	All	46.54	All	46.54
			2.25	47.01	5.0	50.11	1.0	49.56
			5.00	40.96	0.0	49.72	1.5	49.67
			10.00	24.99	0.0	49.56	2.0	49.56
			20.00	15.29	0.0	49.38	2.5	49.42
1977	3	Dublin	0.75	30.22	All	30.22	All	30.22
			2.25	30.69	5.0	34.07	1.0	33.30
			5.00	30.71	5.0	35.27	1.0	34.11
			10.00	20.30	0.0	34.47	2.0	34.47
			20.00	7.0	0.0	34.19	2.0	34.19
1977	4	Waite	0.75	31.42	All	31.42	All	31.42
			2.25	32.19	5.0	37.79	1.0	36.19
			5.00	32.23	5.0	45.16	0.0	38.15
			10.00	29.91	0.0	40.28	1.5	38.71
			20.00	2.16	0.0	39.76	1.5	38.67

4.5 Discussion

Inspection of the results in Tables 4.1 to 4.4 shows that the problem of within site variation is very complex. The aim of the analysis was to determine the best way to compensate for field heterogeneity which was expected to occur in the F_4 experiments described in the next chapter. Rather than directly answering this question, it illustrated more complex problems and thus the work in this chapter should be viewed as a preliminary investigation rather than a definitive study.

4.5.1 Site Variations

Table 4.1 shows the amount of variance observed at each site. Up to tenfold differences in the total variances are observed between different sites in the same experiment (Table 4.1 Clinton and Mortlock, 1977). This variation is not just due to genotypic differences within the experiment - if this were true then each experiment should have a similar total variance at each site. Similarly, as shown in Table 4.1, the environmental effects manifest themselves differently from site to site; at Palmer (1976) and Mortlock (1977) the control plot variance is approximately equal to the experimental plot variance, yet in the same experiments at different sites the control plot variance is less than half of the experimental plot variance. The ratio of control plot variance to experimental variance seems to be independent of the magnitude of the total variance for each site. These observations indicate that non-additive environmental effects such as soil fertility factors and site block effects will not explain all the variance. It is apparent that

genotype-environmental interactions have a notable influence.

From the plant breeder's point of view, breeding to compensate for a genotype-environmental interaction may not be possible. As with specific combining ability, genotype-environment interactions may not be predictable, they may only be observed. If, however, similar genotypes are grown over a number of years then environmental x additive genotypic interactions may be predictable (eg. Goodchild & Boyd, 1975). Thus the breeder must rely on the additive environmental effects (e.g. block effects and control plot effects) to provide some of the information required. These additive effects, whilst not all-encompassing, at least give the breeder information on how the experimental material may fair at other sites and in other years. Again this supports the procedure of testing at many sites rather than at one site with replication. The more sites that are used, the more confident the breeder may be that a variety being bred is widely adapted. This is especially important when it is noted that the same sites (but in different paddocks) behave differently in different years.

All the sites used in these experiments are within a one hundred and fifty kilometre radius of Adelaide and all within commercially cropped areas. It can be seen from Table 4.1 that if breeding programmes were only grown at one site, then the crop might not be well suited to different sites.

4.5.2 Reduced Variation

Tables 4.2 to 4.4 show similar patterns in the amount of the variance that is removed. The least variance is removed when only

the experimental plots are adjusted, with marginally more variance being accounted for in the analysis when the control plots are also adjusted. This is to be expected, as the control plots, by definition, should reduce to zero variance after the analysis.... where the conditions are perfect. Table 4.5 shows the percentages by which the control plot variances are reduced by the analysis. Comparing Table 4.3 to Table 4.5 it can be seen that the less the control plot variance is reduced the higher is the regression SS/total SS ratio for the experiment. This at first seems contradictory as it might be expected that the more the control plot variance is reduced, the more the experimental plot variance would be reduced. However, in order to reduce the control plot variance substantially (e.g. Windsor, 1975) the variation within the site would have to show trends over the site rather than be "patchy" with high and low yielding patches occurring irregularly. Such a "smooth" continuum would give reduced variance to the adjusted experimental plots. However when the control plot variance is not reduced as much (e.g. Waite, 1976), it is probably due to an uneven change in soil fertility throughout the experimental site. This means that proximal control plots may be exerting opposing effects on each other in the analysis. For example, if the control plots formed the following uneven grid:

699	205	862	215
215	115	112	862
115	864	725	306

it would be difficult for an analysis procedure to "smooth" out these variations over the entire experiment. Although the variance of these control plots is reduced it would not be reduced by as much as the following example grid:

199	220	699	862
190	210	725	870
230	290	750	864

The experimental plots' variances would still be adjusted in both of these examples. In the first example the control plot variance may not be greatly reduced but the experimental plot variances will be. In the second example the control plot variance will certainly be greatly reduced, but as in the first example the experimental plot variance may or may not be greatly reduced. Coupling this problem with the varying ratios of control plot variance to experimental plot variance may explain the seeming inconsistency.

4.5.2.1 Moving Mean Variances

The "moving mean" regression SS/total SS (Table 4.4) is considerably higher in many cases than the same factor shown in Tables 4.2 and 4.3, in which only the control plots are used for adjusting the observed values. This "moving mean" analysis may thus seem a better alternative if the breeder is only interested in reducing this regression SS/total SS statistic. However, in this case, biological interpretations of the analysis are not as straightforward. Because the variances of the plots are adjusted by the experimental plots themselves, problems of bias are introduced. A genotypically low yielding plot between two genotypically high yielding plots will be artificially lowered when it is adjusted even if it is in a low yielding section of the field site. This does not occur if only the control plots are used, as here the control plot is only deemed to be a "high" yielding plot if it is yielding high compared to its neighbouring

Table 4.5

The % reduction of the control plot variance when the control plot covariate analysis is used to adjust the experimental and control plots.

Year	Site	Distance		
		10	20	30
1975	1 Windsor	90.9	92.1	92.6
	2 Clinton	62.4	69.1	72.5
	3 Mortlock	92.1	93.1	93.8
1976	1 Waite	33.6	39.3	44.6
	2 Palmer	89.1	92.4	93.3
	3 Gulnare	87.0	89.4	90.8
1977	1 Clinton	37.1	42.8	47.7
	2 Mortlock	85.6	89.8	92.3
	3 Dublin	93.5	96.8	97.6
	4 Waite	82.6	89.2	91.7

control plots (all of which are of the same genotype). Thus the randomisation of the experiments could introduce chance bias in the "moving mean" soil fertility adjustment procedure. A replicated experiment would remove much of this bias (see Section 1.3), as now the adjoining experimental plots could be compared to their own genotypic replicates within the experiment before they are considered high or low yielding. Hence relativity would be reintroduced. However, as was stated earlier, plant breeders often do not have the resources for such replication; therefore, although a moving mean type analysis could reduce the within site environmental variances more than a control plot analysis, the problem of introducing bias or having to increase (create?) the replication makes the utility of this "moving mean" type analysis suspect.

If the number of proximal experimental plots used in the analysis is large enough, and thus encompasses a large range of genotypes, then the bias mentioned above may be removed. However, as it is difficult to measure whether or not the moving mean analysis is biased, it would appear safer not to use moving means until this and other problems are satisfactorily eliminated.

4.5.3 Distance

Tables 4.2 and 4.3 show that the distances used for deciding which control plots would or would not be used for calculating the covariate influence the results only marginally. That is, if control plots within 10, 20 or 30 metres are used the results of the covariate analysis are consistent - in general the 10 and 20 metre distances give extremely close results with both of them

sharing evenly the "honour" of having the highest percentage reduction of the sums of squares. Occasionally the 30 metre distance gives the best percentage result.

As the purpose of the analyses carried out in this chapter was to determine a method to use in the F_4 experiment (which will be described in Chapter Five) to reduce the within site variation, a decision has to be made regarding which of these distances should be used.

If a distance of 20 metres is used then it appears that sufficient information will be gained by using control plots. The advantage of repeating the analysis for various distances and then picking the optimum would be lost once the extra work involved and the subsequent inferential and interpretational difficulties, when two sites are analysed with different distances, are considered. The moving mean results of Table 4.4 show that a distance of only five metres would be adequate and sufficient for this form of analysis.

4.5.4 Power Function

The various powers used to give weightings to the distances were more varied in their effects than the three distances used. The optimum powers were much less consistent than the optimum distances. The optimal powers ranged from zero to four; however, in general a power of two (i.e. the distance squared) gave results only marginally different from the optimal results.

It should be noted that the optimum power functions for the

"moving mean" analyses were lower than for the control plot analyses. A power of two was, however, still only marginally worse, in most cases, than the optimal result. It should be observed that at distances of 0.75 metres all the power functions gave the same results for the "moving mean" analysis. At 0.75 metres, only one plot on each side of the experimental plots is used and thus weighting the distances between plots used in the analysis has no effect.

4.5.5 Effects of Analysis

The effects of the analyses described in this chapter can be observed by using the covariate analysis to adjust the observed values and these adjusted values can then be compared to the observed values. The plots were adjusted using the following formula:

$$\hat{\text{obs}}_i = \text{obs}_i - b.(\overline{\text{cov}} - \text{cov}_i)$$

where:

b = the regression coefficient given by the covariate analysis.

obs_i = the observed measurement of plot i.

cov_i = the covariate for plot i.

$\overline{\text{cov}}$ = the mean value of the covariates.

In each of the experiments four commercial wheat varieties were included in the experimental design, with replicates of 4, 4 and 6 in 1975, 1976 and 1977 respectively. The ranking of the means of these varieties can be compared to each other before and after they have been adjusted for soil fertility factors.

The results of these comparisons appear in Table 4.6. As

Table 4.6

The ranking of the four wheat check plots before and after the plots have been adjusted for soil heterogeneity. Three sets of analyses results are shown: all plots (AP); experimental plots only (EO); and all plots using the "moving mean" (MM) rather than the control plot method. The ranking given immediately after the site name is the observed ranking before analysis. All analysis use a distance power weighting of two.

Year	Site		Distance					
			2.25	5	10	20	30	
1975 1	Windsor		1432					
		AP				1432	1432	1432
		EO				1342	1342	1342
1975 2	Clinton	MM	1432	1432	1432	1432		
		AP			3241	3241	3241	
		EO			3241	3241	3241	
1975 3	Mortlock	MM	4312	4312	4321	4321		
		AP			3241	3241	3241	
		EO			3241	3241	3241	
1976 1	Waite	MM	3412	3412	3412	3412		
		AP			3214	3214	3214	
		EO			3214	3214	3214	
1976 2	Palmer	MM	3412	3412	3412	3412		
		AP			4132	4123	4123	
		EO			4312	4312	4312	
1976 3	Gulnare	MM	3412	3412	3412	3412		
		AP			4231	2431	2431	
		EO			2431	2431	2431	
1977 1	Clinton	MM	1234	1234	1234	1234		
		AP			1423	1423	1423	
		EO			1423	1423	1423	
1977 2	Mortlock	MM	3124	3124	3124	3124		
		AP			3214	3214	3214	
		EO			3214	3214	3214	
1977 3	Dublin	MM	2413	2413	2413	2413		
		AP			1423	4123	4123	
		EO			1423	4123	4123	
1977 4	Waite	MM	3142	3142	3142	3142		
		AP			3421	3412	3412	
		EO			3421	3412	3412	

already stated, making these comparisons is easy, it is their interpretation which is difficult. They are presented here more in order to convince the reader that the analysis affects the interpretation of the experiment rather than to draw any specific conclusions. All the results in Table 4.6 are based on using a distance power weighting of two.

In general only marginal rank differences occurred, but in some sites the rank change was significant, e.g. in Dublin 1977 the rank order was almost ^{totally} reversed! All the control plot analyses gave similar results irrespective of distance and whether or not the control plots were included in the covariate analyses. The "moving mean" results were also consistent over the various distances but were often significantly different from the rank order of both the observed means and the control plot adjusted means. From the data it was observed that when the adjusted means did change ranks as the distances were altered, the means were extremely close and often the rank changes were due only to changes in the first or second decimal places. In these cases a plant breeder would not discriminate between these rankings, so such small changes in rank due to the different distances used were not considered important.

4.6 Conclusion

Despite the difficulty in determining black and white answers from these varied and often confusing results a number of guidelines may be suggested from the analyses presented:

1. A good reduction in local environmental variance is

The advantages, reported by Townley-Smith and Herd (1973) and Lawrence and Townley-Smith (1975), presuppose that the experimenter is able to use replication, as well as randomisation. Thus, in experiments similar to those described in this Chapter, where replication is not possible, the advantages of using the moving mean method may well be lost.

obtained using control plots within twenty metres of the experimental plot to be adjusted, and inversely weighting these control plots by the square of their distance. This reduction may not be optimal but its difference from an optimal value would in most cases be marginal.

2. The use of moving mean analysis without the aid of replication is difficult to assess because of unknown biases which are probably present. ^{INSERT OPPOSITE PAGE HERE} Much of the variance reduction advantage is probably due to the use of more proximal plots than the control plot analyses used. Thus using control plots at more frequent intervals may be a more viable approach than the use of moving means.
3. As many sites as possible should be used within the region in which the plant breeder is working so as to avoid breeding a plant adapted to a specific small environment, which may only occur rarely within the region. The large site variabilities and their subsequent genotypic interactions imply that only a plant which is bred for general adaptation to the regional environments will succeed.

The many unknowns encountered when dealing with variation within a site should make the breeder as cautious and perhaps as conservative as possible. The control plot adjustment procedures suggested in this chapter are both cautious and conservative. The caution manifests itself in the selection of a single distance and

power function rather than suggesting that each site should be optimised for both these variables. Interactions between distance and power are by no means made clear by the results obtained, let alone interactions between these two variables, the sites and the genotypes. Thus a cautious approach, until a better understanding can be obtained, is to use the same variables (20 metre distance, power of 2) at each site so that the user may feel more confident in making comparisons.

Conservatism is manifested by not using moving means. Here, although considerable advantages may be gained in variance reduction and by not having to plant control plots, the inability to test for, and hence reduce, bias makes use of the method dubious. Increasing replication would more than account for the resources saved by not having to use control plots and would probably mean that less sites could be used in plant breeding trials.

5. The F₁₁ Diallel

5.1 Introduction

In Chapter Three the results of a twelve parent diallel of triticale were presented. These results showed that the simulations presented in Chapter Two could be used to accurately describe observed plant material. However, in plant breeding programmes the ability to make predictions about the F₁ generation is not always critical. A high yielding F₁ plant will not necessarily produce later generation selections which are high yielding, and, more importantly, a low yielding F₁ plant may have high yielding later generation progeny. Thus low yielding F₁ plots should not necessarily be rejected as they may, like the higher yielding F₁'s, produce later generation high yielding progeny.

In most cereal breeding, the breeder's aim is to obtain a high yielding homozygous line which contains advantageous traits from two or more parents. Of course, hybrid crops may have the F₁ as the end point of a breeding programme, and in this case the F₁ diallel is ample for the plant breeder's needs.

In order to evaluate the use of the incomplete partial diallel for breeders who will ultimately wish to obtain a new homozygous line, later generations beyond the F₁ will have to be evaluated. For this study, the F₁ diallel described in Chapter Three was observed at the F₄ generation. Although the F₄ generation of a

self-pollinating crop cannot be considered homozygous, it may be said to have lost much of its heterozygosity. [In the F_4 generation, if there is no linkage, it would be expected that 87% ($1-0.5^3$) of loci would be homozygous.] Growing two generations a year, the F_4 progeny can be evaluated two years from the time the initial cross is made. Thus the F_4 generation is a good compromise between evaluating a cross when it reaches homozygosity and evaluating it as rapidly as possible.

The F_4 diallel described in this chapter will be analysed for a number of uses. These are:

1. The applicability of incomplete partial diallel analyses on the F_4 generation.
2. The use of more than one site for F_4 evaluations.
3. The use of control plots.
- [4. Comparison of F_1 traits with F_4 traits (Chapter Six)
5. The use of means and variances to describe an F_4 family (Chapter Six).]

5.2 Growing the Diallel

As discussed in Chapter One, the number of possible genotypic variations from a single cross becomes extremely large as the generations advance. Because of this it is impossible to grow all the possible F_4 's from a single cross; only a subset can be grown. As the purpose of growing the F_4 generation was to observe the potential of each of the sixtysix cross families, the observed F_4 's had to be an unselected sample of each F_4 family. In order to obtain such a sample the following method was used:

- (i) Three plants of each F_1 cross were grown in a glasshouse over the 1976/7 summer (out of season).
- (ii) The F_2 seed from (i) above was bulked for each cross (i.e. the three F_1 plants) and this seed was planted as a four row, 3.5 metre plot in 1977 (in season).
- (iii) At the conclusion of the 1977 season, thirty five F_2 heads were selected at random from each plot. Any of these randomly selected heads which contained less than five seeds was rejected and a further head was selected, at random, to replace it. The remainder of the F_2 plot was machine harvested as a bulk.
- (iv) The heads from the F_2 plants [(iii) above] were threshed and planted as small "hill plots" in the 1977/8 summer (out of season). These hill plots consisted of the F_3 seed from each head being scattered randomly within a 25 cm. diameter circle. These circular 25 cm. plots were planted on a 30 cm. (between plots) square grid.
- (v) Each hill plot was harvested and the grain was used to plant a 2.5 metre F_4 plot in 1978 (in season). Thus each cross family was represented by thirty five F_4 plots, each of which was derived from a single F_2 head selection.

Although the term random selections was used in (iii) above, this is not completely accurate as sterile genotypes were rejected and, presumably, some natural selection had occurred in the two

generations grown before the selection was made. Because of meiotic irregularities which may occur when chromosomal mismatching occurs in the third genome (see Section 3.2), the range of genotypic combinations available for sampling was probably less in some crosses than in others. However, as the overall number of possible combinations is so large it was felt that this would not significantly narrow the range of genotypes sampled.

In (v) (above) the hill plot yields were not as high as was hoped and some plots did not yield enough seed to grow an F_4 plot. It was only intended that thirty F_4 plots from each cross family would be grown and thus five F_3 plots which did not have a high enough yield could be discarded. Despite this, there were still not enough high yielding F_3 plots to plant the F_4 plots. As the four row F_4 plots required 20 gms. of seed it was decided to grow some two row plots which would only require 10 gms. of seed.

5.2.1 Experimental Design

The F_4 plots were grown at three sites. Each site contained ten F_4 selections (derived from the F_2) from each cross family, as well as ten plots of each of the twelve parental lines. Thus six hundred and sixty F_4 plots and one hundred and twenty parental plots were grown at each site. The three sites used were:

Waite: a field site within the grounds of the Waite Agricultural Research Institute, Adelaide, South Australia.

Strathalbyn: the Waite Agricultural Research Institute's
C.S. Charlick Experimental Station at
Sandagrove, south of Strathalbyn, South
Australia.

Roseworthy: Roseworthy Agricultural College, Roseworthy,
South Australia.

The Waite and Strathalbyn sites had four row plots sown and Roseworthy had the two row plots sown (the choice of Roseworthy as the two row plot site was arbitrary). Within each cross family all the F_3 hill plots which yielded 20 gms. of seed or more were grouped together. Twenty of these were randomly allocated to the Waite and Strathalbyn sites. Of the remaining F_3 hill plots, those yielding less than 10 gms. were discarded and ten of the remaining plots were selected at random for planting at Roseworthy.

Within each site the 780 plots were randomised within ten blocks of 78 genotypes (the sixty six F_4 's and the twelve parents). It should be stressed that although the ten plots of each parent are replicates at each site, the ten plots of each F_4 family are not, strictly speaking, replicates as they are individual F_2 derived selections. These F_4 plots are genotypically related, not genotypically identical.

The experiment was laid out using a computer programme written and devised by the plant breeding section of the Agronomy Department of the Waite Institute (Rathjen, 1972).

A control plot grid was also grown within the experiment at each

site. The control plot placement consisted of a wheat plot being placed in every eighth grid position of the site. Wheat was used for the control plots in these triticale experiments, as a commercial variety of triticale adapted to the S.A. region was not available. As the purpose of the control plots is to measure field fertility variations, it was felt that a well adapted wheat variety would serve this purpose. The wheat variety used was the Waite Institute variety Warimba. One hundred and thirteen control plots of Warimba were grown at each site. Each experimental site contained fifteen rows and sixty columns, giving a total of nine hundred plots at each site. As the 780 experimental plots and 113 control plots only add to 893 plots, seven additional plots were added to the experiment to make the total up to 900. These seven plots were of the wheat variety Kite.

The plant breeding section of the Agronomy Department at the Waite Institute has designed and built its own equipment for sowing and harvesting this type of plot experiment. Fiftyfive thousand plots were grown for the various cereal programmes engaged in by the Agronomy Department in 1978, and the two thousand seven hundred plots described in this chapter were grown and harvested in essentially the same manner as all these other experiments. Plots are sown at commercial densities with 300 plots being planted per hour. The plots are harvested at a rate of approximately 100 plots per hour. No supplementary irrigation was used.

5.3 Characters Measured on the Diallel

The following four characters were measured on the plots:

1. Yield : Each plot was mechanically harvested and the weight of the seed was measured to the nearest gram.
2. Height : In a plot of 400 or more plants, some height segregation did occur, thus it was necessary to measure the approximate height of the plot by visually scanning the level of the tallest tillers in the plot. This was then measured to the nearest 5 centimetres.
3. Days to Heading : This character was measured when more than five plants in the plot had fully emerged heads. It was measured once a week.
4. Days to Anthesis : This character was recorded when more than five plants in the plot had anthers which had dehisced. It was also measured weekly.

Characters one and two were recorded at all three sites, whilst characters three and four were only recorded at the Waite site.

The control plots were measured at all sites for characters one and two.

5.4 Control Plot Analysis

All sites were analysed by using the control plots to create a covariate for each experimental plot. The analysis was of the form described in Chapter Four, using all control plots within a twenty metre distance of the experimental plot and weighting the effect of the control plot by the square of its distance from the experimental plot.

The variances of these experiments, for yield and height, are shown in Tables 5.1.1 and 5.1.2. Here the total variance is shown as well as the variance of the control plots only and the variance

Table 5.1.1.

The variances associated with the F_4 yields at the three experimental sites used. The regression $SS/total$ SS represents the amount of variance in the experiment reduced by the control plot covariate analysis.

Site	Total Variance	Experimental Plot Variance	Control Plot Variance	Regression SS/ Total SS
Waite	49627	38293	24744	7.0%
Roseworthy	16723	16883	14152	1.2%
Strathalbyn	15257	15737	11461	3.4%

Table 5.1.2

The variance associated with the F_4 heights at each of the three experimental sites used. The regression $SS/total$ SS represents the amount of variance in the experiment reduced by the control plot covariate analysis.

Site	Total Variance	Experimental Plot Variance	Control Plot Variance	Regression SS/ Total SS
Waite	230	186	12	1.43%
Roseworthy	194	177	23	6.58%
Strathalbyn	180	169	156	2.33%

of the experimental plot only. The {regression SS/total SS} percentage refers to the experimental plot sums of squares removed by the covariate regression analysis over the total sums of squares of the experimental plots.

Table 5.2 shows the mean values of the observed characters for each of the experimental sites. The mean values for the sixtysix F_4 families and the twelve parental lines are given in Appendix III; the values adjusted for soil heterogeneity are also given in Appendix IV.

5.5 Diallel Analysis

Because of the statistical complexity of any programme which would analyse this type of experiment, a statistical programming package was used to perform the analysis. The statistical programming package used was GENSTAT (Rothamsted 1977). A copy of the programme (Baghurst, 1979) which performed the analysis appears in Appendix VI. The programme treated the F_4 selections as replicates and thus each cross was presented to the GENSTAT programme as thirty replicates (ten from each site). This ensured that the variance of the F_4 families was used in the analysis as well as their means (cf. the F_1 diallel analysis). The partial diallel was compared to its incomplete partial diallels in the same manner as the F_1 diallel described in Chapter Three.

The within site variation had already been removed as far as possible from the data by the use of the control plot analysis. Additive site effects were removed by the GENSTAT programme. The results of the least squares analysis for estimating the gca

Table 5.2

The means of the F_4 characters measured at the three experimental sites.

Site	Yield	Height	Days to Heading	Days to Anthesis
Waite	651	118	110	129
Roseworthy	304	108	-	-
Strathalbyn	340	93	-	-

values of the F_4 diallel are presented in Tables 5.3.1 to 5.3.4. Because these analyses used replicated data, the "sca variance" given in Tables 5.3.1 to 5.3.4 has to be interpreted differently than the values given for the simulated results, and the F_1 diallel results presented in Chapters Two and Three respectively.

Whereas the simulated and F_1 data could be partitioned into only three effects [that is, the mean effect, the additive genetic effect (gca) and the non-additive genetic effects (sca)], the F_4 data, being replicated, also yield environmental interaction effects as well as error effects. Each of these additional two effects can be partitioned separately from the additive (gca) and non-additive (sca) genetic effects. The sca variance presented in Tables 5.3.1 to 5.3.4 represents all the effects other than the mean effect and the additive genetic and environmental effects.

This allows Tables 5.3.1 to 5.3.4 to be compared directly with Tables 3.3.1 to 3.3.11 (Chapter Three).

From the plant breeder's point of view, this combining of all the effects except the additive effects is certainly advantageous. All the effects which have been grouped here under the title of "sca variance" are only partitionable when all the interactions can be observed, and thus they have no use as a predictive tool. In this set of data, additive environmental effects are used in the analysis, all non-additive effects having been grouped under the title "sca variance". The accuracy of calculating these additive environmental effects as the diallel is reduced will be discussed later in this chapter.

Tables 5.3.1 - 5.4.2.

The following tables show the ranks of the gca estimates for each of the parents in the diallel. The ranks for the incomplete partial diallels are also shown, as are the ranks of the parental means. The bracketed numbers indicate the differences in rank of the I.P.D.'s (or parental means) when compared to the ranks in the partial diallel.

Table 5.3.1

F4	Character 1	<u>Adjusted Yield</u>					
		gca variance 2062	sca variance 2372	gca/sca variance ratio 0.869			
Variety	gca Ranks						
(Bracketed numbers indicate deviation from P.D.ranks)							
	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p	Parent Rank
T28	6	8(2)	8(2)	9(3)	10(4)	10(4)	10(4)
T31	5	5	5	5	5	3(2)	3(2)
T33	3	3	1(2)	2(1)	3	4(1)	4(1)
T34	8	9(1)	9(1)	8	9(1)	8	9(1)
T58	9	7(2)	7(2)	7(2)	6(3)	7(2)	8(1)
T106	11	11	11	11	11	12(1)	12(1)
T246	4	4	4	4	4	5(1)	6(2)
T686	10	10	10	10	8(2)	9(1)	7(3)
T702	1	1	3(2)	3(2)	1	2(1)	2(1)
T710	7	6(1)	6(1)	6(1)	7	6(1)	5(2)
T896	12	12	12	12	12	11(1)	11(1)
T937	2	2	2	1(1)	2	1(1)	1(1)
Mean of Abs. Residuals		39.06	39.02	39.14	39.88	41.12	44.58
S.D. of Abs. Residuals		29.16	30.07	31.20	30.21	29.67	33.69

Table 5.3.2.

F4	Character 2	<u>Adjusted Height</u>					
		gca variance 28.47	sca variance 8.52	gca/sca variance ratio 3.34			
Variety	gca Ranks						
(Bracketed numbers indicate deviation from P.D. ranks)							
	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p	Parent Rank
T28	7	7	7	7	7	7	8(1)
T31	6	6	6	5(1)	5(1)	5(1)	4(2)
T33	8	8	8	8	8	9(1)	9(1)
T34	10	9(1)	9(1)	9(1)	9(1)	8(2)	7(3)
T58	5	5	5	6(1)	6(1)	6(1)	6(1)
T106	1	1	1	1	1	1	1
T246	9	10(1)	10(1)	10(1)	10(1)	10(1)	10(1)
T686	11	11	11	11	11	11	11
T702	12	12	12	12	12	12	12
T710	2	2	2	2	2	2	2
T896	3	3	3	3	3	3	3
T937	4	4	4	4	4	4	5(1)
Mean of Abs. Residuals		2.22	2.22	2.28	2.31	2.32	2.46
S.D. of Abs. Residuals		1.92	1.96	1.92	1.99	2.00	2.10

Table 5.3.3

Variety	Days to Heading						Parent Rank
	P.D.	10c/p	8c/p	6c.p	4c/p	2c/p	
F4 Character 3							
gca variance 9.95 sca variance 8.82 gca/sca variance ratio 1.13							
gca Ranks (Bracketed numbers indicate deviation from P.D. ranks)							
T28	9	9	8(1)	7(2)	7(2)	7(2)	8(1)
T31	10	10	9(1)	8(2)	8(2)	8(2)	9=10
T33	3	2(1)	3	3	3	3	3=4
T34	12	12	11(1)	11(1)	11(1)	11(1)	12
T58	8	8	10(2)	9(1)	9(1)	10(2)	9=10(1)
T106	2	3(1)	2	2	1(1)	1(1)	1(1)
T246	5	5	5	6(1)	6(1)	6(1)	7(2)
T686	11	11	12(1)	12(1)	12(1)	12(1)	11
T702	6	6	6	5(1)	5(1)	4(2)	3=4(2)
T710	4	4	4	4	4	5(1)	5(1)
T896	7	7	7	10(3)	10(3)	9(2)	6(1)
T937	1	1	1	1	2(1)	2(1)	2(1)
Mean of Abs. Residuals							
	2.36	2.43	2.55	2.62	2.69	2.89	
S.D. of Abs. Residuals							
	1.78	7.73	1.68	1.73	1.91	1.95	

Table 5.3.4

Variety	Days to Anthesis						Parent Rank
	P.D.	10c/p	9c/p	6c/p	4c/p	2c/p	
F4 Character 4							
gca variance 4.92 sca variance 4.49 gca/sca variance ratio 1.10							
gca Ranks (Bracketed numbers indicate deviation from P.D. ranks)							
T28	10	10	10	10	10	10	7=9 (1)
T31	9	9	9	9	9	9	7=9
T33	2	1(1)	2	1(1)	1(1)	1(1)	2
T34	12	12	12	11(1)	12	12	12
T58	7	8(1)	7	7	7	8(1)	7=9
T106	3	3	3	3	3	3	4(1)
T246	5	5	5	5	5	5	10(5)
T686	11	11	11	12(1)	11	11	11
T702	8	7(1)	8	6(2)	6(2)	6(2)	5=6(2)
T710	4	4	4	4	4	4	3(1)
T896	6	6	6	8(2)	8(2)	7(1)	5=6
T937	1	2(1)	1	2(1)	2(1)	2(1)	1
Mean of Abs. Residuals							
	1.73	1.76	1.78	1.82	1.84	1.93	
S.D. of Abs. Residuals							
	1.22	1.22	1.21	1.32	1.30	1.24	

Tables 5.4.1 and 5.4.2 show the results of the diallel analysis for yield and height when no adjustment is made for field homogeneity (i.e. the control plots are not used to adjust the experimental plot data).

The four measured characters together with the unadjusted yield and height measurements (characters one and two) are presented in Table 5.5 with their gca/sca variance ratio. In this case, the ratios are different from those of the F_1 characters (cf. Table 3.4), the F_4 yield and height gca/sca ratios being much higher than their F_1 counterparts. Conversely, the F_4 heading and anthesis gca/sca variance ratios are lower than the same character traits in the F_1 's.

Tables 5.6, 5.7 and 5.8 can be directly compared to their F_1 counterparts (Tables 3.5, 3.6 and 3.7).

5.5.1 Additive Site Effects

A critical part of analysing experiments grown at a number of sites is the calculation of an additive site effect {interactive (non-additive) effects will be discussed in the next chapter}. It is expected that the larger the number of plots (and genotypes) grown at each site, the more accurate the calculation of the additive environmental effect would be. Thus, as the diallel is reduced, and hence less plots are grown at each site, the ability to accurately calculate these site effects should be reduced. Table 5.9 shows the additive site effects for the two characters observed at all sites. The effect of reducing the diallel is also shown in this table.

Table 5.4.1

Variety	gca Ranks (Bracketed numbers indicate deviation from P.D.ranks)						Parent Rank
	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p	
T28	6	8(2)	8(2)	9(3)	10(4)	10(4)	10(4)
T31	5	5	5	5	5	3(2)	3(2)
T33	3	3	2(1)	3	3	4(1)	4(1)
T34	7	7	9(2)	8(1)	9(2)	8(1)	9(2)
T58	9	6(3)	7(2)	7(2)	6(3)	7(2)	8(1)
T106	11	11	11	11	11	12(1)	12(1)
T246	4	4	4	4	4	5(1)	5(1)
T686	10	10	10	10	8(2)	9(1)	7(3)
T702	2	1(1)	3(1)	2	1(1)	2	2
T710	8	9(1)	6(2)	6(2)	7(1)	6(2)	6(2)
T896	12	12	12	12	12	11(1)	11(1)
T937	1	2(1)	1	1	2(1)	1	1
Mean of Abs. Residuals	39.59	39.59	39.58	40.32	41.16	43.89	
S.D. of Abs. Residuals	29.13	30.01	31.17	30.01	30.07	34.14	

Table 5.4.2

Variety	gca Ranks (Bracketed numbers indicate deviation from P.D.ranks)					Parent Rank
	P.D.	10c/p	8c/p	6c/p	4c/ 2c/p	
T28	7		7	7	7	8(1)
T31	6		6	6	5(1)	4(2)
T33	8		8	8	8	9(1)
T34	10		9(1)	9(1)	9(1)	8(2)
T58	5		5	5	6(1)	6(1)
T106	1		1	1	1	1
T246	9		10(1)	10(1)	10(1)	10(1)
T686	11		11	11	11	12(1)
T702	12		12	12	12	11(1)
T710	2		2	2	2	2
T896	3		3	3	3	3
T937	4		4	4	4	4
Mean of Abs. Residuals	2.25		2.30	2.32	2.36	2.50
S.D. of Abs. Residuals	1.94		1.94	2.02	2.03	2.10

Table 5.5

The gca/sca variance ratios of the F_4 characters observed in the twelve parent triticales diallel.

Character	gca/sca Variance ratio
Adjusted Yield	0.87
Adjusted Height	3.34
Yield	0.86
Height	3.24
Heading	1.13
Anthesis	1.10

Table 5.6

The percentage of parents in the 12 parent triticales diallel which did not change in rank by more than four when the partial diallel was reduced.

Character	I.P.D.	Var.	Rank Changes				
			0	≤1	≤2	≤3	≤4
Adjusted Yield	6c/p	0.87	50.0	75.0	91.6	100	100
	4c/p		66.6	75.0	83.3	91.6	100
	2c/p		8.3	75.0	91.6	91.6	100
Adjusted Height	6c/p	3.34	66.6	100	100	100	100
	4c/p		66.6	100	100	100	100
	2c/p		58.3	91.6	100	100	100
Yield	6c/p	0.86	66.6	75.0	91.6	100	100
	4c/p		41.6	66.6	83.3	91.6	100
	2c/p		16.6	66.6	91.6	91.6	100
Height	6c/p	3.24	83.3	100	100	100	100
	4c/p		66.6	100	100	100	100
	2c/p		41.6	91.6	100	100	100
Heading	6c/p	1.13	33.3	75.0	91.6	100	100
	4c/p		16.6	75.0	91.6	100	100
	2c/p		8.3	58.3	100	100	100
Anthesis	6c/p	1.10	50.0	83.3	100	100	100
	4c/p		66.6	83.3	100	100	100
	2c/p		58.3	91.6	100	100	100

Table 5.7

The percentage of parents in the observed 12 parent triticale diallel which did not change rank by more than four when the ranks of the parental means are compared to the gca ranks from the partial diallel analysis.

Char.	gca/sca Var. Ratio	Rank Changes				
		0	≤1	≤2	≤3	≤4
Adjusted Yield	0.87	0	58.3	83.3	91.6	100
Adjusted Height	3.34	41.6	83.3	91.6	100	100
Yield	0.86	16.6	58.3	83.3	91.6	100
Height	3.24	50.0	75.0	91.6	100	100
Heading	1.13	33.3	83.3	100	100	100
Anthesis	1.10	58.3	83.3	91.6	91.6	91.6

Table 5.8

The gca/sca variance ratios predicted from the mean of the absolute values of deviations, (Observed - Predicted) of the twelve parent triticales diallel. The bracketed numbers indicate the calculation of the mean of the absolute deviations were from the crosses sampled.

Character	Ovserved gca/sca ratio	P.D.	Estimated gca/sca variance ratio	
			6 crosses / parent	4 crosses / parent
Adjusted Yield	0.87	0.77	0.88 (0.99)	0.81 (0.92)
Adjusted Height	3.34	3.27	3.94 (6.51)	4.04 (7.87)
Yield	0.86	0.75	0.89 (0.96)	0.84 (0.92)
Height	3.24	3.16	3.87 (6.16)	3.91 (7.87)
Heading	1.13	1.01	0.89 (1.13)	0.89 (1.26)
Anthesis	1.10	0.93	0.77 (0.99)	0.86 (1.00)

Table 5.9

The additive environmental effects associated with the characters observed for each of the three experimental sites. The three sites effects are listed for the Waite, Roseworthy and Strathalbyn sites respectively. F_4

Character	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p
Adjusted Yield	218	218	217	213	210	210
	-127	127	-129	-125	-122	-111
	-90	-92	-89	-88	-88	-99
Adjusted Height	11	11	11	11	11	11
	2	2	2	3	3	3
	-13	-13	-13	-13	-14	-14
Yield	217	219	216	212	208	208
	-127	-127	-129	-125	-122	-110
	-90	-92	-87	87	-86	-98
Height	11	11	11	11	11	11
	2	2	2	2	3	3
	-13	-13	-13	-13	-14	-14

5.6 Discussion

5.6.1 Control Plot Analysis

The removal of the within site variation by the use of control plots gave similar results in this F_4 experiment as were observed in the experiments described in Chapter Four. Only characters one and two were adjusted for field heterogeneity factors, as the remaining two characters were effectively constant for all the control plots.

Seven percent of the observed variation was the maximum that was reduced by the covariate analysis (Tables 5.1.1, 5.1.2). As in the results in Chapter Four, there appears to be no pattern relating the percentage reduction in variance to any of the observed variance statistics. Appendices III & IV show the effects of the control plot analysis on the means of characters one and two. It can be seen that although the mean values were altered, the change, in most cases, was not great. Because of uncertainties involved in the control plot analysis (Chapter Four) the unadjusted data were also analysed in order to discover whether differences occurred between the two sets of data in the diallel analysis.

By comparing Tables 5.3.1 and 5.3.2 to Tables 5.4.1 and 5.4.2, slight differences in the analysis results can be observed. The fifth and sixth ranked parents (based on parent mean yield) swap ranks when the yield and height data are adjusted for field

heterogeneity. The gca ranks are, however, less stable, and a number of gca rank changes do occur between the two sets of data. The most striking change is that the highest yield gca becomes the second highest yield gca when the control plot grid is used to adjust the data. For the remainder of this chapter only the adjusted data will be referred to, for although differences do occur between the raw and adjusted data, in general they both lead the plant breeder to similar conclusions. The adjusted data, having had as much of the within site variation removed as possible, form the data set with which the breeder should deal.

5.6.2 GCA Ranking

As can be seen from Tables 5.3.1 to 5.4.2, the ranks of the gca for the various incomplete partial diallels do not change from those in the partial diallel. The only rank changes which remove one of the top five ranked parents from the top five occur between the fifth and sixth ranked parents. Yield, the most important character to the plant breeder, has none of the top five ranked parents incorrectly ranked outside of the top five.

Table 5.6, which shows the percentage of gca estimates which change in rank, confirms that there is little chance of a gca rank changing by more than two. A comparison of Table 5.6 with Table 3.5 shows that the simulation results, the F_1 results and the F_4 results are similar. All show a remarkable lack of rank change.

5.6.3 SCA Variance

As previously explained, the term "sca" variance in the variance

of the F_4 experiment actually refers to the non-additive effects, but for simplicity and as an aid for comparison with the simulated and F_1 results the term sca variance will be retained. Table 5.5 lists the gca/sca variance ratios for the F_4 character traits measured.

An unexpected result, and certainly an encouraging result for the plant breeder, is the increase in the gca/sca variance ratio for yield when the F_4 's are compared to the F_1 's. The F_1 diallel gave a gca/sca variance ratio of 0.21 for yield whereas the F_4 diallel has a variance ratio of 0.87. This makes a large difference as to how the F_4 diallel analysis may be used. Variance ratios which are much less than unity mean that spurious results have a relatively high probability of occurring when the incomplete partial diallels are analysed for gca ranks. In the F_1 diallel, yield cannot be confidently analysed in the incomplete partial diallels because of the low gca/sca ratio. However, in the F_4 diallel the yield gca/sca ratio is within the range of variance ratios which can be accurately analysed. This means that yield, the most commercially important agronomic trait, can be evaluated in incomplete partial diallels of F_4 material. This potential accuracy in the F_4 is especially welcome as it is the yielding behaviour of later generation progeny (e.g. F_4) which is the most important factor to the breeder of self-pollinating cereals.

The gca/sca variance ratio of height also increased in the F_4 generation. However, this character already had a high variance ratio in the F_1 diallel and its agronomic importance is nowhere near as great as that of yield. Days to heading and anthesis both

decrease in the gca/sca variance ratio when the F_4 diallel is compared to the F_1 diallel. However, their magnitude is still sufficiently large to enable the incomplete partial diallels to be analysed with confidence.

Table 5.8 shows the accuracy with which the gca/sca variance ratios may be estimated by using the means of the absolute values of the residuals, when the observed data are compared to the estimated data. Here, as with the F_1 data, the gca/sca variance ratio estimation is extremely accurate when the incomplete partial diallels are used. As in Table 3.7, the bracketed numbers in Table 5.8 represent the estimations when only the crosses sampled in the incomplete partial diallel are used for the sca estimation (compared with calculating the gca values from the I.P.D. and then calculating the mean of the absolute values of the residuals from the P.D.).

The F_4 character, height, is the only trait which gave a gca/sca variance estimate significantly different from the observed variance ratio. An explanation for this phenomenon may be in the way in which the F_4 heights were measured. As they were measured to the nearest five centimetres in the F_4 (cf. 0.5 centimetres in the F_1), considerable "rounding off" errors may have occurred in the measurement of this character. These "round off" errors may bias the subsets of crosses in the various incomplete partial diallels. For example, in the F_4 two measurements of 90 cm and 92 cm would both have been rounded off to 90; though if the second measurement had been 93 cm it would have been recorded as 95 cm. Thus in the F_4 diallel this 1 cm difference would have been recorded as a 5 cm difference, whereas

because of segregating heights in the F_4 plot data, it was not possible to measure plot height to the nearest centimetre as was done on a single plant basis in the F_1 .

in the F_1 diallel, which was measured to the nearest centimetre, it would have been recorded as a 1 cm difference. ^{INSERT OPPOSITE PAGE HERE} It should also be noted that the gca/sca variance ratio jumped to approximately seven in the incomplete partial diallels when it should have been four. This jump should not influence decisions made by the plant breeder as both of these values are within the same range in terms of their subsequent interpretation by the plant breeder.

5.6.4 Additive Environmental Effects

Table 5.9 shows the additive environmental effects of the three experimental sites. These values were calculated by the GENSTAT programme which performed the diallel analysis. The observed values less the values given in Table 5.9 serve to adjust each plot value so that all sites can be compared and analysed together. This additive environmental effect slightly changes the diallel analysis model presented in chapter one. The equation of the model used in this F_4 experiment becomes:

$$P_{ijk} = \mu + gca_i + gca_j + site_k + e_{ij} \quad (v.i)$$

where: $site_k$ represents the additive environmental effect of site k.

As can be seen from this table, the reduction of the partial diallel has only a minor effect on these statistics. Thus the plant breeder is able to use incomplete partial diallels to calculate these additive site environmental effects with a high degree of confidence. This result is probably independent of the number of genotypes used but rather dependent on the number of plots, so it may be more accurate to say that the calculation of the additive site environmental effects was not significantly

influenced by reducing the number of plots which were observed at each site.

5.6.5 Parental Ranks

The mean values of the twelve parents were ranked for the observed characters and these ranks are also given in Tables 5.3.1 to 5.4.2. The differences between these ranks and the gca ranks are illustrated in Table 5.7. As in the F_1 data, the ranks of the parental means are different from the ranks of the parental gca estimates. More rank changes occur when the parental ranks are compared to the gca ranks from the partial diallel, than when the incomplete partial diallels are compared to the partial diallel.

5.7 Conclusion

The reduction of the F_4 partial diallel to its incomplete partial diallel subsets did not give significantly lower accuracy in the gca rank estimations. The results in this chapter reinforce the results of the simulations presented in Chapter One. Because the additive genetic effects of the cross families are measured by the diallel analysis, the allelic interaction which take place within the individual F_4 selections were buffered. This buffering was aided by analysing the F_4 's as family populations rather than as individual genotypes. Thus the diallel analysis was able to calculate the additive genetic effect of the F_4 family populations and hence individual allelic combinations within the F_4 's did not appear to detract from the results of the analysis.

As the results of the triticales experiments showed a higher tolerance to low gca/sca ratios, ratios of less than unity may now be considered to be significantly high.

Complete information about the best parents is contained in Appendix III, but given the lack of replication over sites, use of this information might be misleading in the present case.

The appearance of a relatively high gca/sca variance ratio for yield in the F_4 diallel makes this method of cross evaluation viable for the plant breeder. Using the methods described in this, and earlier chapters, a plant breeder will be able to evaluate parental material for its later generation (F_4) yielding potential. Both the four and six crosses per parent incomplete partial diallels give the breeder accurate rankings of the top five parental gca's. In addition to this, accurate calculations of the gca/sca variance ratio may also be gained from these incomplete partial diallels.

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Using the gca ranks and the gca/sca variance ratios, the plant breeder is able to make sound decisions as to which crosses should be incorporated into a breeding programme. This concept will be further discussed in Chapter Seven.

It can be seen that the plant breeder gains different information by using the ranks of the parental means than by using the ranks of the gca's. The diallel analysis gives the breeder further critical information regarding the ratio of the additive genetic effects to the non-additive effects. This additional information will influence the breeder's ability to predict the later generation characteristics of crosses made between the parental varieties evaluated.

6. A Further look at the Triticale Diallels

6.1 Introduction

In this chapter three further topics relating to the breeding of a self-pollinating species will be examined. They are:

- the correlations between the character traits observed in the F_1 and F_2 triticale diallel;
- the genotype-environment interactions observed in the F_4 diallel experiment;
- use of the means and the variances of measured character traits to describe the later generation cross families.

Although these three topics all relate to breeding methodologies, they will be described individually in this chapter. In the following chapter the interrelations of these issues together with those which were presented in previous chapters will be discussed.

6.2 Correlations

As discussed in Chapter One, the relationship between the phenotypes of the F_1 of a cross and its later generation homozygous progeny is usually not predictable for quantitative traits. Allelic permutations and the interactions which occur after the F_1 generation are so plentiful that the isolation of a single (predetermined) genotype and the prediction of its

phenotype effectively impossible. However, as the primary objective of most cereal breeding programmes is to increase yield, an early generation predictor of later generation yielding ability would be of considerable importance.

As stated in Chapter Five, the F_4 generation is an effective compromise for the plant breeder between observing a cross at homozygosity and being able to make an evaluation of a cross as soon as possible. The F_1 generation, on the other hand, is the earliest cross generation which can be observed and it contains all the parental alleles (assuming that the parents are homozygous). The F_1 generation is the most heterozygous generation, as from this generation onwards further homozygous allelic combinations may occur (the F_1 may not be totally heterozygous as the parents may have common alleles). For this reason the F_1 generation will display all the dominance effects of the various loci as well as their heterotic effects. If characteristics of this generation can be related to the characteristics of the later generations, then a large amount of selection can be performed, by the breeder, at the F_1 generation. Only those F_1 's with a high potential for the desired later generation character trait need be taken on towards homozygosity. Although this argument relies on the character being mainly (or wholly) controlled by major and/or dominant genes, this problem will be ignored for the remainder of this section. This concept will, however, be discussed in Chapter Seven.

In order to investigate the possible relationships between the F_1 and the F_4 generations, Pearson's correlation coefficients were calculated for all the observed characters in the triticales

diallel. The eleven F_1 character traits and the four F_4 character traits were treated in this way. Each character was represented by the mean values of the sixty-six cross families.

The F_1 generation is genetically identical within replicates of the cross and thus these mean values represent a unique genotype.

The F_4 generation, however, has its mean values calculated from thirty randomly selected F_2 derived F_4 plots (see Chapter Five) and they thus represent the mean value of a family of genotypes.

The parent lines were not included in the correlations made with these diallels. As the parents were included in the F_1 as well as the F_4 diallel experiment, they had to be excluded from the diallel for the purpose of calculating correlations between generations.

The correlations within the F_1 generation, within the F_4 generation and between the F_1 and F_4 generations will be presented separately.

6.2.1 The F_1 Generation

Pearson's correlation coefficients for the eleven F_1 characters observed are presented in Table 6.1. In these tables significances at the 5% and 1% level are denoted by a and b respectively.

Although most of these correlation coefficients are statistically significant, in many cases they are not biologically significant. For example, a highly significant positive correlation occurs between the number of days to heading and the

Table 6.1

Pearsons's correlation coefficients between the eleven character traits observed in the F₁ diallel. The five percent (a) significance level is 0.25 and the one percent (b) significance level is 0.32.

	1	2	3	4	5	6	7	8	9	10	11
	Days to Heading	Days to Anthesis	Hgt.	Tiller No.	Biological Weight	Head length	Spikelet No.	No. of Seed	Sd. Wt.	Yld.	Harvest Index
1 Head	1.0000	0.8888b	0.5683b	0.4130b	0.4229b	0.2431	0.6485b	0.0596	0.0267	0.0041	-0.3522b
2 Anth.		1.0000	0.5226b	0.4394b	0.4508b	0.3963b	0.7184b	0.0366	0.1025	0.0869	-0.2968a
3 Hgt.			1.0000	0.3710b	0.6826b	0.4454b	0.6397b	-0.2536a	0.0674	0.0359	-0.5795b
4 Till.				1.0000	0.7384b	0.5365b	0.6532b	0.1784	0.4804b	0.4450b	-0.1424
5 B.Wt.					1.0000	0.7560b	0.7932b	0.2313	0.5931b	0.5644b	-0.2297
6 Hdlng.						1.0000	0.8306b	0.2425	0.3902b	0.3835b	-0.2687a
7 Spik.							1.0000	0.1076	0.2853a	0.2659a	-0.4138b
8 Seed.								1.0000	0.7649b	0.8061b	0.7537b
9 Sd.Wt.									1.0000	0.9969b	0.6133b
10 Yld.										1.0000	0.6465b
11 H.I.											1.0000

number of days to anthesis. This is statistically significant but biologically trivial. Such trivial relationships can be seen between a number of the characters presented in Table 6.1. Because the entire correlation matrix is presented, other problems, besides trivial correlations, may be seen. The major one is that correlations between harvest index and its components (i.e. total Biological Weight and Grain Yield) are shown in this table. Here an obvious statistical flaw is illustrated as these two components of harvest index are effectively being compared to a ratio of themselves. Because of this the correlation coefficients (-0.2297 and 0.6465) cannot be reasonably interpreted, either statistically or biologically.

These two correlation coefficients were not, however, removed from the table as they are merely less subtle examples of what also occurs elsewhere in Table 6.1. Whereas harvest index correlated with its ratio components can easily be seen to be statistically as well as biologically meaningless, other correlations are only biologically meaningless. For example, height and number of tillers are all obvious biological components of total biological weight, and the question must therefore arise as to what importance should be placed on the correlation between height and total biological weight or between height and harvest index. It is not that the two characters have to be independent before computations can be made (after all that would defeat the purpose of calculating the correlation coefficients), it is that the measurement of the two characters must be independent. The measurement of the weight of the seed in the whole plant is clearly not independent of the measurement of the weight of the seed in the tallest tiller, thus their correlation coefficient

should be treated warily; hence the correlation between harvest index and weight of seed in the tallest tiller should be treated just as cautiously as the correlation of harvest index and yield.

An example of two characters which are independently measured is height and days to anthesis. It can be thus seen that the interpretation of Table 6.1 is far from straightforward, as there are many subtle as well as obvious measurement dependencies between the characters observed. Because some of these more subtle interdependencies tend to be subjective (height and total biological weight?) all the correlation coefficients are presented in order to emphasise the need to be cautious in interpreting their biological significance.

The above discussion serves to illustrate the dangers in interpreting the black and white computer-generated results as the definitive answer to biological problems. However, rather than going to the opposite extreme and rejecting totally the value of these correlations, they should be used to give the plant breeder guidelines as to the interrelations between the observed characters. The following such information may be gleaned from Table 6.1:

- although yield correlates very positively with the number of productive tillers and the length of the spike (tallest tiller), it is only just significantly positively correlated with the number of spikelets on the tallest tiller. This indicates that the plant does not utilize all the spikelets, and that the larger head (and more spikelets) compensates for this

lack of utility. If the spikelets were fully utilized, the number of spikelets per head would be expected to correlate with yield at the same level as headlength and number of tillers. This trend is also shown when the number of seed in the tallest tiller is compared to the number of spikelets, head length and number of heads.

- the above comments for yield are also true for harvest index. Harvest index, however, has three distinct sets of statistically significant correlations. The first set of correlations comprises the trivial ones between harvest index and its components. These should be ignored. The second set of significant correlations is important. These are the correlations between harvest index and heading and anthesis time. As these two characteristics are measures of the maturity time of the plant it shows that as the plant matures later, its harvest index decreases (or vice versa). Although correlations cannot be used to show cause and effect relationships, it would seem logical to assume that the low harvest index result from the late maturity time. As the plant delays its reproductive (seed formation) phase, so it has more time for vegetative growth and less time for seed development. Thirdly, significant negative correlations are present between harvest index and the number of heads, the length of head and the number of spikelets on the head. These three characters increase in their correlation with

harvest index in the opposite manner to that in which they react to yield. Here the most significant character seems to be the number of spikelets. As the increase in the number of spikelets is detrimental to harvest index, this again reinforces the concept that it is the utility of spikelets which is important to yield, not the number of them. Harvest index would be far more sensitive to this utility than yield alone. If the plant breeder wanted to increase this utility^{of spikelets}, by comparing yield and number of spikelets, the task would be difficult in that a significant positive correlation would have to be made larger. However, if the breeder uses harvest index as the guide, then the goal is clearer, here a significant negative correlation has to be converted to a significant positive correlation.

- later maturity seems to be more related to the number of spikelets in a head than both the number of heads and the length of the head. This indicates the direction of physiological studies which could be fruitfully undertaken in conjunction with a triticales breeding programme.
- height is significantly negatively correlated with the number of seed in the tallest tiller, yet there is no correlation observed between height and the weight of the seed in the tallest tiller, nor with the grain yield of the entire plant. This is another important physiological anomaly, the answer to which could be

important in a triticales breeding programme.

It is these types of observations from correlation coefficient tables such as Table 6.1 which should be made by plant breeders, as the more restrictive "x is correlated to y" approach may, for the reasons stated earlier, be misleading.

6.2.1.1 The F₄ Generation

The general discussion in the preceding section also applies to correlations between the characters measured in the F₄ diallel.

In the F₄ diallel only a subset of the characters measured in the F₁ was observed, so much of the discussion on the dependence between the measurements of the character traits is not relevant for the F₄ characters (the exception being heading and anthesis times).

Because of the small number of correlations involved here only a few observations can be made. The Pearson's correlation coefficients for the four F₄ observed character traits are presented in Table 6.2.

From Table 6.2 it can be seen that a significant negative correlation occurs between height and yield. This correlation is not evident in the F₁ diallel. A significant positive correlation is evident between height and maturity (heading, anthesis time), which is also evident in the F₁ diallel.

Table 6.2

Pearsons' correlation coefficients between the eleven character traits observed in the F_4 diallel. The five percent (a) significance level is 0.25 and the one percent (b) significance level is 0.32.

	12	28	14	15
	Yld.	Hgt.	Head	Anth.
12 Yld.	1.0000	-0.3330 ^b	0.1191	0.1215
13 Hgt.		1.0000	0.4986 ^b	0.4027 ^b
14 Head.			1.0000	0.9162 ^b
15 Anth.				1.0000

6.2.1.2 Correlating the F_1 and F_4 Characters

The Pearson's correlation coefficients between the F_1 and the F_4 character traits are presented in Table 6.3. The following three major items of information can be obtained from this table:

- yield is the most important agronomic character measured in the F_4 diallel and thus correlations between this character and the F_1 characters are of major importance. F_4 yield correlates significantly (and positively) with all the F_1 characters which measure seed (i.e. F_1 characters 8 to 11), with the highest correlation being with harvest index. The next highest correlation is not with the F_1 yield but with the F_1 weight of seed in the tallest tiller. The reason for the measurement of this F_1 character was to approximate the F_1 plant's potential for seed fill rather than the average seed fill of all the heads on the plant. It seems that this measurement of "potential" is better than the plant's average measurement (yield). A significant negative correlation occurs between F_1 height and F_4 yield. This negative correlation does not exist between F_1 yield and F_1 height (Table 6.1).
- whilst having a strong positive correlation with F_4 yield, F_1 harvest index is significantly negatively correlated with F_4 height and maturity time (heading, anthesis). This contrasts markedly with F_1 yield (or number of seed in tallest tiller, or weight of seed in tallest tiller) which only correlates significantly with F_4 yield.

Table 6.3

Pearson's correlation coefficients between the eleven character traits observed in the F_1 diallel and the four character traits observed in the F_4 diallel. The five percent (a) significance level is 0.25 and the one percent (b) significance level is 0.32.

	12 Yld.	13 Hgt.	14 Head	15 Anth.
1 Head	0.0314	0.5962b	0.7480b	0.6754b
2 Anth.	0.0448	0.5140b	0.7397b	0.7042b
3 Hgt.	-0.3882b	0.7510b	0.5116b	0.4933b
4 Till.	0.1355	0.0886	0.4251b	0.48888b
5 B.Wt.	-0.0779	0.3762b	0.4615b	0.5382b
6 Hdng.	-0.1170	0.1656	0.4334b	0.5486b
7 Spik.	-0.1172	0.4140b	0.6515b	0.6902b
8 Seed	0.4861b	-0.2153	0.0694	0.1218
9 Sd.Wt.	0.3961b	-0.1259	0.1251	0.2071
10 Yld.	0.4041b	-0.1366	0.1134	0.2002
11 H.I.	0.5547B	-0.4472b	-0.2848a	-0.2557a

- F_4 height, anthesis and heading time correlate with nearly all the F_1 characters which do not directly measure seed. The only F_1 character, which includes the measurement of seed and which does significantly correlate with these three F_4 characters is harvest index. These correlations are all negative.

These relationships between the F_1 and the F_4 diallels imply that F_4 characteristics may be predicted by certain F_1 characteristics. If this is true, then correlation coefficients and subsequently regression equations, would be a powerful tool to the triticale breeder. The implications of these results for plant breeding methodologies will be discussed in the following chapter.

6.2.2 Discussion

In conclusion, it appears that whilst definitive answers may not be obtainable from correlations, as described in this chapter, important interrelationships are certainly made visible. The most difficult task for the plant breeder, in relation to correlations such as those presented here, is to be able to make biological interpretations, rather than merely statistical interpretations of the correlation coefficients.

The statistical significances are often difficult to define with certainty. Part of the reason for this is that not all the measured characteristics are normally distributed and thus parametric significance tests do not always apply. Use of

non-parametric correlation coefficients (e.g. Spearman's rank correlation coefficient) may solve this problem statistically, however such non-parametric tests analyse the ranks of the data rather than their observed value and thus some information is lost. The Spearman's rank correlation coefficient was used to compare the gca ranks in the diallel simulations (Chapter Two). However, in that case it was the rank changes which were the important values, whereas in the correlations presented in this chapter the measured values were themselves important.

Using Pearson's correlation coefficient introduces a statistical problem of determining significance when the data are not normally distributed (e.g. tiller number). However, the correlation itself is more meaningful biologically than a rank correlation coefficient as the distances between two observations are appraised as well as the number of other observations ranked between them.

Provided that the plant breeder is aware of the statistical problems involved, the correlation coefficient can be used to give biological guidelines for further breeding and/or physiological experiments which could be carried out. Interpretation is easier than for relevant multivariate methods which also have the same problems with non-Gaussian data.

6.3 Genotype-Environment Interactions

6.3.1 Introduction

In Chapter Five the results of an F_4 diallel experiment grown at three sites was presented. In the GENSTAT computer programme which analysed those data, the additive site effects ($site_k$) were removed so that the observations from the three sites could be analysed collectively. The model for the diallel analysis thus became:

$$P_{ijk} = \mu + gca_i + gca_j + site_k + e_{ijk}$$

The term e_{ijk} here, incorporates all the non-additive effects. One of these non-additive effects is the interaction between the additive genetic effects (gca) and the environment. [That is, the change in the gca values for the different sites.] To incorporate this into the model the diallel equation becomes:

$$P_{ijk} = \mu + gca_i + gca_j + site_k + site_k.gca_i + site_k.gca_j + e_{ijk} \quad (vi.i)$$

where:- $site_k.gca_i$ represents the interaction between the gca value and the environment for parent i at side k.

The GENSTAT programme was modified to include these additional site interaction effects, and the F_4 experimental data were analysed according to the model illustrated in equation (vi.i).

6.3.2 Results

The $\text{site}_k \cdot \text{gca}_i$ values calculated for the yield and height of the F_4 plots are shown in Tables 6.4.1 and 6.4.2 respectively. Table 5.2 shows the mean values for the F_4 yield and heights at the three sites. As can be seen from Tables 6.4.1 and 6.4.2 the interactions are large and often change dramatically from site to site. The magnitude of these interaction effects is of approximately the same range as the gca values for the same sites. In order to show the effect of these interactions the three sites were analysed independently and the ranks of the gca values at each site were recorded. These ranks appear in Tables 6.5.1 and 6.5.2 for the F_4 characters yield and height respectively. The average value for the three sites is also presented in this table. The "All Sites" column in this table represents the analysis which removes only the additive environmental effects and the last column represents the gca analysis when both the additive environmental effects and the gca by environment interactive effects are partitioned by the programme.

6.3.3 Discussion

As the interaction values shown in Tables 6.4.1 and 6.4.2 are so large, it would be expected that the gca values, and hence their ranks, would change at the three sites. Tables 6.5.1 and 6.5.2 show that these changes do occur and the bracketed numbers in these tables show the extent of the rank changes compared to the results given in Chapter Five (the "all sites" column in Tables 6.5.1 and 6.5.2).

Table 6.4.1

The site_k.gca (additive genetic effect by environment) interaction for the F₄ character yield.

Variety	Site		
	Waite	Roseworthy	Strathalbyn
T28	- 7.80	- 8.40	16.20
T31	15.74	- 9.92	- 5.82
T33	27.16	-27.30	0.14
T34	6.44	- 1.47	- 4.97
T58	1.46	-10.88	9.41
T106	-28.00	36.66	- 8.66
T246	27.94	- 2.64	-25.30
T686	17.38	-17.74	0.36
T702	-24.08	- 5.93	30.02
T710	- 6.23	- 1.17	7.40
T896	-64.25	32.98	31.26
T937	34.25	15.79	-50.05

Table 6.4.2

The site \times gca_i (additive genetic effect by environment) interaction for the F_4 character height

Variety	Site		
	Waite	Roseworthy	Strathalbyn
T28	0.05	0.14	0.19
T31	0.20	0.32	0.52
T33	- 1.26	- 1.38	2.64
T34	- 1.15	- 0.63	1.78
T58	1.67	- 0.62	- 1.05
T106	4.67	2.00	- 6.67
T246	- 0.90	- 0.55	1.45
T686	- 1.49	- 0.95	2.44
T702	- 2.81	- 0.47	3.28
T710	0.78	1.19	- 1.97
T896	0.12	0.25	- 0.37
T937	0.11	0.72	- 0.83

Table 6.5.1

The gca ranks of the F_{11} triticales diallel for the character trait yield. Six sets of ranks are shown. They are: the three sites analysed independently; the mean of these ranks from the three sites; the analysis of all sites removing additive environmental effects and the analysis when both the additive environmental effect and the gca x site interactive effect. The bracketed numbers represent the rank deviation from the "All Sites" column.

Variety	Waite	Site Roseworthy	Strathalbyn	Mean of all sites	All sites	All sites & gca/envir. Int.
T28	9(3)	8(2)	4(2)	7.0(1)	6	6
T31	5	5	5	5.0	5	5
T33	2(1)	3	2(1)	2.3(0.7)	3	3
T34	6(2)	7(1)	9(1)	7.3(0.7)	8	8
T58	8(1)	9	8(1)	8.3(0.7)	9	9
T106	11	10(1)	12(1)	11.0	11	11
T246	3(1)	4	6(2)	4.3(0.3)	4	4
T686	10	12(2)	10	10.7(0.3)	10	10
T702	4(3)	2(1)	1	2.3(1.3)	1	1
T719	7	6(1)	7	6.7(0.3)	7	7
T896	12	11(1)	11(1)	11.3(0.7)	12	12
T937	1(1)	1(1)	3(1)	1.7(0.3)	2	2

Table 6.5.2

The gca ranks of the F_4 triticales diallel for the character trait height. Six sets of ranks are shown. They are: the three sites analysed independently; the mean of these ranks from the three sites; the analysis of all sites removing additive environmental effects; and the analysis when both the additive environmental effect and the gca x site interactive effect are removed. The bracketed numbers represent the rank deviation from the "All Sites" column.

Variety	Waite	Site Roseworthy	Strathalbyn	Mean of all sites	All sites	All sites & Gca/env. Inter.
T28	7	7	10(3)	8.0(1.0)	7	7
T31	6	5(1)	6	5.7(0.3)	6	6
T33	8	10(2)	5(3)	7.7(0.3)	8	8
T34	10	9(1)	7(3)	8.7(1.3)	10	10
T58	5	6(1)	8(3)	6.3(0.7)	5	5
T106	1	1	1	1.0	1	1
T246	9	8(1)	9	8.7(0.3)	9	9
T686	11	11	12(1)	11.3(0.3)	11	11
T702	12	12	11(1)	11.07(0.3)	12	12
T710	2	2	2	2.0	2	2
T891	3	3	3	3.0	3	3
T937	4	4	4	4.0	4	4

These results show that the same sets of genotypes grown at different locations (but all within the S.A. wheat region) perform differently from site to site and that the ranks of nearly all the parents are affected. For example, T33 has gca-site interactions of 27.16, -27.30 and 0.14 for yield at the three sites (Table 6.4.1). The same parent has its gca's ranked as second, third and second at these three sites respectively.

The clear indication is that the plant breeder cannot grow plant material at only one site as there is no guarantee that the genotypes at one site will react in the same way as they would at different sites. In fact, the opposite would be expected to happen. This again emphasises the need for plant breeding programmes to be evaluated over as many sites as possible.

Because these effects are interactions they cannot be predicted beforehand but can only be obtained once the experiment has been grown at a site. The results in Chapter Four indicate that even the same site, at different years and in different paddocks, imposes different effects on experiments grown there. While the evidence in Chapter Four does not show that gca x site interactions will be different at the same site between years (and in different paddocks), it would be prudent for the plant breeder to believe so until proven otherwise.

By growing material at as many different sites as possible the breeder would hope to average out the gca-environment interactions and thus breed a plant which is well adapted to most sites within the region for which seed is being bred. This will probably mean

that no site will be ideally suited to a variety commercially released. However, the regional sites should all be within the range of environments for which the variety is adapted. This compares favourably with the concept of breeding at only one site, as here the variety would be unadapted to the other sites in the region (and perhaps also unadapted to the same test site in a different year and in a different paddock!).

As these gca-environment interactions are specific for each site used, and may also be specific to the paddocks and seasons within that site, prediction of this effect is not possible. However, as this interactive effect does not affect the values of the gca estimates themselves, it does not affect the overall use of diallels as cross predictors. That is, the gca environmental interactions are part of the "sca" variance component discussed in Chapter Five, and thus tabulating their values does not effect the gca values; it merely partitions the remaining interaction effect into one of its components (still remaining in this "sca" component are the sca values themselves, the sca-environment interaction effects and an error term). The values of the gca estimates for F_4 yield are shown, as an example, in Table 6.6. The estimates when the gca environment interactions are accounted for and when they are not accounted for is shown in this table in order to illustrate that the interaction effect does indeed come from the "sca" (and not the gca) component of the diallel analysis.

It is also worth noting that the diallel analysis for yield and height in the F_4 material removes approximately 60% (yield: 60.1%, height: 57.8%) of the variance by the procedure described

Table 6.6

GCA Estimates for the F_{II} yield in the triticales partial diallel. The estimates are shown for the case when the GENSTAT programme removes additive environmental effects and for the case when the programme also removes the gca environmental interaction effects.

Parent	GCA Estimate (Additive environmental effect)	GCA Estimate (Additive and interactive environmental effects)
T28	-6.66	-6.54
T31	9.45	9.26
T33	51.84	51.75
T34	-9.84	-9.51
T58	-14.57	-15.13
T106	-63.00	-62.84
T246	26.61	26.86
T686	-32.43	-32.10
T702	63.10	63.22
T719	-7.30	-7.29
T896	-78.02	-78.87
T937	60.83	61.19

in Chapter Five. When gca environment interactions are also removed by the analysis, the total variance removed by the least squares programme only increases by approximately two percent (yield: 62.2%, height: 60.3%).

In summary, a parallel can be drawn between the interactive environmental effects (sca as well as gca interactions) and the additive environmental effects, and the gca and sca effects previously described. In both cases the specific interactions (non-additive) are of importance but the breeder must work on the assumption that the additive effects alone will allow prediction of what would happen to cross families which have not been observed.

6.4 Describing the F_{II} Generation

6.4.1 Introduction

In plant breeding experiments replicates of a single genotype are often grown, and a mean and variance of these replicates are used by the plant breeder to objectively describe the genotype. Similarly, selections from families of genotypes may be grown, and then appraised according to their means and variances.

In the case of the single genotype grown in a replicated experiment, the variation within replicates reflects the genotype's responses to its different environments (within a single experimental site the environment would vary - refer to Chapter Four). When the replicates are of a family of genotypes, the variation reflects genotypic variation as well as environmental variation.

A problem for the plant breeder is to compare the different genotypes and/or families of genotypes which are represented in a breeding experiment. Clearly, two sets of genotypic observations with the same means but different variances should be evaluated differently by the plant breeder.

6.4.2 The F_{II} Diallel

The F_{II} diallel, as described in Chapter Five, illustrates a breeding experiment in which both replicates of a single genotype

(the parental lines) and selections from a family of genotypes (the F_4 's) are present. The means and standard deviations (square root of the variance) of the characters measured from these F_4 's are presented in Appendices III & IV.

If only the means of these genotypes, or genotype families, were to be appraised then the seventy-eight sets of genotypes (12 parents, 66 cross families) could easily be ranked and compared. However, if the variances are considered important then the comparison is more difficult. Statistically, comparisons may still be made between the genotypes by use of multiple comparison tests, such as Duncan's Multiple Range Test (Duncan, 1955), which takes into account both the mean and the variance of the samples. However, the plant breeder needs to appraise the genotypes in other ways than by just ranking them.

An F_4 family with a low mean but a high variance may be just as important to the breeder as an F_4 family with a high mean but a low variance. The breeder is interested in the F_4 selections within each family which have extremely high yield; the genotype family with the low mean but high variance may well have more genotypes in this extremely high yielding range than the genotype family with a high mean but a low variance.

If it is assumed that yield is normally distributed, then these relationships may be graphically represented. Given a mean and variance value, a probability distribution function for any bivariate normal distribution [$N(\text{mean}, \text{variance})$] may be plotted. Two such distributions are plotted in Figure 6.1; here both distributions have the same mean, but different variances. In

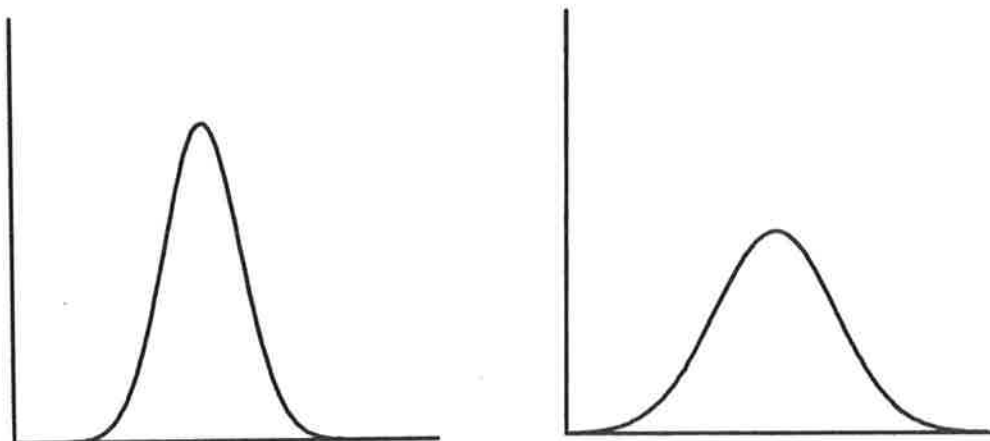


Figure 6.1: Two normal probability density functions with the same means but different variances.

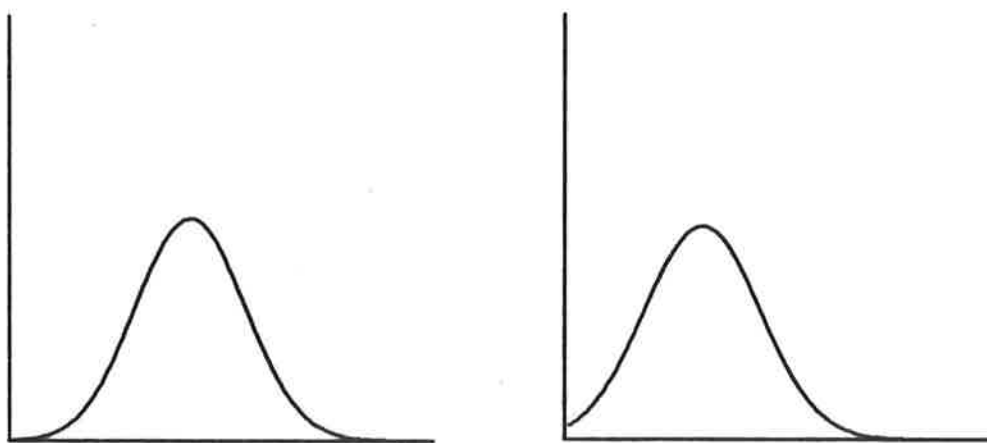


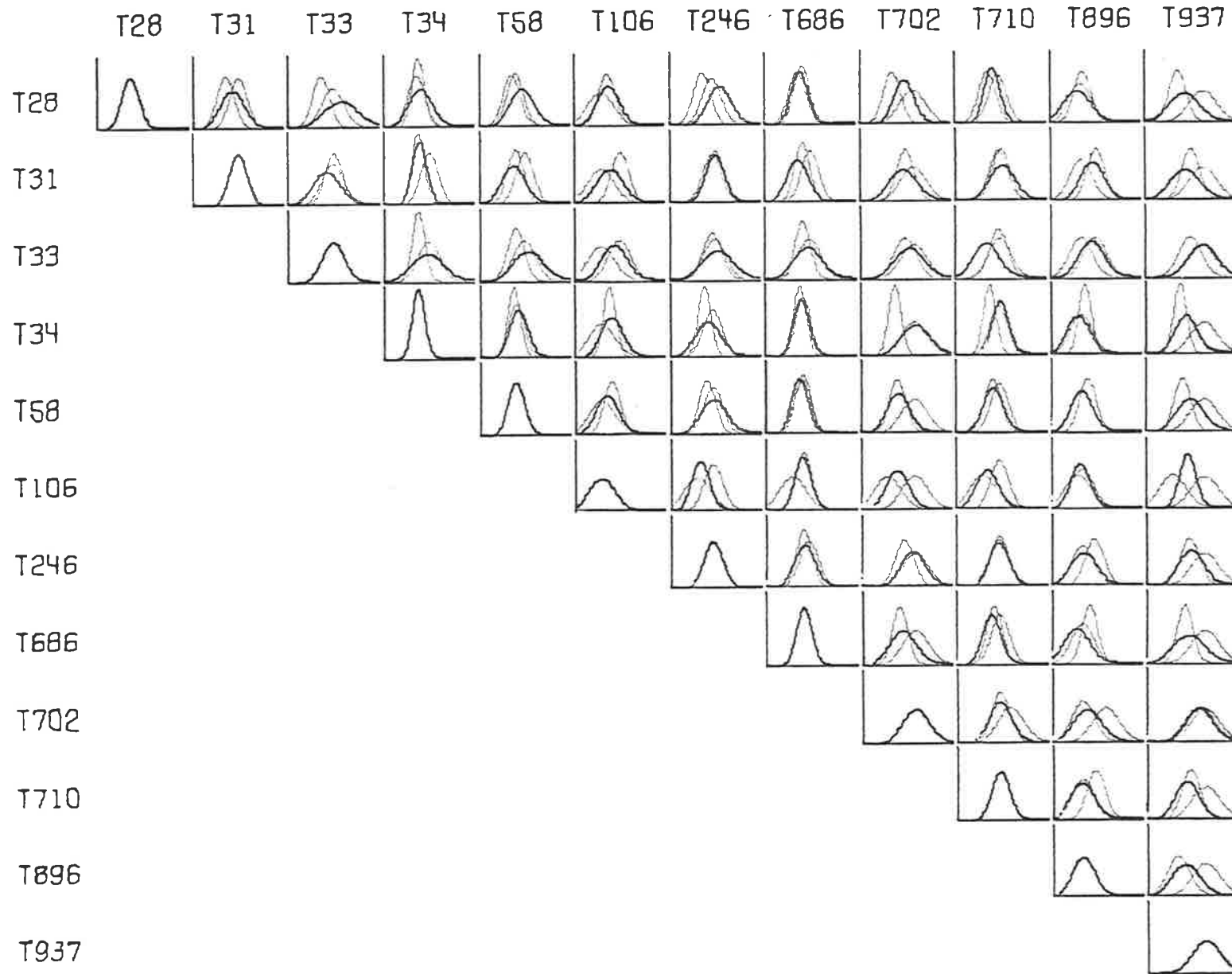
Figure 6.2: Two normal probability density functions with the same variances but different means.

Figure 6.2, both have the same variance but different means. [To aid comparisons axis scales on all these figures are the same.] As the area under each of these curves represents the probability of a particular x-axis value occurring, the total area under the curve is one. As would be expected, when the value of x is the mean value for the particular normal distribution, the area under the curve (from minus infinity to x) is equal to one half. Probability distribution functions such as these can therefore be used to approximate the probability of a particular range of x values occurring. For example, the probability of an x value falling between 100 and 200 is the area under the probability distribution function (PDF) between these two x coordinates (i.e. 100 and 200). Further explanation and details of the use of the univariate and bivariate normal probability distribution functions may be obtained from most elementary statistical textbooks (e.g. Sokal and Rohlf, 1969).

6.4.3 A Diallel of Probability Distribution Functions

Using the bivariate normal probability distribution function, graphs of the seventy-eight genotypes and/or genotype families of the F_4 triticales diallel are presented in Figure 6.3 (the yield values, after they had been adjusted for field heterogeneity are used here). All of these graphs are drawn to the same scale and thus direct comparisons may be made between these graphs. Three PDF's are drawn for each cross. These three PDF's represent the PDF of the cross (the thirty F_4 selections) and the two parental PDF's. The parental PDF's are the lighter plots and the F_4 PDF's are drawn in bold (as are the parents in the leading diagonal).

Figure 6.3: The normal probability density function for the F_4 triticales diallel described in this thesis. The light lines represent the parent PDF superimposed over the PDF of their F_4 progeny



These probability distribution functions can be evaluated by the breeder visually, by use of Figure 6.3, or statistically, by use of the areas under the curves. Both of these methods will be presented here separately and they will be further discussed in Chapter Seven.

6.4.3.1 Visually Appraising the Diallel of PDF's

A number of observations may be made from Figure 6.3. Perhaps the most notable, at least from the plant breeder's point of view, is that the variances of the F_4 's are no greater than, and in some cases less than, the parental variances. This can be numerically verified (cf. Appendix IV) and will be further discussed in Chapter Seven.

According to classical genetic theory, the cross families should have a higher variance than their (nearly) homozygous parents and that their mean should lie intermediate to the two parents. The cross of T28 x T31 is one such example. However, in most cases this type of result does not occur (e.g. T28 x T686). In many cases the PDF of the F_4 is virtually the same as one of the parents, whilst the other parent appears to have little effect (e.g. T106 x T686). To aid interpretation of these PDF's it should be noted that the higher the peak of each plot, the lower the variance, and that a higher mean is represented by the peak being shifted to the right. Thus T106 x T937, for example, has a mean intermediate between the two parents, but its variance is lower than both parents (cf. T686 x T937).

The cross T33 x T246 is a good example of what may be the ideal

distribution as far as the breeder is concerned. Here, the mean of the F_4 is higher than the mean of both parents and the variance of this F_4 is also higher than that of the two parents. The area between the right hand side of the PDF for this F_4 and the right hand side of the parental PDF's represents the probability of obtaining more F_4 individual selections in this range than would be obtained from the parents. However, it can also be seen that parent T937 has such a high mean and variance that any cross family would have difficulty beating it. As these graphs only describe the plot yields, F_4 's which do not have a yield higher than the parental means may still be important, provided that their yield is not significantly worse than the diallel parents.

As an example, T937 is a very high yielding triticale, however it has poor threshability (separation of the seed from the head is not easily done). The specialised equipment and the time available for harvesting in an experimental breeding programme cannot be economically mimicked by the farmer and thus the high yielding ability of T937 needs to be incorporated into an easily threshable variety. T702, although not as high yielding as T937, is easily threshed. The PDF of the T702 x T937 cross shows that little of the yielding ability of both parents is lost by the F_4 's. Thus a high yielding easily threshable F_4 may be able to be found from this cross. This cross should be compared to T34 x T937. Here, although T34 is easily threshable, and this characteristic may be found in the F_4 , much of the yielding ability of T937 has been lost.

Most breeding strategies suggest that a highly variable F_4

generation (that is, the F_4 selections are variable when viewed collectively) is a good thing for which to breed as this means that the extremes are more likely to occur. The more extremes of yield present in an F_4 the more chance a plant breeder has of selecting and isolating (genetically) these extremes. In the triticales diallel, however, this strategy is clouded by the high variance of the parental lines. In terms of variability a plant breeder would surely rather see a variety like T34 than T937. It may be that the genotype of T34 is more able to buffer itself against local environmental changes than T937. This "buffering" characteristic would certainly be desired by the plant breeder, as it would indicate a genotype which is adaptable to many environmental situations. [The gca site interactions for these two parents, presented in Section 6.3, also suggest this interpretation.]

If this interpretation is correct, then perhaps the breeder should be selecting from F_4 's with a small variance in order to ultimately release a variety which also has a small variance. The inheritance of variance will be discussed later in this Chapter. The question as to whether T106 x T937 is a better cross from which to select than T686 x T937, exemplifies the difficulty in deciding whether to select from an F_4 with low variance (low probability of extremes) or one with a high variance (high probability of extremes). [Both of the crosses have approximately the same means.]

6.4.3.2 Numerically Appraising the Diallel of PDF's

In Chapter Five the F_4 diallel was analysed by a least squares computer programme which used both the mean and variance of the

data "replicates" to obtain gca and other estimates. Table 6.7 shows the results of analysing the yield of the F_4 diallel by using only the mean values of each genotype, and/or genotype family, of the diallel. This is identical to the method used for the F_1 diallel. The results shown in this table are almost identical to those in the corresponding table in Chapter Five (Table 5.3.1). However, if the plant breeder wished to breed for a high (or low) yield variance rather than yield mean, the parents would be ranked in a completely different order. The results of using the variances of each of the F_4 's, for yield, are presented in Table 6.8.

Before discussing these tables in more detail, further extension of this idea will be presented, by using the area under the normal curve as the data points representing the genotypes in the diallel. Here, when a yield value of, say, 400 is chosen from the PDF of each of the genotypes in the diallel, a probability of exceeding (or not exceeding) this value may be obtained. It is these probabilities which may now be used as the data representing each of the genotypes in the diallel. Tables 6.9.1 to 6.9.3 show the results of a diallel analysis using these data values. The x values used for these tables are based on the sample population statistics for the entire diallel. They were, the mean plus one standard deviation, the mean plus one and a half standard deviations and the mean plus two standard deviations, for Tables 6.9.1 to 6.9.3 respectively. The probabilities used were the probabilities of not exceeding the particular value of x used. That is, the twelfth ranked parent has the highest probability of exceeding the values of x .

Table 6.7

F4	Yield		Mean				
	gca variance 2039	sca variance 2352	gca/sca variance ratio 0.87				
Variety	gca Ranks						Parent Rank
	(Bracketed numbers indicate deviation from P.D.ranks)						
	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p	
T28	6	8(2)	8(2)	9(3)	10(4)	10(4)	10(4)
T31	5	5	5	5	5	3(2)	3(2)
T33	3	3	1(2)	3	3	4(1)	4(1)
T34	8	9(1)	9(1)	8	9(1)	8	9(1)
T58	9	6(3)	7(2)	7(2)	6(3)	7(2)	8(1)
T106	11	11	11	11	11	12(1)	12(1)
T246	4	4	4	4	4	5(1)	6(2)
T686	10	10	10	10	8(2)	9(1)	7(3)
T702	1	1	3(2)	2(1)	1	2(1)	2(1)
T710	7	7	6(1)	6(1)	7	6(1)	5(2)
T896	12	12	12	12	12	11(1)	11(1)
T937	2	2	2	1(1)	2	1(1)	1(1)
Mean of Abs. Residuals	38.00	37.78	37.85	38.68	39.69	44.68	
S.D. of Abs. Residuals	29.83	39.83	31.92	30.95	30.71	32.91	

Table 6.8

F4	Yield		Variance				
	gca variance 8748227	sca variance 24344356	gca/sca var. ratio 0.36				
Variety	gca Ranks						Parent Rank
	(Bracketed numbers indicate deviation from P.D.ranks)						
	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p	
T28	7	7	6(1)	5(2)	5(2)	6(1)	9(2)
T31	5	5	8(3)	9(4)	9(4)	7(2)	8(3)
T33	1	1	1	1	1	2(1)	5(4)
T34	10	10	12(2)	10	11(1)	8(2)	12(2)
T58	8	9(1)	9(1)	8	7(1)	12(4)	10(2)
T106	9	8(1)	7(2)	7(2)	6(3)	4(5)	3(6)
T246	6	6	5(1)	6	8(2)	11(5)	6
T686	11	11	10(1)	11	12(1)	9(2)	11
T702	3	3	4(1)	3	3	3	2(1)
T710	12	12	11(1)	12	10(2)	10(2)	7(5)
T896	4	4	3(1)	4	4	5(1)	4
T937	2	2	2	2	2	1(1)	1(1)
Mean of Abs. Residuals	3875	3914	3972	3976	4016	4336	
S.D. of Abs. Residuals	3023	3019	3093	3087	3260	3368	

Table 6.9.1

F4 Yield Area 1 S.D. Under Normal Curve
 gca variance 0.0069 sca variance .0091 gca/sca var. ratio 0.76

Variety	gca Ranks						Parent Rank
	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p	
T28	7	7	7	6(1)	7	2(5)	2(5)
T31	8	8	8	8	6(2)	9(1)	9(1)
T33	10	10	11(1)	11(1)	10	10	10
T34	6	5(1)	3(3)	4(2)	4(2)	6	1(5)
T58	5	6(1)	5	7(2)	8(3)	5	4(1)
T106	1	1	1	1	3(2)	4(3)	6(5)
T246	9	9	9	9	9	8(1)	7(2)
T686	3	3	4(1)	3	2(1)	3	3
T702	11	11	10(1)	10(1)	11	11	11
T710	4	4	6(2)	5(1)	5(1)	7(3)	8(4)
T896	2	2	2	2	1(1)	1(1)	5(3)
T937	12	12	12	12	12	12	12
Mean of Abs. Residuals	0.072	0.070	0.071	0.072	0.073	0.079	
S.D. of Abs. Residuals	0.063	0.066	0.068	0.067	0.067	0.079	

Table 6.9.2

F4 Yield Area 1.5 S.D. Under Normal Curve
 gca variance 0.0025 sca variance 0.0044 gca/sca var. ratio 0.57

Variety	gca Ranks						Parent Rank
	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p	
T28	8	7(1)	7(1)	8	8	2(6)	2(6)
T31	7	8(1)	8(1)	5(2)	4(3)	9(2)	9(2)
T33	10	10	11(1)	11(1)	10	10	10
T34	6	6	3(3)	6	6	8(2)	1(5)
T58	5	5	6(1)	7(2)	7(2)	4(1)	4(1)
T106	1	1	2(1)	1	5(4)	6(5)	6(5)
T246	9	9	9	9	9	7(2)	8(1)
T686	3	3	4(1)	4(1)	3	3	3
T702	11	11	10(1)	10(1)	11	11	11
T710	4	4	5(1)	2(2)	2(2)	5(1)	7(3)
T896	2	2	1(1)	3(1)	1(1)	1(1)	5(3)
T937	12	12	12	12	12	12	12
Mean of Abs. Residuals	0.046	0.046	0.047	0.049	0.050	0.053	
S.D. of Abs. Residuals	0.047	0.049	0.050	0.048	0.048	0.057	

Table 6.9.3

F4 Yield Area 2 S.D. Under Normal Curve

gca variance 0.00067 sca variance 0.00161 gca/sca var.ratio 0.42

Variety	gca Ranks						Parent Rank
	P.D.	10c/p	8c/p	6c/p	4c/p	2c/p	
T28	6	8(2)	8(2)	9(3)	9(3)	2(4)	3(3)
T31	8	6(2)	6(2)	2(6)	3(5)	7(1)	8
T33	11	11	11	11	10(1)	10(1)	10(1)
T34	7	7	1(6)	6(1)	5(2)	9(2)	1(6)
T58	5	5	7(2)	7(2)	8(3)	5	4(1)
T106	1	4(3)	3(2)	3(2)	6(5)	8(7)	9(8)
T246	9	9	9	8(1)	7(2)	6(3)	7(2)
T686	4	3(1)	5(1)	5(1)	4	3(1)	2(2)
T702	10	10	10	10	11(1)	11(1)	11(1)
T710	2	1(1)	4(2)	1(1)	1(1)	4(2)	6(4)
T896	3	2(1)	2(1)	4(1)	2(1)	1(2)	5(2)
T937	12	12	12	12	12	12	12
Mean of Abs. Residuals	0.026	0.026	0.027	0.028	0.029	0.031	
S.D. of Abs. Residuals	0.030	0.030	0.031	0.029	0.029	0.034	

These five tables (Tables 6.7 to 6.9.3) give five different gca rank orders by which the plant breeder could make the selection of the best parents, and thus the best crosses. The area under the normal curve (Tables 6.9.1 to 6.9.3) combines many of the attributes discussed in previous sections of this chapter. The individual breeder would have to decide which of these gca ranks should be used for parental selection. As the gca/sca variance ratios for these five "character descriptors" range from 0.36 to 0.87, the critical nature of this statistic (refer to Chapter Two) may well influence the decision.

The stability, and hence the accuracy, of the gca ranks conforms, in these sets of analysis, to those of the simulated diallels (Chapter Two). Here, as in the simulated data and the previously presented F_1 and F_4 data, the incomplete partial diallels give the plant breeder most of the ranking information which could be obtained from the partial diallel. In most cases the six crosses per parent incomplete partial diallel ranks the gca's in a similar, or identical manner to the partial diallel.

The mean values of the parents, when ranked, give greatly different rankings from those of the partial diallel and thus cannot be used as an alternative to the incomplete partial diallel. [See discussions in Chapters Two, Three and Four for a more detailed account of interpreting, and evaluating the use to the plant breeder, of these tables (Tables 6.7 to 6.9.3).]

6.4.4 Discussion

The breeding strategies involving the further use of Tables 6.7

to 6.9.3 and Figure 6.3 will be examined in the following chapter.

As yield is the major agronomic trait concerning the cereal plant breeder, yield has been used as the example character throughout this section. However, as the behaviour of yield conformed with the other observed characters described in previous chapters, and as these in turn conformed with the more general simulations of Chapter Two, it was concluded that other quantitative characters could be treated and/or described in the same manner as yield.

General Discussion and Conclusions7.1 Introduction

The aim of this study was to investigate ways in which computers could be effectively used by plant breeders, other than for large-scale data analysis and information storage and retrieval. At the best of times quantitative genetics is a complex subject; for plant breeders, environmental effects and experimental errors make the subject even more complex. Because plant breeding involves large numbers of genotypes, grown in a large range of environments and usually with uncertainty regarding the relatedness of the plants, a computer could be an important tool to the plant breeder in rationalising this "chaos".

The previous chapters described a set of computer programmes which were written to investigate some of the problems faced by the plant breeder. Unless otherwise stated, all programmes were written in the PASCAL programming language, by the author. Before discussing the results of the various sets of analyses presented in this thesis, the way in which the programmes were designed and how they are used should be discussed. Obviously, if every plant breeder must first obtain a degree in computer science before these programmes can be used, then the programmes are of no benefit. For this reason the programmes have been written to be as general and as widely applicable as possible. The programmes are not in a "package" form but could easily be adapted for this purpose. The aim of this thesis was to evaluate the use of such

programmes rather than to develop them as a "software package"; once evaluated, the task of making them readily accessible can begin.

7.2 Using the Computer Programmes

The "master" programme reads data in the form of:

name, female parent, male parent, character set, site, observations.

The first three data are ten letter (or digit) names which are used to describe the genotype. If the parentage of a genotype is unknown or if it is an homozygous variety then "nil" is used to describe the parents. The next datum, "character set", defines the amount of information that will be supplied for this genotype. As storage in digital computers is an expensive resource, this datum is used to initiate a complex series of space saving actions involving the allocation of storage for each genotype.

In this study eleven F_1 characters and four F_4 characters were measured. To prevent having to use different programmes (or the same programme in a modified form) to ensure that only four sets of storage were allocated to the F_4 , whilst eleven were provided for the F_1 , the "character set" data is essential. For this thesis only two storage possibilities were defined, though provision was made to extend this to a much larger number of possibilities.

Once the genotype name and the "character set" of observations have been read by the computer, a set of "housekeeping" programmes

are initiated. Firstly a check is made to see whether that genotype already exists in "memory". If it does not then storage is allocated to it and the parental information given is used to insert it into a pedigree structure within computer memory. Once "placed" genetically within the programme, the data are read in and the mean, variance and N (number of observations) values for the genotype for the site at which it was grown are recorded. The programme will accept as many replicates from each site as the user wishes.

When all the data have been read by the programme the user has the following information:

- (a) The pedigree of each genotype . Procedures can be called to list all related genotypes (in order of relatedness).
- (b) The means and variances of all the genotypes for each site, as well as an overall mean (this overall mean will not, however, be adjusted to compensate for site effects).
- (c) The means and variances for each observed character at each site, for all the genotypes.

The user may, for example, wish to list all genotypes related to T937, with some or all of their respective mean and variance values for the measured character traits. This type of information is available to the user (plant breeder) by issuing a single procedure call (four words).

When the data have been read, the least squares procedures can be utilised to perform the "diallel type" analysis illustrated in earlier chapters. The PASCAL programme will only perform such analyses for each site independently; if all sites are to be analysed, then the programme creates a data file suitable for analysis by the GENSTAT programme. Further PASCAL and FORTRAN procedures then read the GENSTAT programme output and store the information for easy presentation to the plant breeder.

Similarly, another programme reads in the field data (in plot order), sorts the data into the appropriate genotypes (unrandomises the experiment), performs the control plot analysis and then prepares a data file for the "master" programme.

In preparing the statistical components of these programmes, flow charts, advice, and in some cases similar FORTRAN subroutines were provided by Dr. P.A. Baghurst and Mr. T.W. Hancock of the Waite Institute's Biometry Section.

Once combined into a "software package", the workings of these programmes would be effectively hidden from the plant breeder, so that only the knowledge regarding the preparation of the initial data and how to ask for the required information is needed (i.e. about twenty commands). Integration of these programmes with the experimental field layout programmes used by the Agronomy Department, Waite Institute (Rathjen & Lamacraft, 1972) would simplify the use of this programme even further.

7.3 Genotypic Analyses

The results presented in the previous chapters show that the simulation of a plant breeding experiment can be used to accurately describe certain genetic and agronomic conditions. The use of the word "diallel" is perhaps unfortunate, as the crossing designs which may be analysed by the least squares analyses, presented here, do not have to be so rigidly defined. The programme will in fact attempt to analyse a "diallel" consisting of only one cross, or any combination or number of crosses.

Use of this procedure to analyse a random set of crosses was discussed in Chapter Two. The simulation results show that such random crossing designs, although having limitations, are capable of providing important and accurate information to the plant breeder. Although virtually any set of crosses may be analysed by the programme, the breeder must be prepared to exercise judgement in their interpretation. If the crosses used are systematic (e.g. incomplete partial diallels suggested in this thesis, top cross method, North Carolina II) then the plant breeder can interpret the results more confidently.

This study has also implied that these other crossing designs may also be simulated in order to observe their effectiveness. The diallel method was not selected because it was considered to be the optimum or "best possible" crossing system, but because it is easily generalised and because it is well suited to a relatively unselected inbreeding crop such as triticale. The term "diallel" can be generalised to such an extent that its incomplete partial diallel can be used to describe all crossing systems

(except those involving backcrosses or the hybridisation of already hybridised material, e.g. F/1xF/1). Hinkelmann (1976), in a review of diallels and multi-cross designs, concludes by saying:

"How can one utilize this information [from a crossing design] to the maximum possible extent in breeding work? That ultimately determines the usefulness of these experiments."

One of the purpose of this study was to determine whether this "utility" could in fact be tested for various designs. The simulation testing of various designs may be approached with a high degree of confidence in view of the confirmation, of these simulation methods, given by the triticales diallel results.

The difficulty in simulating designs is, of course, that large plant breeding resources are needed in order to test that the simulations do in fact reflect a biological situation. The similarities between the triticales diallel and the simulation results cannot of course be extrapolated to all species under all conditions, however they do show that the principle of simulating a crossing design works effectively.

7.4 Implications for the Plant Breeder

It must be stressed that the information gained by plant breeders from the types of analyses proposed in this thesis is not intended to give them definitive instructions. Rather it is

intended to supply them with as much clear and concise information as possible so that informed decisions may be made. If information is not detailed enough, or if the information is too detailed (so that an overview is not possible) then modifications in the presentation of the material should be made.

Examples of uses to which the programmes outlined in this thesis could be put by the plant breeder are summarised below:

- A set of potential parents is chosen. As six crosses per parent yields an incomplete partial diallel which gives accurate gca rank information, this would be a good size IPD to use (Chapters Two, Three and Five). The number of parents used depends on the number of crosses that the breeder can manage. [The six crosses per parent IPD requires $3 \times P$ F_1 's, where P is the number of parents.]
- F_1 plants can then be grown out of season (if possible) so that the F_2 generation can be grown as soon as possible. Using the scheme outlined for the triticale diallel in this thesis, the remaining F_1 seed can be grown in the same season as the F_4 diallel. [In an half-year seasonal crop, this process would take two years - if some generations were grown out of season.]
- The diallel analysis can now be used in order to determine which are the highest ranking gca parents for the character traits considered important by the

plant breeder. If the gca/sca variance ratio is estimated to be approximately one or greater, then the additive genetic component of that character will be a good predictor of cross potentials. In this case only the most promising crosses need be further investigated. If the gca/sca variance ratio is unfavourable, then more crosses will have to be used. Some of these crosses will already have been made; thus thirty random F_4 selections from these selections will already be available from which the plant breeder may select. Other crosses will have to be made.

It is at this final point that the plant breeder has to make a set of decisions based on the information available. Assuming that the plants have been ranked according to their gca values, and therefore a set of "optimum" crosses may be forecast, important decisions still have to be made. If the crosses which the breeder already has at the F_4 generation are ignored (for the purposes of this discussion), then the breeder has to decide on the breeding methodology which will be used (Section 1.4).

With a low gca/sca variance ratio, many parents and thus many crosses would have to be used by the breeder, as the ranking and importance of the gca effects are not accurately known. Using many crosses, the breeder would probably be limited to the use of a bulk selection method or a method which selects in early generations (Section 1.3). However, with many crosses, methods which select in early generations are usually expensive in both resources and time, and they are also often ineffective within crosses.

A high gca/sca variance ratio means that only a few parents, and

thus crosses, need be made. Here, then, the pedigree or the F_2 selection method may be employed. The diallel analysis of the F_4 , is effectively an example of this method, except of course that selection at the F_2 generation was random. Use of this method may now be reassessed in view of the additional information the plant breeder has about the crosses to be made.

One of the main disadvantages of the pedigree method is that selection in the F_2 may cause potentially high yielding lines to be discarded. [Yield, being the most important agronomic character for most crops, will be discussed for most of this section. As yield is only one of the quantitative characters treated in this thesis, the discussion may also be applied to other quantitative characters.] The only way to ensure that high yielding lines are not lost is to carry all lines on towards homozygosity before making any selection. This is, of course, impossible, because of the large number of homozygotes which would have to be grown. However, the larger the number of F_4 selections grown, the greater the probability that promising lines will be found.

The problem for all plant breeders is that, because of economical and physical constraints, only a certain amount of material can be grown in any one year. Thus, for example, if a breeder could only grow 1000 F_4 plots, a decision would have to be made as to how many genotypes should be represented in these 1000 plots.

Here the breeder's problem becomes philosophical. If the best cross is known (by prediction from the diallel results), then

perhaps only one cross family should be grown, with 1000 selections. The breeder can then pick "the best from the best". If the breeder is unsure of the diallel predictions (because of a low gca/sca variance ratio), then more genotypes should be grown, but not necessarily with the same number of selections from each genotype. The best predicted cross may have 500 selections, the next best 250 selections, etc.

On the other hand, the opposite strategy could be used. If the breeder knows (predicts) that a cross will give a high proportion of high yielding F_4 's, then not many F_4 selections need be grown in order to isolate a high yielding one. Conversely, if it is known (predicted) that a cross will give a low proportion of high yielding F_4 plots, then perhaps a large number of this cross should be grown in order to try to find the high yielders. This argument is subjective and many other factors will also influence the breeder's decision. For example, if the plant breeder is trying to breed for more than one quantitative character (e.g. yield and maturity time), then more than one set of gca ranks must be appraised by him. It is not intended that diallel analysis should answer the "philosophical" problems, but rather that it should provide the plant breeder with the necessary information on which to base the debate.

Ranking the parental gca's is a relatively easy task; ranking the potential crosses is not so simple. The highest potential cross is, trivially, that of the two highest ranking parents (ranked according to gca). The second highest ranking cross, however, may be parent two x parent three, or parent one x parent three. It is, therefore, safest for the plant breeder to choose

the top P parents and then use all the crosses between these parents. For example, a fifty parent six crosses per parent incomplete partial diallel would involve one hundred and fifty crosses; if after the diallel analysis the top five (gca) ranked parents are to be used by the breeder, then only ten crosses need be made $[(5 \times 4) / 2]$.

The gca estimates themselves, however, are not accurate for the incomplete partial diallel, only their ranks are. Thus the range of the gca estimates is not accurately known. For example, if the five top ranked parents had gca values of 5, 4, 3, 2 and 1 they would be ranked in the same order as if their gca values had been 500, 499, 200, 20 and 1. The ranks remain constant but the gca values themselves are different relative to each other. In the first example all the parents are fairly close in their gca values and thus there is not a great difference between the first and the fifth ranked parents. In the second example, however, there is a large difference between the first and the fifth ranked parents. As accurate estimation of the gca values (as opposed to their ranks) is not obtainable from the incomplete partial diallels, the plant breeder cannot measure these distances and thus should treat all the top (gca) ranked parents as equal (for the purpose of intercrossing them). Table 7.1 shows the gca values for the F_4 character yield as calculated from the partial and the incomplete partial diallels. It can be seen from this table that the ranks of the gca values are far more stable than their numeric values when the diallel is reduced to its incomplete partial diallel subsets.

The results from the F_4 triticales diallel show that the

Table 7.1

The gca values, and their ranks, for the F₄ character yield. The gca values for the partial and the incomplete partial diallels are shown [i.e. 2, 4, 6, 8 and 10 crosses per parent (c/p)]

	Incomplete Partial Diallels					Partial diallel
	2 c/p	4 c/p	6 c/p	8 c/p	10 c/p	
T28	-40.61	-23.09	-22.58	-15.42	-13.27	- 6.66
T31	27.53	3.30	5.55	13.66	15.48	9.45
T33	24.56	53.80	62.93	65.69	54.67	51.84
T34	-12.46	-16.48	-17.46	-21.64	-14.29	- 9.84
T58	- 7.45	0.31	-10.20	-11.90	-12.36	-14.57
T106	-77.11	-64.89	-65.86	-67.06	-62.97	-63.00
T246	10.69	17.68	20.96	18.91	20.02	26.61
T686	-15.69	-14.84	-26.16	-26.66	-26.62	-32.43
T702	66.20	66.71	62.81	57.59	66.04	63.10
T710	4.74	- 9.91	- 4.96	- 0.13	-11.78	- 7.30
T896	-66.87	-75.74	-74.18	-75.40	-75.74	-78.02
T937	86.46	63.14	69.15	62.36	60.85	60.83

prediction of cross performance from the incomplete partial diallel ranks does reflect the performance of these crosses. The highest ranked parents for yield were T937, T33 and T702 (for the six crosses per parent IPD - Table 5.3.1). Appendix Three shows the observed values of the F_4 diallel (all sites); the cross T33xT937 is in fact the highest yielding F_4 family. T33xT702 is merely the seventh highest yielding F_4 family, but only one of the six crosses which are higher yielding did not have a parent in the top three ranked parents [T246xT28 (rank 4xrank 9)]. Thus the gca ranks for the triticale diallel do reflect the yield potential of the crosses. If the top five ranked parents from the six crosses per parent IPD were used, then the above cross, T246xT28, would still not have been used; however, most of the high yielding crosses would have been. [see Appendices Two, Three and Four for comparison with the results of Tables 3.3.1 to 3.3.11 and Tables 5.3.1 to 5.4.2 and Tables 6.7 to 6.9.3].

In addition to the gca ranks, the plant breeder may be able to use graphical information of the type provided in Chapter Six (Figure 6.3). Here the plant breeder may make a further visual appraisal of the high ranking gca parents. The top three ranked parents are identifiable from Figure 6.3. T33, T702 and T937 all have a high mean and variance value. T33 has F_4 's with a variance value which tends to be larger than the parental variance, T702 has similar F_4 variance to the parental variance and T937 tends to have a higher variance than its F_4 's. Strategies for selecting F_4 families with high or low variances were discussed in Chapter Six, and this is a subjective decision which would have to be made by the plant breeder.

A disturbing feature of the F_4 diallel is the relatively high variance of the parental lines as compared to the F_4 families. If the parental lines are homozygous, then their observed variances should be small. This creates a large conceptual problem for the plant breeder: when a high yielding parental plot is harvested, and as many plots are grown in the next season, the mean and variance (excluding seasonal and environmental effects) over the two years for the parental genotype plots should be the same. Conversely, if the same procedure was carried out on an F_4 family, the plant breeder would expect the subsequent years' plots to have a higher mean value (and perhaps a lower variance value). This latter concept is the basis of all breeding strategies. It should, however, be noted that site x year and variety x year effects are frequently very large (Patterson et al. 1977).

A possible explanation of this feature is that the variance of the parental plots is due to environmental effects (cf. Qualset, 1968). These same environmental influences must be operating on the F_4 families. However, unless the F_4 family variance is due largely to genotypic differences, breeder selection would be a useless process.

This paradoxical situation may be due to the mixture of (partially) heterozygous genotypes in the F_4 plots being able to compensate, or buffer, against local environmental effects. The parental lines, being a pure (homozygous) stand, would have no such buffering ability. Thus by the mixture (F_4) compensating for environmental differences between plots, the F_4 families would be less variable than the parental lines. As this "mixture" effect would be counterbalanced by the genotypic differences

between F_4 family plots, the "status quo" between the F_4 families and the parents would remain, and similar variances would be observed. This hypothesis is an attempt to explain the apparent anomaly which occurs between the parental variances and the F_4 family variances; its validity would have to be established by future experimentation.

The correlations that are evident between the F_1 and the F_4 characters were discussed in Chapter Six. It is clear that a number of F_1 character traits are positively correlated with yield; however, as explained in the previous chapter, it is difficult to interpret these correlations from a plant breeding standpoint.

One of the major significant correlations present in Chapter Six is the relationship between F_1 harvest index and the F_4 yields. It appears that an F_1 with a high harvest index should produce high yielding F_4 progeny. The number of seed in the tallest tiller also correlated highly with F_4 yield [Spearman's correlation coefficient between F_4 yield and F_1 harvest index was 0.5547 and between F_4 yield and the number of seeds in the tallest tiller was 0.4861, see Table 6.3]. If a plant breeder was going to use such correlations for a breeding programme, then it would probably be to his advantage to use "seed in tallest tiller" rather than "harvest index". For harvest index is a ratio of two other measured F_1 traits, and the biological effect of this ratio may or may not be independent. If the components of harvest index (total biological weight and grain yield) are not independent, then correlations using harvest index may cause spurious results. Because the interpretation of harvest index is controversial, and

because there is another viable alternative (seed in tallest tiller), it seems that the best course is the conservative one (for a more detailed treatment of the use of harvest index, as a selection criteria, see Donald & Hamblin (1976)).

Assuming that a correlation exists between any F_1 character trait and F_4 yield, it is nevertheless debatable whether this correlation should be used as the sole selection criterion. As only dominance effects will be observed in the F_1 generation, later generation progeny would have the opportunity to display many phenotypic variations which would not be visible in the F_1 . Some of these combinations may be desired by the plant breeder; however, if only the "promising" F_1 's are taken on to further generations, it is likely that many of these desirable phenotypes would not be found. Similarly, as alleles at many loci control one quantitative trait, it is their interaction in genotypes segregating for different combinations of these alleles which may be of interest to the plant breeder. These segregating "multigene" lines would also only be observable in generations beyond the F_1 .

If selection is delayed as long as possible, then a measure can be made of the range of these allelic combinations. The F_4 triticales diallel described in this thesis was designed to measure, as far as possible, this variation. The more F_4 selections that are grown, the more accurate will be the measure of this genotypic variation within an F_4 family. However, here the problem of resources available to the plant breeder is often the deciding factor as to how many selections are actually grown.

The number of F_4 plots observed in each family also dictates the degree of certainty with which the normal distribution curves (Figure 6.3) can be interpreted. Deviations from normality can be measured by two statistics - skewness and kurtosis. Skewness occurs when more observations are found near one end of the curve than the other; kurtosis is characterised by a disproportionate number of observations either near the mean or near the tails of the normal PDF curve. Unfortunately, thirty observations is too few to obtain accurate measurements of these two deviations from normality. If the thirty observations did show signs of these deviations, then perhaps more F_4 selections should have been grown, in order to determine these statistics accurately. [This would presumably have to be at the expense of investigating fewer families.] Fortunately, but not definitively, the seventy-eight genotypes observed in the diallel, with only three exceptions, showed little or no deviation from the normal in terms of these measures.

7.5 Conclusion

Many of the results given in this thesis were produced by a computer programme in order to mimic the thought processes that a plant breeder may follow when evaluating a breeding programme. Data are summarised, tabulated and presented in various ways so that the plant breeder may have as much information available as possible.

Despite the genetic and environmental complexities of evaluating parents for a breeding programme, accurate computer simulations, using the diallel model, are possible. These simulations have

accurately reflected the phenotypic observations of a twelve parent triticales diallel.

Also, it has been shown that a substantial proportion of environmental variation (within and between sites) can be removed from experimental breeding trials. The extent of this environmental variation and the inconsistency of genotypic interactions within and between sites make it imperative for the plant breeder to use as many sites as possible.

In principle, as soon as a design, analysis, storage or presentation problem is converted by the breeder to a pragmatic rather than a theoretical one, a computer programme should be capable of solving it, thus freeing the plant breeder to pursue further theoretical problems.

Appendix I

The means and standard errors of the percentage of parents, in all the simulated diallels, which did not change rank, or which changed in rank by up to nine or less (ten tables for each diallel size), when the incomplete partial diallel analysis is compared to the partial diallel analysis.

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 0 OR LESS. REPLICATES = 100. NUMBER OF PARENTS=15.

GCA/SCR Variance Ratio	2 C/P 15/ 105	14.3%	4 C/P 30/ 105	28.6%	6 C/P 45/ 105	42.9%	8 C/P 60/ 105	57.1%	10 C/P 75/ 105	71.4%
1024.0	95.47	0.69	95.87	0.68	97.73	0.54	97.33	0.54	98.53	0.42
256.0	91.03	0.66	93.40	0.63	93.17	0.64	95.07	0.55	97.03	0.44
64.0	83.58	0.78	85.58	0.74	87.49	0.68	90.38	0.62	93.60	0.50
16.0	69.33	0.80	75.03	0.76	78.98	0.73	82.82	0.67	87.03	0.60
4.0	54.27	0.75	59.73	0.70	65.49	0.70	71.35	0.66	77.13	0.66
1.0	33.69	0.59	38.74	0.65	45.16	0.64	52.06	0.63	60.31	0.64
0.2500	22.57	0.55	25.92	0.57	31.79	0.61	36.08	0.63	43.53	0.69
0.0625	15.33	0.52	18.13	0.52	21.92	0.58	25.22	0.64	32.18	0.74
0.0156	13.69	0.52	15.49	0.61	17.58	0.59	21.91	0.70	26.51	0.74
0.0039	13.40	0.61	15.00	0.64	16.03	0.73	18.97	0.87	23.63	0.86
0.0010	10.93	0.86	13.40	0.89	14.93	1.03	19.20	1.18	24.93	1.30

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 1 OR LESS. REPLICATES = 100. NUMBER OF PARENTS=15.

GCA/SCR Variance Ratio	2 C/P 15/ 105	14.3%	4 C/P 30/ 105	28.6%	6 C/P 45/ 105	42.9%	8 C/P 60/ 105	57.1%	10 C/P 75/ 105	71.4%
1024.0	99.87	0.13	100.00	0	100.00	0	100.00	0	100.00	0
256.0	99.57	0.14	99.67	0.12	99.70	0.12	99.93	0.05	99.97	0.03
64.0	98.09	0.26	98.80	0.19	99.16	0.19	99.62	0.10	99.76	0.08
16.0	94.07	0.39	95.52	0.33	97.20	0.27	97.83	0.22	98.87	0.17
4.0	85.61	0.51	90.11	0.40	92.96	0.37	95.17	0.30	96.77	0.25
1.0	68.43	0.58	74.51	0.55	80.30	0.49	85.31	0.47	89.96	0.41
0.2500	50.99	0.61	56.71	0.64	63.79	0.64	70.12	0.61	78.27	0.58
0.0625	38.38	0.69	43.30	0.71	50.17	0.72	55.85	0.73	64.13	0.72
0.0156	33.76	0.73	38.29	0.78	42.58	0.79	48.89	0.84	57.36	0.85
0.0039	33.80	0.87	37.07	0.92	39.93	0.94	45.57	1.09	52.50	1.04
0.0010	29.67	1.28	33.60	1.31	37.80	1.34	45.73	1.56	52.80	1.52

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 2 OR LESS. REPLICATES = 100. NUMBER OF PARENTS=15.

GCA/SCR Variance Ratio	2 C/P 15/ 105	14.3%	4 C/P 30/ 105	28.6%	6 C/P 45/ 105	42.9%	8 C/P 60/ 105	57.1%	10 C/P 75/ 105	71.4%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	99.73	0.09	99.93	0.04	99.98	0.02	99.96	0.03	100.00	0
16.0	99.13	0.14	99.45	0.11	99.72	0.08	99.80	0.07	99.97	0.02
4.0	96.27	0.25	97.45	0.21	98.88	0.15	99.25	0.11	99.51	0.10
1.0	84.87	0.46	89.98	0.38	93.40	0.31	95.74	0.27	97.84	0.20
0.2500	69.37	0.61	75.84	0.56	82.12	0.53	86.77	0.47	92.13	0.39
0.0625	55.92	0.68	62.03	0.70	68.20	0.69	74.53	0.69	82.03	0.61
0.0156	50.89	0.82	56.27	0.82	61.49	0.82	67.20	0.78	75.36	0.73
0.0039	49.53	1.00	52.63	1.00	58.07	0.94	64.70	1.07	72.43	0.98
0.0010	45.00	1.52	51.13	1.36	55.60	1.47	64.60	1.40	73.07	1.23

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 3 OR LESS. REPLICATES = 100. NUMBER OF PARENTS=15.

GCA/SCR Variance Ratio	2 C/P 15/ 105	14.3%	4 C/P 30/ 105	28.6%	6 C/P 45/ 105	42.9%	8 C/P 60/ 105	57.1%	10 C/P 75/ 105	71.4%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	99.98	0.02	100.00	0	100.00	0	100.00	0	100.00	0
16.0	99.80	0.07	99.90	0.05	99.97	0.02	99.98	0.02	100.00	0
4.0	99.11	0.13	99.53	0.09	99.85	0.04	99.95	0.03	99.93	0.04
1.0	93.18	0.33	96.19	0.24	97.87	0.19	98.86	0.15	99.44	0.11
0.2500	81.95	0.53	87.29	0.43	91.28	0.39	94.31	0.33	97.32	0.24
0.0625	69.65	0.67	75.33	0.61	81.60	0.56	86.68	0.52	91.25	0.43
0.0156	64.07	0.86	69.00	0.85	74.62	0.79	79.60	0.66	86.04	0.60
0.0039	62.97	0.96	66.47	0.96	71.37	0.90	77.03	0.92	83.67	0.79
0.0010	58.87	1.44	65.33	1.32	69.27	1.46	76.60	1.29	85.13	1.05

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 4 OR LESS. REPLICATES = 100. NUMBER OF PARENTS=15.

GCA/SCR Variance Ratio	2 C/P 15/ 105	14.3%	4 C/P 30/ 105	28.6%	6 C/P 45/ 105	42.9%	8 C/P 60/ 105	57.1%	10 C/P 75/ 105	71.4%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	99.93	0.04	99.98	0.02	100.00	0	100.00	0	100.00	0
4.0	99.79	0.06	99.91	0.04	99.99	0.01	100.00	0	100.00	0
1.0	97.24	0.22	98.76	0.14	99.28	0.11	99.64	0.08	99.89	0.04
0.2500	89.65	0.44	93.25	0.33	96.08	0.26	97.87	0.20	99.01	0.14
0.0625	79.93	0.57	85.08	0.52	89.92	0.44	93.47	0.38	96.62	0.28
0.0156	73.76	0.78	79.02	0.77	84.22	0.67	88.27	0.58	92.40	0.47
0.0039	73.17	0.91	76.83	0.83	82.00	0.82	85.53	0.76	91.30	0.63
0.0010	70.13	1.37	75.53	1.16	80.80	1.09	86.33	0.94	92.20	0.89

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 5 OR LESS. REPLICATES = 100. NUMBER OF PARENTS=15.

GCA/SCR Variance Ratio	2 C/P 15/ 105	14.3%	4 C/P 30/ 105	28.6%	6 C/P 45/ 105	42.9%	8 C/P 60/ 105	57.1%	10 C/P 75/ 105	71.4%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	99.98	0.02	100.00	0	100.00	0	100.00	0	100.00	0
4.0	99.97	0.02	99.99	0.01	100.00	0	100.00	0	100.00	0
1.0	99.02	0.12	99.56	0.08	99.72	0.07	99.89	0.05	99.97	0.02
0.2500	94.53	0.30	97.03	0.21	98.57	0.16	99.33	0.11	99.80	0.06
0.0625	87.13	0.46	91.50	0.42	94.38	0.32	96.92	0.26	98.93	0.14
0.0156	81.84	0.65	86.53	0.60	90.80	0.53	93.38	0.43	96.36	0.35
0.0039	80.63	0.83	84.77	0.73	88.90	0.68	91.97	0.60	96.13	0.39
0.0010	77.67	1.23	83.33	1.06	87.53	0.94	91.53	0.75	96.47	0.61

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 6 OR LESS. REPLICATES = 100. NUMBER OF PARENTS=15.

GCA/SCR Variance Ratio	2 C/P 15/ 105	14.3%	4 C/P 30/ 105	28.6%	6 C/P 45/ 105	42.9%	8 C/P 60/ 105	57.1%	10 C/P 75/ 105	71.4%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
4.0	99.99	0.01	100.00	0	100.00	0	100.00	0	100.00	0
1.0	99.64	0.07	99.86	0.05	99.90	0.04	99.96	0.03	99.99	0.01
0.2500	97.49	0.20	98.71	0.13	99.61	0.08	99.85	0.05	99.92	0.03
0.0625	92.13	0.39	94.92	0.31	97.07	0.23	98.77	0.16	99.67	0.09
0.0156	87.42	0.55	91.80	0.45	94.67	0.41	96.42	0.33	98.36	0.21
0.0039	87.40	0.65	90.07	0.57	93.13	0.55	95.23	0.44	97.93	0.28
0.0010	86.07	1.00	89.33	0.86	93.00	0.74	95.40	0.60	98.40	0.38

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 7 OR LESS. REPLICATES = 100. NUMBER OF PARENTS=15.

GCA/SCR Variance Ratio	2 C/P 15/ 105	14.3%	4 C/P 30/ 105	28.6%	6 C/P 45/ 105	42.9%	8 C/P 60/ 105	57.1%	10 C/P 75/ 105	71.4%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
4.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
1.0	99.87	0.04	99.94	0.03	99.99	0.01	99.99	0.01	100.00	0
0.2500	98.56	0.15	99.45	0.09	99.91	0.04	99.95	0.03	99.96	0.02
0.0625	95.67	0.28	97.48	0.22	98.60	0.17	99.55	0.09	99.95	0.03
0.0156	91.98	0.46	95.20	0.36	96.82	0.30	98.16	0.22	99.31	0.13
0.0039	92.20	0.50	94.27	0.42	96.23	0.35	97.70	0.33	99.23	0.17
0.0010	91.33	0.86	93.67	0.72	96.20	0.49	97.80	0.39	99.40	0.19

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 8 OR LESS. REPLICATES = 100. NUMBER OF PARENTS=15.

GCA/SCR Variance Ratio	2 C/P 14.3%		4 C/P 28.6%		6 C/P 42.9%		8 C/P 57.1%		10 C/P 71.4%	
	15/ 105		30/ 105		45/ 105		60/ 105		75/ 105	
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
4.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
1.0	100.00	0	99.98	0.02	100.00	0	100.00	0	100.00	0
0.2500	99.36	0.09	99.79	0.05	99.97	0.02	99.99	0.01	99.99	0.01
0.0625	97.75	0.20	98.82	0.14	99.38	0.12	99.83	0.05	99.98	0.02
0.0156	95.38	0.34	97.31	0.25	98.31	0.21	99.11	0.17	99.73	0.08
0.0039	95.40	0.42	96.53	0.35	98.03	0.27	98.87	0.20	99.73	0.09
0.0010	94.73	0.59	97.27	0.39	98.00	0.35	98.93	0.26	99.93	0.07

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 9 OR LESS. REPLICATES = 100. NUMBER OF PARENTS=15.

GCA/SCR Variance Ratio	2 C/P 14.3%		4 C/P 28.6%		6 C/P 42.9%		8 C/P 57.1%		10 C/P 71.4%	
	15/ 105		30/ 105		45/ 105		60/ 105		75/ 105	
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
4.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
1.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
0.2500	99.77	0.05	99.96	0.02	100.00	0	100.00	0	100.00	0
0.0625	99.00	0.13	99.55	0.09	99.80	0.06	99.93	0.03	100.00	0
0.0156	97.33	0.25	98.40	0.20	99.22	0.15	99.60	0.10	99.91	0.04
0.0039	97.03	0.33	98.23	0.26	99.00	0.18	99.47	0.13	99.97	0.03
0.0010	96.87	0.48	98.40	0.30	99.13	0.24	99.60	0.16	100.00	0

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 0 OR LESS. REPLICATES = 50. NUMBER OF PARENTS=20.

GCA/SCR Variance Ratio	2 C/P 20/ 190	10.5%	4 C/P 40/ 190	21.1%	6 C/P 60/ 190	31.6%	8 C/P 80/ 190	42.1%	10 C/P 100/ 190	52.6%
1024.0	91.00	1.12	93.40	1.05	94.00	1.03	94.30	1.05	95.60	1.04
256.0	87.30	0.99	88.60	1.03	90.90	0.97	91.85	0.88	92.95	0.77
64.0	77.87	1.03	81.27	0.99	85.23	0.90	86.70	0.88	88.30	0.87
16.0	62.82	0.91	68.45	0.99	72.30	0.87	76.25	0.84	78.63	0.83
4.0	43.54	0.81	49.48	0.87	55.56	0.93	59.56	0.92	64.40	0.87
1.0	25.67	0.64	29.95	0.69	36.22	0.70	39.52	0.80	44.95	0.80
0.2500	15.78	0.58	19.62	0.57	22.24	0.66	24.86	0.67	28.42	0.66
0.0625	11.95	0.52	13.87	0.55	15.20	0.63	16.70	0.64	19.65	0.71
0.0156	9.00	0.53	10.33	0.55	11.80	0.68	12.17	0.68	15.13	0.64
0.0039	8.95	0.64	9.90	0.72	12.10	0.80	13.40	0.81	15.80	0.81
0.0010	9.60	0.99	10.90	1.00	10.30	0.84	14.40	1.34	14.40	1.21

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 1 OR LESS. REPLICATES = 50. NUMBER OF PARENTS=20.

GCA/SCR Variance Ratio	2 C/P 20/ 190	10.5%	4 C/P 40/ 190	21.1%	6 C/P 60/ 190	31.6%	8 C/P 80/ 190	42.1%	10 C/P 100/ 190	52.6%
1024.0	100.00	0	100.00	0	100.00	0	99.90	0.10	100.00	0
256.0	99.10	0.26	99.20	0.24	99.50	0.19	99.65	0.16	99.65	0.16
64.0	97.30	0.37	97.70	0.35	98.23	0.33	98.77	0.28	98.93	0.24
16.0	90.78	0.59	93.15	0.51	94.97	0.43	95.65	0.40	96.60	0.37
4.0	77.84	0.71	83.00	0.69	86.94	0.59	89.92	0.54	92.82	0.43
1.0	56.67	0.75	63.02	0.75	69.00	0.66	73.05	0.72	77.78	0.64
0.2500	38.82	0.81	45.16	0.75	49.04	0.77	54.10	0.79	58.66	0.76
0.0625	29.00	0.73	34.55	0.78	36.82	0.82	40.22	0.87	45.85	0.86
0.0156	25.53	0.76	26.37	0.82	29.40	0.88	33.37	0.95	38.43	0.93
0.0039	24.40	1.13	25.30	0.97	31.80	1.13	32.90	0.98	36.80	1.10
0.0010	25.10	1.52	24.60	1.55	28.30	1.49	33.40	1.58	32.20	1.82

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 2 OR LESS. REPLICATES = 50. NUMBER OF PARENTS=20.

GCA/SCR Variance Ratio	2 C/P 20/ 190	10.5%	4 C/P 40/ 190	21.1%	6 C/P 60/ 190	31.6%	8 C/P 80/ 190	42.1%	10 C/P 100/ 190	52.6%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	99.67	0.15	99.80	0.09	99.83	0.09	99.93	0.05	99.97	0.03
16.0	97.82	0.29	98.73	0.20	99.25	0.17	99.57	0.12	99.72	0.10
4.0	92.58	0.41	94.92	0.39	96.38	0.34	97.84	0.25	98.56	0.21
1.0	74.38	0.70	80.52	0.60	85.18	0.55	88.35	0.57	91.72	0.45
0.2500	55.24	0.80	62.42	0.74	68.10	0.79	72.76	0.74	77.82	0.75
0.0625	43.97	0.85	49.40	0.81	53.40	0.85	57.77	0.86	64.52	0.82
0.0156	38.70	0.91	40.83	0.95	44.77	1.00	50.50	0.93	54.93	0.93
0.0039	35.50	1.22	38.60	0.99	45.05	1.13	48.30	1.31	53.15	1.13
0.0010	36.90	1.50	38.40	1.62	42.50	1.38	48.20	1.55	48.70	1.84

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 3 OR LESS. REPLICATES = 50. NUMBER OF PARENTS=20.

GCA/SCR Variance Ratio	2 C/P 20/ 190	10.5%	4 C/P 40/ 190	21.1%	6 C/P 60/ 190	31.6%	8 C/P 80/ 190	42.1%	10 C/P 100/ 190	52.6%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	99.97	0.03	99.97	0.03	99.97	0.03	100.00	0	100.00	0
16.0	99.43	0.14	99.57	0.13	99.90	0.06	99.95	0.04	99.92	0.04
4.0	97.64	0.24	98.62	0.20	99.18	0.15	99.58	0.10	99.74	0.10
1.0	85.33	0.58	90.25	0.48	93.85	0.40	95.32	0.35	96.82	0.28
0.2500	68.76	0.77	74.78	0.67	79.40	0.70	84.62	0.62	88.38	0.55
0.0625	55.85	0.85	60.67	0.84	65.72	0.83	70.65	0.82	76.85	0.74
0.0156	49.37	0.89	53.93	0.95	58.40	1.03	63.63	0.97	67.70	0.94
0.0039	46.75	1.30	51.05	1.16	56.90	1.13	59.75	1.35	66.50	1.18
0.0010	47.10	1.60	48.40	1.55	53.50	1.49	60.40	1.65	63.40	1.72

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 4 OR LESS. REPLICATES = 50. NUMBER OF PARENTS=20.

GCA/SCR Variance Ratio	2 C/P 20/ 190	10.5%	4 C/P 40/ 190	21.1%	6 C/P 60/ 190	31.6%	8 C/P 80/ 190	42.1%	10 C/P 100/ 190	52.6%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	99.88	0.06	99.92	0.06	99.98	0.03	100.00	0	100.00	0
4.0	99.12	0.15	99.66	0.10	99.78	0.10	99.92	0.04	99.96	0.04
1.0	92.62	0.42	95.67	0.33	97.47	0.25	98.32	0.22	98.98	0.14
0.2500	78.36	0.65	83.58	0.63	87.12	0.60	91.78	0.47	94.34	0.41
0.0625	64.88	0.85	70.67	0.80	76.00	0.81	80.18	0.75	85.87	0.65
0.0156	59.03	0.97	64.50	0.92	68.10	1.05	73.40	0.89	78.17	0.86
0.0039	57.55	1.31	61.55	1.28	66.75	1.23	70.15	1.33	76.80	1.08
0.0010	55.50	1.49	58.50	1.40	63.50	1.52	68.70	1.60	74.70	1.48

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 5 OR LESS. REPLICATES = 50. NUMBER OF PARENTS=20.

GCA/SCR Variance Ratio	2 C/P 20/ 190	10.5%	4 C/P 40/ 190	21.1%	6 C/P 60/ 190	31.6%	8 C/P 80/ 190	42.1%	10 C/P 100/ 190	52.6%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	99.98	0.03	100.00	0	100.00	0	100.00	0	100.00	0
4.0	99.82	0.07	99.90	0.05	99.98	0.02	99.98	0.02	99.98	0.02
1.0	96.53	0.32	98.28	0.21	99.12	0.14	99.37	0.12	99.73	0.06
0.2500	84.90	0.59	89.48	0.51	92.92	0.45	95.56	0.33	97.20	0.26
0.0625	72.80	0.82	78.90	0.70	83.65	0.67	87.30	0.63	91.18	0.47
0.0156	67.47	0.96	73.00	0.84	76.77	0.92	80.80	0.80	85.23	0.78
0.0039	66.35	1.15	69.60	1.19	74.55	1.12	79.40	1.14	84.00	0.96
0.0010	62.70	1.32	67.30	1.47	72.90	1.55	77.40	1.59	81.20	1.53

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 6 OR LESS. REPLICATES = 50. NUMBER OF PARENTS=20.

GCA/SCR Variance Ratio	2 C/P 10.5%		4 C/P 21.1%		6 C/P 31.6%		8 C/P 42.1%		10 C/P 52.6%	
	20/ 190		40/ 190		60/ 190		80/ 190		100/ 190	
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
4.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
1.0	98.15	0.23	99.27	0.12	99.67	0.08	99.70	0.08	99.97	0.02
0.2500	90.26	0.48	93.54	0.41	95.94	0.34	97.68	0.24	98.84	0.16
0.0625	80.30	0.74	84.93	0.64	88.95	0.60	91.95	0.51	94.67	0.40
0.0156	74.83	0.86	79.97	0.74	83.50	0.79	87.17	0.67	90.57	0.67
0.0039	72.65	1.12	76.80	1.05	81.30	0.93	84.95	0.99	88.40	0.78
0.0010	71.70	1.41	75.80	1.37	81.00	1.25	83.20	1.39	86.20	1.24

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 7 OR LESS. REPLICATES = 50. NUMBER OF PARENTS=20.

GCA/SCR Variance Ratio	2 C/P 10.5%		4 C/P 21.1%		6 C/P 31.6%		8 C/P 42.1%		10 C/P 52.6%	
	20/ 190		40/ 190		60/ 190		80/ 190		100/ 190	
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
4.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
1.0	99.25	0.13	99.80	0.07	99.92	0.04	99.98	0.02	100.00	0
0.2500	93.96	0.38	96.20	0.31	97.96	0.24	98.70	0.18	99.28	0.13
0.0625	85.63	0.66	89.58	0.58	92.85	0.54	94.85	0.41	96.95	0.31
0.0156	81.33	0.74	85.20	0.66	88.77	0.66	91.17	0.61	93.97	0.54
0.0039	78.60	1.07	82.10	0.98	87.20	0.83	90.10	0.74	92.80	0.66
0.0010	77.40	1.20	80.70	1.29	86.10	1.06	87.90	1.30	90.60	1.02

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 8 OR LESS. REPLICATES = 50. NUMBER OF PARENTS=20.

GCA/SCR Variance Ratio	2 C/P 20/ 190	10.5%	4 C/P 40/ 190	21.1%	6 C/P 60/ 190	31.6%	8 C/P 80/ 190	42.1%	10 C/P 100/ 190	52.6%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
4.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
1.0	99.65	0.10	99.97	0.02	99.98	0.02	100.00	0	100.00	0
0.2500	96.20	0.32	97.98	0.23	98.98	0.16	99.48	0.10	99.70	0.09
0.0625	89.62	0.58	93.47	0.47	95.23	0.42	97.10	0.32	98.37	0.22
0.0156	86.17	0.65	89.40	0.60	92.17	0.55	93.70	0.51	96.13	0.42
0.0039	83.95	0.90	86.30	0.83	90.70	0.75	93.10	0.62	95.65	0.47
0.0010	84.70	1.13	86.20	1.16	90.00	1.04	92.20	1.03	94.20	0.95

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 9 OR LESS. REPLICATES = 50. NUMBER OF PARENTS=20.

GCA/SCR Variance Ratio	2 C/P 20/ 190	10.5%	4 C/P 40/ 190	21.1%	6 C/P 60/ 190	31.6%	8 C/P 80/ 190	42.1%	10 C/P 100/ 190	52.6%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
4.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
1.0	99.80	0.07	100.00	0	100.00	0	100.00	0	100.00	0
0.2500	97.74	0.24	99.00	0.17	99.52	0.10	99.82	0.06	99.82	0.07
0.0625	92.90	0.49	95.60	0.39	97.12	0.31	98.37	0.22	99.22	0.14
0.0156	89.63	0.59	93.03	0.48	95.33	0.44	95.67	0.41	97.77	0.30
0.0039	88.05	0.79	90.30	0.63	93.65	0.61	95.05	0.51	97.50	0.40
0.0010	88.80	1.06	90.50	1.00	92.40	0.98	95.00	0.77	96.30	0.74

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 0 OR LESS. REPLICATES = 30. NUMBER OF PARENTS=30.

GCA/SCR Variance Ratio	2 C/P 30/ 435	6.9%	4 C/P 60/ 435	13.8%	6 C/P 90/ 435	20.7%	8 C/P 120/ 435	27.6%	10 C/P 150/ 435	34.5%
1024.0	86.67	1.41	89.67	1.23	91.11	1.21	92.56	1.15	94.44	1.06
256.0	80.28	1.38	81.67	1.22	86.44	0.96	87.00	1.16	88.22	1.04
64.0	66.00	1.22	71.44	1.18	74.81	1.18	78.04	1.07	81.63	1.06
16.0	45.50	1.04	51.47	1.03	55.11	1.00	58.94	1.13	62.36	1.07
4.0	26.44	0.80	32.42	0.87	36.67	0.86	39.62	0.80	44.53	0.93
1.0	15.04	0.55	18.87	0.59	21.87	0.63	24.63	0.69	26.94	0.71
0.2500	10.36	0.46	11.24	0.51	12.13	0.49	14.31	0.56	14.42	0.54
0.0625	6.81	0.43	8.11	0.46	9.08	0.51	10.58	0.50	11.36	0.55
0.0156	5.56	0.50	5.56	0.46	6.67	0.50	7.89	0.56	8.30	0.58
0.0039	5.50	0.69	5.83	0.55	6.56	0.70	7.28	0.67	7.44	0.67
0.0010	5.00	0.71	6.22	0.73	5.89	0.84	8.00	0.91	9.33	0.82

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 1 OR LESS. REPLICATES = 30. NUMBER OF PARENTS=30.

GCA/SCR Variance Ratio	2 C/P 30/ 435	6.9%	4 C/P 60/ 435	13.8%	6 C/P 90/ 435	20.7%	8 C/P 120/ 435	27.6%	10 C/P 150/ 435	34.5%
1024.0	99.11	0.42	99.67	0.19	100.00	0	99.89	0.11	100.00	0
256.0	98.11	0.41	98.44	0.31	98.78	0.33	98.89	0.29	99.28	0.25
64.0	94.78	0.48	96.37	0.46	97.30	0.37	97.67	0.36	98.48	0.26
16.0	80.83	0.76	86.17	0.65	88.22	0.66	90.19	0.59	92.72	0.52
4.0	61.84	0.87	68.67	0.75	73.42	0.74	77.62	0.75	81.29	0.72
1.0	39.04	0.74	45.04	0.69	51.72	0.70	55.89	0.72	59.69	0.71
0.2500	26.71	0.66	28.89	0.65	32.49	0.70	35.84	0.75	39.49	0.78
0.0625	19.33	0.66	20.81	0.65	23.89	0.70	24.72	0.70	27.28	0.74
0.0156	16.00	0.66	17.44	0.70	18.30	0.70	20.26	0.85	23.19	0.86
0.0039	15.00	1.03	16.11	1.03	17.28	0.89	19.39	1.03	22.00	1.11
0.0010	16.89	1.08	15.44	1.34	15.67	1.09	20.22	1.27	21.33	1.22

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 2 OR LESS. REPLICATES = 30. NUMBER OF PARENTS=30.

GCA/SCR Variance Ratio	2 C/P 30/ 435	6.9%	4 C/P 60/ 435	13.8%	6 C/P 90/ 435	20.7%	8 C/P 120/ 435	27.6%	10 C/P 150/ 435	34.5%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	99.83	0.12	99.83	0.09	99.89	0.08	99.89	0.08	99.94	0.06
64.0	99.07	0.23	99.52	0.13	99.59	0.14	100.00	0	99.96	0.04
16.0	94.00	0.41	96.69	0.34	97.25	0.32	98.03	0.32	98.81	0.22
4.0	81.36	0.67	86.07	0.61	89.40	0.49	91.47	0.44	93.58	0.42
1.0	57.85	0.75	64.67	0.70	71.52	0.63	76.17	0.63	79.87	0.62
0.2500	40.22	0.76	43.76	0.76	49.02	0.76	53.31	0.83	57.76	0.77
0.0625	28.92	0.77	31.86	0.79	35.72	0.82	37.89	0.80	41.69	0.82
0.0156	24.89	0.75	26.81	0.86	28.44	0.84	31.85	1.02	35.56	0.87
0.0039	24.22	1.18	25.22	1.24	25.50	1.02	30.61	1.20	32.78	1.14
0.0010	23.89	1.24	23.67	1.57	25.67	1.37	30.78	1.60	31.78	1.34

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 3 OR LESS. REPLICATES = 30. NUMBER OF PARENTS=30.

GCA/SCR Variance Ratio	2 C/P 30/ 435	6.9%	4 C/P 60/ 435	13.8%	6 C/P 90/ 435	20.7%	8 C/P 120/ 435	27.6%	10 C/P 150/ 435	34.5%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	99.81	0.08	99.89	0.06	99.96	0.04	100.00	0	100.00	0
16.0	98.58	0.20	99.33	0.14	99.47	0.12	99.64	0.11	99.81	0.08
4.0	91.40	0.49	94.47	0.39	95.87	0.35	97.09	0.29	98.02	0.24
1.0	72.04	0.66	79.46	0.61	84.20	0.52	87.48	0.51	90.30	0.46
0.2500	51.64	0.78	56.98	0.79	61.40	0.77	65.98	0.82	71.82	0.72
0.0625	37.64	0.81	41.14	0.83	45.92	0.85	49.08	0.86	53.53	0.84
0.0156	32.26	0.90	34.26	0.92	38.48	0.92	41.48	1.05	44.59	0.85
0.0039	32.83	1.26	34.72	1.36	36.56	1.15	39.33	1.22	41.94	1.34
0.0010	31.44	1.48	31.67	1.64	35.00	1.71	38.44	1.51	39.89	1.55

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 4 OR LESS. REPLICATES = 30. NUMBER OF PARENTS=30.

GCA/SCR Variance Ratio	2 C/P 30/ 435	6.9%	4 C/P 60/ 435	13.8%	6 C/P 90/ 435	20.7%	8 C/P 120/ 435	27.6%	10 C/P 150/ 435	34.5%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	99.96	0.04	100.00	0	100.00	0
16.0	99.69	0.10	99.97	0.03	99.92	0.05	99.94	0.04	99.94	0.04
4.0	96.49	0.30	98.11	0.22	98.71	0.20	99.07	0.16	99.38	0.13
1.0	82.19	0.59	87.70	0.51	91.63	0.37	94.17	0.36	95.93	0.30
0.2500	61.44	0.79	67.49	0.75	72.22	0.77	76.84	0.72	81.31	0.69
0.0625	46.81	0.81	50.92	0.87	55.36	0.84	58.44	0.83	63.08	0.83
0.0156	40.41	0.90	42.59	0.87	46.44	0.97	50.15	1.06	52.63	0.89
0.0039	40.06	1.33	43.89	1.35	45.06	1.18	47.61	1.22	49.94	1.31
0.0010	38.56	1.53	40.11	1.62	43.44	1.89	48.44	1.66	48.44	1.49

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 5 OR LESS. REPLICATES = 30. NUMBER OF PARENTS=30.

GCA/SCR Variance Ratio	2 C/P 30/ 435	6.9%	4 C/P 60/ 435	13.8%	6 C/P 90/ 435	20.7%	8 C/P 120/ 435	27.6%	10 C/P 150/ 435	34.5%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	99.97	0.03	100.00	0	99.97	0.03	100.00	0	100.00	0
4.0	98.89	0.17	99.40	0.11	99.58	0.11	99.73	0.09	99.89	0.06
1.0	89.13	0.50	93.07	0.39	95.54	0.31	97.30	0.25	97.94	0.22
0.2500	69.78	0.80	75.98	0.69	80.13	0.70	84.38	0.66	88.51	0.56
0.0625	54.50	0.89	58.06	0.93	63.28	0.87	67.44	0.83	71.00	0.83
0.0156	47.15	0.97	49.67	0.84	54.11	0.97	58.04	1.10	60.78	0.96
0.0039	47.06	1.38	50.61	1.32	51.83	1.03	55.17	1.22	57.11	1.35
0.0010	44.67	1.69	45.33	1.50	50.00	1.64	53.78	1.78	56.11	1.57

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 6 OR LESS. REPLICATES = 30. NUMBER OF PARENTS=30.

GCA/SCR Variance Ratio	2 C/P 30/ 435	6.9%	4 C/P 60/ 435	13.8%	6 C/P 90/ 435	20.7%	8 C/P 120/ 435	27.6%	10 C/P 150/ 435	34.5%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
4.0	99.73	0.08	99.84	0.06	99.93	0.05	99.93	0.04	99.98	0.02
1.0	93.76	0.38	96.65	0.27	98.11	0.21	98.69	0.18	99.07	0.15
0.2500	76.33	0.78	82.36	0.60	86.33	0.66	90.00	0.56	92.47	0.50
0.0625	61.00	0.88	64.67	0.89	69.97	0.78	73.94	0.77	78.14	0.76
0.0156	54.07	1.01	56.44	0.89	60.78	0.99	64.44	1.06	68.11	0.93
0.0039	53.44	1.39	56.56	1.36	58.94	1.10	62.00	1.17	64.50	1.24
0.0010	51.44	1.56	52.22	1.26	55.89	1.92	60.00	1.76	61.78	1.64

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 7 OR LESS. REPLICATES = 30. NUMBER OF PARENTS=30.

GCA/SCR Variance Ratio	2 C/P 30/ 435	6.9%	4 C/P 60/ 435	13.8%	6 C/P 90/ 435	20.7%	8 C/P 120/ 435	27.6%	10 C/P 150/ 435	34.5%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
4.0	99.91	0.04	99.93	0.04	100.00	0	99.98	0.02	99.98	0.02
1.0	96.28	0.30	98.43	0.19	99.13	0.14	99.43	0.12	99.57	0.09
0.2500	82.13	0.67	87.44	0.57	90.89	0.51	93.76	0.42	95.31	0.37
0.0625	67.66	0.86	71.03	0.86	76.31	0.78	79.22	0.77	83.78	0.68
0.0156	59.37	0.98	62.59	0.87	67.04	0.98	70.93	0.91	74.22	0.90
0.0039	59.67	1.33	62.39	1.42	64.89	1.08	68.06	1.16	70.78	1.24
0.0010	56.56	1.62	58.56	1.36	61.67	1.59	65.89	1.66	69.22	1.78

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 8 OR LESS. REPLICATES = 30. NUMBER OF PARENTS=30.

GCA/SCR Variance Ratio	2 C/P 30/ 435	6.9%	4 C/P 60/ 435	13.8%	6 C/P 90/ 435	20.7%	8 C/P 120/ 435	27.6%	10 C/P 150/ 435	34.5%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
4.0	99.96	0.03	99.98	0.02	100.00	0	100.00	0	100.00	0
1.0	98.26	0.19	99.26	0.13	99.59	0.09	99.78	0.07	99.94	0.03
0.2500	86.64	0.61	91.29	0.51	94.18	0.40	96.36	0.34	97.51	0.25
0.0625	72.67	0.79	76.06	0.76	80.75	0.70	84.25	0.65	87.50	0.61
0.0156	65.56	0.91	68.89	0.88	72.33	0.88	76.00	0.89	79.22	0.80
0.0039	64.67	1.34	67.50	1.28	70.17	1.13	73.28	1.19	75.61	1.18
0.0010	61.78	1.86	64.33	1.55	66.89	1.67	69.00	1.53	73.89	1.57

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 9 OR LESS. REPLICATES = 30. NUMBER OF PARENTS=30.

GCA/SCR Variance Ratio	2 C/P 30/ 435	6.9%	4 C/P 60/ 435	13.8%	6 C/P 90/ 435	20.7%	8 C/P 120/ 435	27.6%	10 C/P 150/ 435	34.5%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
4.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
1.0	99.06	0.15	99.70	0.09	99.76	0.08	99.89	0.04	99.98	0.02
0.2500	90.13	0.54	94.02	0.45	96.27	0.32	97.91	0.26	98.51	0.20
0.0625	77.17	0.82	81.17	0.72	85.42	0.66	88.06	0.60	90.47	0.54
0.0156	71.07	0.87	73.93	0.79	76.78	0.84	79.56	0.85	83.44	0.69
0.0039	70.06	1.31	72.44	1.27	75.00	1.06	77.72	1.12	79.67	1.11
0.0010	66.11	1.66	69.44	1.61	72.67	1.67	74.67	1.51	77.56	1.70

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 0 OR LESS. REPLICATES = 14. NUMBER OF PARENTS=50.

GCA/SCR Variance Ratio	2 C/P 50/1225	4.1%	4 C/P 100/1225	8.2%	6 C/P 150/1225	12.2%	8 C/P 200/1225	16.3%	10 C/P 250/1225	20.4%
1024.0	85.00	1.58	88.00	1.79	88.00	2.27	89.86	1.82	91.71	1.20
256.0	70.21	1.55	72.79	1.33	74.50	1.31	76.43	1.31	80.07	1.42
64.0	46.52	1.23	54.57	1.23	59.90	1.53	60.24	1.26	65.86	1.18
16.0	29.21	0.94	33.96	1.06	37.36	0.95	41.75	1.08	44.57	1.06
4.0	16.60	0.68	18.80	0.76	20.74	0.79	23.63	0.82	26.14	0.79
1.0	8.29	0.49	11.60	0.51	12.17	0.51	13.48	0.53	15.40	0.58
0.2500	5.40	0.38	5.94	0.37	7.00	0.40	7.97	0.45	8.46	0.43
0.0625	3.57	0.33	4.50	0.40	4.79	0.35	5.21	0.43	5.75	0.51
0.0156	3.33	0.37	3.67	0.43	4.76	0.57	4.19	0.45	4.71	0.51
0.0039	2.29	0.29	3.50	0.47	3.14	0.51	3.71	0.47	2.93	0.52
0.0010	2.00	0.47	3.00	0.62	2.00	0.55	2.00	0.59	3.14	0.91

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 1 OR LESS. REPLICATES = 14. NUMBER OF PARENTS=50.

GCA/SCR Variance Ratio	2 C/P 50/1225	4.1%	4 C/P 100/1225	8.2%	6 C/P 150/1225	12.2%	8 C/P 200/1225	16.3%	10 C/P 250/1225	20.4%
1024.0	98.00	0.51	99.14	0.40	99.14	0.40	99.57	0.23	99.43	0.33
256.0	94.71	0.62	96.86	0.59	97.79	0.45	98.14	0.42	98.71	0.36
64.0	85.29	0.96	88.29	0.84	90.43	0.80	92.24	0.73	93.43	0.65
16.0	64.39	1.02	68.61	0.85	73.89	0.89	78.57	0.90	80.18	0.79
4.0	41.40	0.92	47.29	0.84	50.63	0.89	54.69	0.83	59.77	0.87
1.0	23.93	0.76	28.74	0.79	32.52	0.69	35.38	0.69	38.07	0.78
0.2500	14.86	0.51	16.37	0.66	18.54	0.66	20.91	0.66	23.34	0.69
0.0625	10.50	0.57	12.57	0.72	12.61	0.56	14.21	0.67	15.21	0.68
0.0156	9.48	0.64	10.00	0.58	10.95	0.82	11.14	0.72	12.19	0.79
0.0039	8.07	0.77	8.79	0.58	10.07	0.72	11.43	0.94	10.43	0.65
0.0010	7.57	0.92	8.43	1.13	7.14	0.93	8.29	1.11	9.86	1.04

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 2 OR LESS. REPLICATES = 14. NUMBER OF PARENTS=50.

GCA/SCR Variance Ratio	2 C/P 50/1225	4.1%	4 C/P 100/1225	8.2%	6 C/P 150/1225	12.2%	8 C/P 200/1225	16.3%	10 C/P 250/1225	20.4%
1024.0	99.86	0.14	100.00	0	100.00	0	100.00	0	100.00	0
256.0	99.00	0.28	99.57	0.16	99.79	0.16	99.71	0.17	99.79	0.12
64.0	95.95	0.57	97.10	0.49	98.43	0.28	98.71	0.28	99.38	0.17
16.0	83.25	0.82	86.71	0.77	90.36	0.78	92.71	0.60	93.50	0.60
4.0	61.20	0.87	67.71	0.80	71.49	0.79	75.77	0.78	79.49	0.81
1.0	37.00	0.80	43.45	0.88	48.74	0.86	53.05	0.78	56.07	0.80
0.2500	23.94	0.64	26.51	0.79	30.17	0.79	33.51	0.83	36.40	0.88
0.0625	17.32	0.65	18.61	0.80	19.79	0.68	22.64	0.87	24.68	0.89
0.0156	15.38	0.86	15.62	0.75	17.14	0.78	17.38	0.88	18.62	0.77
0.0039	12.79	0.77	13.43	0.88	15.50	0.85	16.71	0.96	17.71	0.92
0.0010	11.57	1.41	12.86	1.12	13.00	1.22	13.14	1.43	17.00	0.96

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 3 OR LESS. REPLICATES = 14. NUMBER OF PARENTS=50.

GCA/SCR Variance Ratio	2 C/P 50/1225	4.1%	4 C/P 100/1225	8.2%	6 C/P 150/1225	12.2%	8 C/P 200/1225	16.3%	10 C/P 250/1225	20.4%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	99.29	0.22	99.67	0.13	99.90	0.07	99.86	0.08	99.81	0.09
16.0	92.54	0.59	94.75	0.50	96.50	0.41	98.00	0.32	98.36	0.30
4.0	74.91	0.77	80.94	0.63	84.14	0.71	87.31	0.67	89.60	0.64
1.0	48.86	0.93	56.36	0.88	62.52	0.76	66.33	0.81	70.26	0.77
0.2500	32.57	0.79	34.63	0.80	39.69	0.95	43.57	0.90	47.34	1.00
0.0625	23.32	0.74	25.07	0.86	27.50	0.80	30.68	0.91	31.86	0.88
0.0156	20.10	0.76	21.24	0.83	23.48	0.92	24.05	0.92	25.71	0.95
0.0039	17.21	0.95	18.07	0.97	21.21	0.68	23.07	1.11	23.50	1.08
0.0010	15.71	1.50	17.29	1.18	18.14	1.30	19.57	1.84	23.14	1.10

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 4 OR LESS. REPLICATES = 14. NUMBER OF PARENTS=50.

GCA/SCR Variance Ratio	2 C/P 50/1225	4.1%	4 C/P 100/1225	8.2%	6 C/P 150/1225	12.2%	8 C/P 200/1225	16.3%	10 C/P 250/1225	20.4%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	99.95	0.05	99.95	0.05	100.00	0	100.00	0	100.00	0
16.0	96.89	0.37	98.18	0.27	98.93	0.20	99.46	0.16	99.57	0.15
4.0	85.60	0.53	89.54	0.51	91.86	0.51	93.69	0.46	95.71	0.37
1.0	59.43	0.85	66.55	0.81	73.05	0.69	76.88	0.74	80.55	0.66
0.2500	41.03	0.83	43.54	0.92	48.51	1.02	52.57	0.97	55.77	1.01
0.0625	28.79	0.82	30.82	0.83	33.50	0.81	37.32	0.97	39.61	0.99
0.0156	25.24	0.89	26.10	0.98	28.10	0.95	29.43	0.92	31.62	1.00
0.0039	21.71	1.02	23.57	0.94	26.21	0.87	29.93	1.43	29.71	1.03
0.0010	18.71	1.37	20.71	1.04	23.29	1.29	23.86	1.86	27.71	1.26

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 5 OR LESS. REPLICATES = 14. NUMBER OF PARENTS=50.

GCA/SCR Variance Ratio	2 C/P 50/1225	4.1%	4 C/P 100/1225	8.2%	6 C/P 150/1225	12.2%	8 C/P 200/1225	16.3%	10 C/P 250/1225	20.4%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	99.00	0.24	99.39	0.15	99.61	0.13	99.79	0.10	99.89	0.06
4.0	91.43	0.49	94.20	0.45	95.51	0.37	97.23	0.30	98.14	0.25
1.0	68.14	0.78	74.71	0.69	80.90	0.61	83.95	0.55	87.33	0.53
0.2500	46.83	0.90	51.37	1.05	56.80	0.97	60.74	0.93	64.09	0.97
0.0625	34.50	0.88	36.32	1.02	39.50	0.89	44.07	0.93	45.96	1.06
0.0156	30.71	0.83	30.57	1.07	34.14	0.93	34.76	1.02	37.38	1.02
0.0039	26.57	1.08	28.50	0.88	31.14	0.95	34.64	1.32	35.14	1.07
0.0010	24.00	1.33	25.00	1.43	27.29	1.40	29.29	2.19	32.86	1.37

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 6 OR LESS. REPLICATES = 14. NUMBER OF PARENTS=50.

GCA/SCR Variance Ratio	2 C/P 50/1225	4.1%	4 C/P 100/1225	8.2%	6 C/P 150/1225	12.2%	8 C/P 200/1225	16.3%	10 C/P 250/1225	20.4%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	99.61	0.13	99.79	0.08	99.96	0.04	99.93	0.05	100.00	0
4.0	95.34	0.37	97.11	0.30	97.91	0.25	99.03	0.17	99.31	0.15
1.0	75.95	0.72	82.76	0.62	87.43	0.53	89.50	0.50	92.02	0.43
0.2500	52.97	0.93	57.86	0.95	64.09	0.95	68.09	0.93	72.03	0.88
0.0625	39.36	0.90	42.32	1.14	45.43	0.95	49.79	0.96	52.04	1.10
0.0156	34.86	0.97	35.43	1.14	39.33	0.95	40.57	1.20	42.48	1.00
0.0039	31.14	1.02	32.71	0.82	36.36	1.01	39.07	1.37	39.57	1.27
0.0010	29.29	1.29	28.86	1.63	33.29	2.05	33.43	2.15	38.29	1.36

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 7 OR LESS. REPLICATES = 14. NUMBER OF PARENTS=50.

GCA/SCR Variance Ratio	2 C/P 50/1225	4.1%	4 C/P 100/1225	8.2%	6 C/P 150/1225	12.2%	8 C/P 200/1225	16.3%	10 C/P 250/1225	20.4%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	99.86	0.07	99.96	0.04	100.00	0	100.00	0	100.00	0
4.0	97.80	0.24	98.71	0.20	99.17	0.16	99.69	0.09	99.71	0.09
1.0	81.33	0.65	88.12	0.55	91.17	0.44	93.48	0.39	95.12	0.39
0.2500	59.06	0.93	63.86	0.93	70.37	0.94	74.60	0.80	77.60	0.85
0.0625	44.82	0.82	47.86	1.09	50.75	0.96	55.11	0.97	58.18	1.08
0.0156	39.14	1.14	39.81	1.18	44.57	0.94	45.14	1.11	47.38	1.05
0.0039	35.36	1.19	37.71	0.88	40.50	1.08	42.57	1.34	45.07	1.27
0.0010	34.14	1.63	34.14	1.67	37.29	2.06	39.71	1.81	43.14	1.45

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 8 OR LESS. REPLICATES = 14. NUMBER OF PARENTS=50.

GCA/SCR Variance Ratio	2 C/P 50/1225	4.1%	4 C/P 100/1225	8.2%	6 C/P 150/1225	12.2%	8 C/P 200/1225	16.3%	10 C/P 250/1225	20.4%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
4.0	98.86	0.21	99.57	0.13	99.77	0.08	99.89	0.06	99.97	0.03
1.0	86.62	0.60	92.19	0.47	93.95	0.37	96.19	0.28	97.26	0.29
0.2500	63.57	0.92	69.63	0.92	75.74	0.88	79.46	0.82	82.54	0.81
0.0625	48.96	0.84	52.39	1.15	55.43	1.03	59.68	0.94	62.96	0.95
0.0156	43.76	1.01	44.90	1.13	48.90	1.01	50.67	1.01	51.57	1.02
0.0039	39.36	1.17	41.71	0.81	44.14	1.06	46.36	1.50	49.93	1.45
0.0010	39.14	1.71	38.57	1.63	41.29	1.95	44.71	1.86	47.14	1.37

CUMULATIVE RANK DIFFERENCES. RANK DIFFERENCE = 9 OR LESS. REPLICATES = 14. NUMBER OF PARENTS=50.

GCA/SCR Variance Ratio	2 C/P 50/1225	4.1%	4 C/P 100/1225	8.2%	6 C/P 150/1225	12.2%	8 C/P 200/1225	16.3%	10 C/P 250/1225	20.4%
1024.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
256.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
64.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
16.0	100.00	0	100.00	0	100.00	0	100.00	0	100.00	0
4.0	99.54	0.13	99.86	0.06	99.97	0.03	99.97	0.03	100.00	0
1.0	90.24	0.57	94.52	0.44	96.24	0.32	97.76	0.25	98.43	0.20
0.2500	68.54	0.90	73.86	0.83	80.20	0.75	83.63	0.74	86.46	0.72
0.0625	52.93	0.87	56.61	1.10	59.86	0.95	63.89	0.94	68.32	0.89
0.0156	48.05	1.01	48.52	1.12	52.48	0.93	54.62	1.06	56.52	0.92
0.0039	43.36	1.13	45.50	0.96	47.14	1.06	51.07	1.54	53.43	1.40
0.0010	43.00	1.88	42.29	1.81	46.57	2.25	48.57	1.57	51.71	1.47

Appendix II

The mean values of the ten observed characters
in the F₁ triticales diallel.

DAYS TO HEADING

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	113.5	106.0	116.0	106.0	112.7	123.0	112.0	106.0	116.0	115.2	106.0	123.0
T31		112.7	116.0	106.0	112.7	121.6	116.0	111.0	109.3	119.5	111.0	119.5
T33			123.0	106.0	119.5	128.2	118.3	116.0	116.0	123.0	116.0	123.0
T34				106.0	106.0	121.6	106.0	108.5	112.7	106.0	112.7	116.0
T58					116.0	123.0	116.0	108.5	116.0	116.0	117.3	119.5
T106						145.0	130.0	116.0	123.0	134.0	124.7	125.8
T246							125.8	113.5	121.2	127.2	121.6	123.0
T686								108.0	112.7	112.7	106.0	115.2
T702									120.7	117.7	112.7	123.0
T710										120.7	121.2	123.0
T896											120.7	116.0
T937												119.5

DAYS TO ANTHESIS

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	128.2	123.0	130.0	123.0	127.7	130.0	125.8	123.0	127.7	126.5	123.0	130.0
T31		127.7	130.0	123.0	123.0	138.0	130.0	126.5	125.3	131.5	126.5	135.0
T33			140.0	126.5	130.0	140.0	130.0	130.0	135.0	140.0	130.0	140.0
T34				123.0	123.0	130.0	124.7	124.7	130.0	123.0	127.7	130.0
T58					130.0	130.0	130.0	124.7	128.2	130.0	130.0	130.0
T106						150.0	140.0	130.0	140.0	142.0	140.0	140.0
T246							136.0	128.2	130.7	138.0	130.0	133.3
T686								124.4	127.7	127.7	123.0	128.2
T702									130.0	130.0	130.7	135.0
T710										136.7	137.5	136.7
T896											133.3	127.7
T937												132.5

HEIGHT

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	112.7	126.3	146.7	110.2	117.7	146.3	107.4	113.7	116.3	128.0	132.8	121.0
T31		117.7	137.3	113.7	122.7	140.4	115.8	121.2	99.3	122.0	128.5	130.2
T33			115.7	126.0	126.0	148.0	129.7	122.0	118.5	140.0	139.3	119.7
T34				110.0	121.5	154.2	112.2	109.0	108.7	110.3	130.7	122.2
T58					129.0	154.0	125.3	118.7	119.0	138.0	139.3	138.5
T106						150.0	154.4	141.5	137.0	150.8	156.5	152.2
T246							107.6	107.5	101.7	124.0	121.6	113.3
T686								96.2	110.0	122.0	117.7	126.7
T702									97.7	119.0	123.5	116.0
T710										128.7	132.5	126.3
T896											128.3	141.3
T937												119.2

NUMBER OF PRODUCTIVE HEADS

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	10.0	8.7	13.0	7.7	5.7	11.5	6.4	7.7	8.7	9.2	7.8	9.5
T31		9.3	12.7	9.7	10.3	10.8	9.4	9.5	10.3	8.0	12.0	11.2
T33			10.7	15.0	12.5	13.0	12.7	10.3	13.0	12.2	10.0	10.3
T34				7.5	9.8	12.0	9.8	8.2	11.7	7.7	11.3	11.7
T58					10.0	10.0	10.7	8.7	9.0	9.0	8.3	13.5
T106						14.5	11.4	10.7	13.7	14.6	10.2	11.6
T246							10.8	10.0	12.5	11.4	9.8	11.7
T686								8.8	12.0	12.7	9.3	11.7
T702									11.3	8.7	10.7	11.0
T710										11.0	8.7	8.7
T896											10.7	11.3
T937												9.5

TOTAL OF BIOLOGICAL WEIGHT

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	73.5	88.0	150.7	70.5	58.7	123.5	53.6	93.7	78.3	81.2	78.0	58.5
T31		73.0	130.3	67.3	100.7	91.8	86.2	98.2	57.3	54.5	89.5	134.7
T33			113.3	151.0	107.0	145.0	136.3	112.3	147.5	109.2	124.7	96.0
T34				54.0	97.2	158.8	79.7	75.5	89.7	68.0	103.7	108.0
T58					101.0	117.0	98.7	83.2	83.5	96.0	85.7	141.5
T106						205.0	138.4	165.5	164.0	159.0	147.0	172.8
T246							102.8	85.2	93.5	89.4	105.4	105.7
T686								55.4	108.0	109.0	104.3	120.0
T702									75.3	77.2	117.2	116.0
T710										103.0	75.0	77.7
T896											132.7	174.3
T937												86.5

HEAD LENGTH

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	10.2	10.8	15.0	11.7	10.7	14.1	11.0	12.7	10.5	11.1	14.3	11.0
T31		9.8	14.0	12.2	11.2	12.9	12.0	14.6	11.7	7.7	13.0	16.9
T33			16.5	16.7	14.0	17.0	15.7	15.3	18.5	16.2	18.7	16.8
T34				12.2	12.0	15.8	13.5	13.4	12.8	13.3	15.8	15.6
T58					11.0	13.5	12.5	13.6	11.1	11.5	14.0	14.2
T106						15.0	14.9	15.6	15.2	16.0	15.4	18.4
T246							13.0	13.7	10.9	11.5	14.5	14.5
T686								13.1	13.5	13.5	16.0	16.0
T702									11.3	11.1	17.2	16.0
T710										12.0	13.1	14.2
T896											15.0	17.8
T937												17.2

NUMBER OF SPIKELETS

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	22.0	22.7	30.3	22.5	22.7	31.5	23.2	22.7	23.3	23.7	25.8	25.0
T31		22.0	27.0	23.3	24.7	29.8	25.8	27.0	24.0	19.5	27.5	29.5
T33			29.3	30.5	28.5	34.5	29.3	28.3	34.0	31.0	32.7	30.3
T34				24.0	24.2	32.4	25.7	25.3	26.0	23.3	28.3	29.7
T58					24.0	29.0	27.3	25.7	24.7	24.5	28.7	28.0
T106						34.5	33.6	29.0	34.0	34.4	31.5	35.6
T246							30.0	26.2	25.3	30.4	30.0	30.7
T686								22.6	25.3	26.0	29.0	29.0
T702									25.3	26.8	30.3	32.0
T710										27.0	29.0	29.0
T896											30.0	31.7
T937												32.3

NUMBER OF SEED

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	69.5	67.7	84.7	81.0	76.0	51.2	62.4	74.0	49.7	57.0	30.2	52.0
T31		70.0	61.3	59.3	71.0	58.8	80.8	86.7	79.3	48.5	34.5	113.7
T33			95.0	65.5	69.0	75.0	63.7	87.7	92.5	51.7	88.3	91.7
T34				87.0	80.2	57.4	76.0	85.2	78.7	79.7	47.3	100.2
T58					84.0	51.0	88.3	82.7	62.5	73.5	25.3	86.0
T106						60.5	38.6	63.2	83.3	49.2	67.2	112.0
T246							103.2	64.2	85.5	82.4	52.2	86.7
T686								63.8	93.0	77.7	57.3	91.7
T702									100.7	91.5	60.5	85.0
T710										86.3	30.7	64.3
T896											95.0	92.7
T937												97.5

WEIGHT OF SEED

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	19.3	25.7	36.0	20.4	16.0	19.4	14.3	26.0	20.1	16.7	4.7	14.5
T31		22.1	24.7	15.9	25.1	17.4	26.4	27.8	15.0	11.7	10.3	35.5
T33			39.9	34.7	14.4	28.3	29.8	35.6	40.2	19.7	27.1	22.6
T34				9.6	31.5	23.3	22.4	22.4	27.0	19.0	14.7	26.5
T58					25.8	9.2	31.7	20.4	18.8	26.2	4.0	48.3
T106						27.3	14.8	29.4	32.2	13.5	28.9	42.0
T246							27.8	21.5	30.8	24.7	8.7	24.3
T686								13.7	29.9	32.9	15.0	33.5
T702									20.3	21.0	16.9	37.6
T710										21.6	4.8	13.9
T896											28.4	48.0
T937												24.2

YIELD

	T20	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T20	23.5	30.1	40.5	25.6	20.5	21.9	17.7	30.4	22.4	19.0	6.0	16.8
T31		25.4	27.4	19.1	29.2	20.2	30.8	32.5	19.0	14.2	11.8	42.0
T33			45.8	38.6	18.0	32.0	33.3	40.7	45.1	22.6	32.6	27.2
T34				14.0	36.8	26.3	27.2	27.2	30.8	24.1	17.4	32.0
T58					29.9	11.6	37.1	25.5	22.5	29.8	5.3	53.5
T106						30.3	16.9	32.6	36.3	15.8	33.2	49.2
T246							33.2	25.5	34.2	28.4	11.2	29.4
T686								17.0	35.2	37.4	17.8	37.5
T702									23.8	25.9	19.7	42.3
T710										25.5	6.3	17.4
T896											33.8	53.4
T937												29.1

Appendix III

The mean and standard deviation values of the four observed characters in the F_4 diallel. Each site is presented individually. The mean values for all sites is also presented, additive site effects having been removed.

YIELD - WAITE

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	366.8 136.2	386.4 192.2	642.7 214.5	354.3 156.6	506.9 196.2	363.0 209.1	582.8 119.3	380.0 76.7	439.4 138.6	452.6 81.3	235.3 203.4	357.7 183.4
T31		582.3 105.1	447.8 192.3	368.9 86.8	331.4 179.4	433.6 206.1	571.6 123.2	365.6 132.3	485.9 153.6	542.0 172.0	438.1 168.2	467.2 210.4
T33			464.2 175.5	494.3 226.8	569.2 194.0	477.8 182.5	561.4 187.7	580.7 174.8	486.8 228.3	296.2 155.2	422.8 184.1	740.4 163.2
T34				393.8 74.6	437.6 147.4	366.5 156.3	537.6 167.1	373.3 82.2	602.5 189.7	552.7 86.6	244.1 98.1	499.6 163.8
T58					373.6 139.7	376.3 202.9	512.2 226.6	369.6 85.3	392.3 171.7	418.0 98.1	223.0 161.8	534.7 213.2
T106						181.6 143.9	285.3 130.0	430.0 115.7	310.0 148.9	311.3 160.7	254.7 124.3	378.6 70.6
T246							488.2 120.6	492.4 111.5	560.7 186.5	490.7 91.4	303.5 188.6	560.7 180.6
T686								412.7 131.5	494.7 162.5	300.5 164.8	169.3 174.3	575.3 229.6
T702									506.3 183.2	447.7 167.4	276.7 183.7	586.5 185.3
T710										453.6 151.4	187.4 89.2	439.9 152.0
T896											269.9 148.9	300.7 168.7
T937												759.0 82.1

YIELD - ROSEWORTHY

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	342.2 51.8	379.2 80.7	462.8 167.5	400.6 124.2	465.6 122.8	371.5 72.3	555.0 164.3	367.2 100.1	460.2 110.9	399.3 106.5	330.8 103.7	526.7 158.1
T31		481.4 103.6	404.7 126.1	418.1 92.0	378.9 97.0	421.8 101.3	487.2 84.9	341.5 88.3	503.2 191.8	454.3 140.9	387.8 113.0	450.8 115.3
T33			524.7 141.5	450.6 153.8	388.4 94.6	433.0 116.0	446.5 173.5	395.2 126.2	483.4 138.4	390.9 170.3	480.5 142.5	567.2 139.9
T34				399.8 77.6	400.3 80.2	445.1 128.2	364.3 71.9	386.5 91.3	581.9 167.9	432.2 81.5	332.2 120.8	438.4 117.0
T58					387.6 79.8	367.5 88.4	441.0 59.9	365.5 89.0	412.4 79.0	416.3 94.3	364.6 101.7	500.5 164.0
T106						410.9 71.7	342.8 78.6	379.2 70.5	408.2 88.1	329.2 112.5	399.7 83.2	511.9 80.1
T246							512.3 82.9	428.5 93.4	582.6 104.8	464.2 132.6	288.4 79.7	499.7 109.3
T686								394.9 81.9	379.0 91.2	381.2 61.9	329.7 115.2	395.5 152.1
T702									608.6 136.3	447.5 122.0	362.8 88.1	577.2 140.6
T710										473.6 67.9	372.3 156.2	441.4 155.6
T896											412.8 95.6	464.9 155.2
T937												676.9 66.1

YIELD - STRATHALBYN

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	366.9 78.6	518.4 53.1	614.3 127.4	466.5 119.5	456.7 55.0	365.1 99.2	521.1 100.9	398.4 87.1	507.3 95.3	394.0 69.9	326.0 104.2	438.4 75.7
T31		443.0 56.8	397.2 155.4	398.6 58.2	416.1 87.1	324.1 64.1	450.2 107.5	374.5 121.7	418.1 107.0	528.9 107.5	544.6 96.5	427.7 156.8
T33			471.7 67.0	459.1 160.3	641.6 119.2	371.2 80.9	531.9 146.2	412.1 97.2	630.2 75.0	315.3 111.3	437.3 69.8	559.3 144.2
T34				320.4 51.4	429.0 79.5	403.1 47.0	342.2 96.5	438.7 101.4	608.3 179.9	508.2 81.9	347.7 103.7	397.9 70.9
T58					418.8 56.7	293.2 51.9	477.5 123.3	366.7 91.2	412.6 110.6	412.3 109.1	342.7 108.8	422.7 85.6
T106						258.6 54.4	350.0 98.1	415.7 83.5	487.7 64.5	371.7 82.1	297.6 65.9	428.8 96.8
T246							398.1 108.1	342.9 80.4	547.5 141.3	427.3 88.6	420.7 134.9	391.8 101.7
T686								420.4 84.7	467.9 134.8	438.4 65.7	307.7 81.0	395.5 79.8
T702									664.3 85.8	499.8 82.0	486.5 98.4	517.6 106.2
T710										468.0 82.2	348.5 102.4	420.4 95.9
T896											313.9 37.5	432.0 84.1
T937												475.9 102.1

YIELD - ALL SITES

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	358.6 93.0	428.0 136.4	577.1 185.1	407.1 137.9	476.0 133.4	366.5 135.1	553.0 128.9	381.9 86.4	469.0 115.9	415.3 88.4	296.2 147.9	440.9 157.8
T31		502.2 106.4	416.6 156.3	396.1 79.8	375.5 128.5	393.2 141.9	503.0 114.9	360.5 112.5	465.4 150.9	508.4 143.1	464.6 138.3	448.6 160.5
T33			486.3 131.5	468.0 177.9	533.1 174.9	427.3 136.1	513.3 171.4	462.7 156.9	533.5 169.4	333.5 146.8	447.7 135.6	622.3 167.4
T34				371.3 75.9	422.3 104.7	404.9 120.2	414.7 145.1	399.5 93.3	597.6 173.5	495.8 94.7	307.2 113.7	443.4 124.3
T58					393.3 97.0	345.7 132.2	476.9 150.5	367.3 85.4	405.8 122.4	415.5 97.2	326.0 125.7	486.0 164.3
T106						283.7 135.4	326.0 105.0	408.3 91.3	399.0 127.2	337.4 121.2	317.3 110.1	439.8 97.8
T246							466.2 113.0	418.9 109.8	563.6 143.6	460.7 105.8	340.5 149.1	484.1 148.6
T686								409.3 99.0	446.5 137.7	373.4 119.5	268.9 144.2	455.4 181.5
T702									593.1 151.3	465.6 126.7	375.3 153.5	560.4 145.8
T710										465.5 101.4	302.7 142.4	433.9 132.8
T896											332.2 117.7	399.2 154.0
T937												635.9 147.8

HEIGHT - WAITE

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	104.2 6.4	106.2 6.3	100.7 4.2	99.7 5.7	102.7 5.7	118.7 14.3	105.2 10.8	99.2 5.0	103.7 6.2	110.2 5.8	110.2 10.8	108.2 13.8
T31		113.7 5.3	105.7 11.4	104.7 8.1	104.7 6.6	111.7 12.1	104.7 7.4	99.2 6.9	108.7 11.3	115.7 3.5	97.7 9.4	102.2 9.4
T33			97.2 4.1	96.2 6.8	106.2 8.9	128.2 14.8	98.7 5.3	98.2 2.8	91.7 7.5	103.2 14.0	109.2 6.9	105.7 6.7
T34				100.2 2.4	106.7 4.8	119.2 10.9	97.2 4.1	97.7 8.4	92.7 5.7	114.7 8.4	97.7 5.7	108.7 12.5
T58					110.2 3.4	125.7 15.7	100.7 8.9	100.7 4.2	97.2 7.1	116.2 8.2	113.2 6.0	116.7 12.5
T106						141.7 6.3	132.7 13.3	120.2 14.3	116.7 8.6	131.2 13.4	135.7 9.2	128.7 8.2
T246							95.2 3.4	93.2 9.0	96.7 5.9	107.2 13.1	110.2 10.3	102.2 6.7
T686								92.7 5.2	87.7 4.6	103.2 8.6	100.7 5.4	106.2 6.8
T702									88.7 4.1	99.2 10.4	97.2 7.5	95.7 9.5
T710										119.7 3.9	106.7 5.9	113.7 13.5
T896											115.2 7.1	113.2 5.0
T937												106.2 4.9

HEIGHT - ROSEWORTHY

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	104.1 8.8	105.1 6.7	102.1 7.0	104.6 6.7	99.1 6.6	109.6 10.6	109.1 10.2	102.1 9.9	99.6 8.2	106.6 7.1	114.6 13.8	116.1 13.4
T31		111.6 7.8	98.1 7.1	104.1 6.6	105.6 6.8	110.1 6.3	103.6 10.7	98.6 7.2	101.1 7.5	117.6 9.8	106.1 10.6	110.1 11.6
T33			100.1 9.5	102.1 8.1	105.1 11.6	120.1 9.2	98.1 12.5	95.6 9.2	97.1 9.9	103.6 14.8	112.1 5.7	106.6 12.5
T34				104.1 7.4	99.1 9.9	114.6 13.3	97.6 9.0	99.1 7.0	96.1 5.4	105.1 14.4	103.1 6.7	104.1 8.1
T58					107.6 12.8	121.1 11.8	106.1 8.9	95.6 6.3	107.1 6.1	110.6 4.9	103.6 15.7	109.1 13.5
T106						147.6 5.0	119.6 17.2	121.6 14.2	116.1 12.1	126.1 14.2	131.6 10.6	125.1 9.5
T246							97.6 2.8	95.1 6.3	93.1 5.8	116.1 6.7	101.6 10.6	104.6 5.3
T686								92.6 7.2	99.1 6.1	107.1 7.4	103.1 9.1	102.1 15.8
T702									91.6 5.8	111.6 10.6	96.6 8.5	94.6 6.3
T710										119.1 8.1	107.6 8.3	115.1 11.8
T896											113.1 7.5	115.1 12.7
T937												111.6 4.7

HEIGHT - STRATHALBYN

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	98.7 8.6	104.2 12.6	106.2 9.2	92.2 28.6	103.2 8.5	112.2 16.6	113.7 9.3	105.7 9.5	105.7 12.5	106.2 12.7	105.2 7.5	109.2 12.2
T31		105.7 9.5	110.2 17.4	100.2 6.3	101.2 6.3	106.7 15.6	107.7 12.3	102.2 11.7	109.7 9.1	108.7 12.1	104.7 9.4	112.2 14.7
T33			108.2 18.1	101.7 11.6	106.2 18.7	119.2 20.9	106.7 6.3	102.7 14.2	96.7 10.6	109.7 14.0	110.7 8.6	109.7 8.5
T34				104.7 11.6	109.2 9.7	114.2 17.4	104.7 11.8	102.7 10.7	99.7 9.4	113.7 8.0	110.7 6.8	107.2 13.1
T58					104.7 6.3	111.7 16.7	102.2 9.7	107.7 10.9	102.2 13.5	108.7 14.6	107.7 11.7	105.2 18.1
T106						127.7 26.6	113.2 15.1	104.2 14.5	110.2 12.5	113.2 16.3	118.2 18.0	114.2 21.3
T246							101.7 14.9	98.2 11.3	102.7 11.2	107.2 6.1	109.2 12.4	104.2 9.9
T686								99.7 9.4	104.7 14.0	104.2 9.1	107.2 4.6	109.2 10.5
T702									101.7 5.8	106.7 10.8	106.2 7.1	103.2 9.4
T710										112.7 7.6	108.2 10.0	110.7 17.8
T896											109.7 11.1	107.2 14.9
T937												104.2 9.9

HEIGHT - ALL SITES

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	102.3 8.2	105.2 8.8	103.0 7.2	98.8 17.4	101.7 7.0	113.5 14.1	109.3 10.4	102.3 8.6	103.0 9.4	107.7 8.9	110.0 11.3	111.2 13.2
T31		110.3 8.2	104.7 13.2	103.0 7.1	103.8 6.6	109.5 11.8	105.3 10.1	100.0 8.7	106.5 9.9	114.0 9.7	102.8 10.2	108.2 12.5
T33			101.8 12.5	100.0 9.1	105.8 13.2	122.5 15.7	101.2 9.2	98.8 10.0	95.2 9.4	105.5 14.1	110.7 7.0	107.3 9.4
T34				103.0 8.0	105.0 9.3	116.0 13.9	99.8 9.2	99.8 8.8	96.2 7.4	111.2 11.2	103.8 8.2	106.7 11.2
T58					107.5 8.5	119.5 15.5	103.0 9.1	101.3 9.0	102.2 10.0	111.8 10.3	108.2 12.1	110.3 15.2
T106						139.0 17.7	121.8 16.9	115.3 16.0	114.3 11.2	123.5 16.1	128.5 14.8	122.7 15.1
T246							98.2 9.1	95.5 9.0	97.5 8.7	110.2 9.9	107.0 11.4	103.7 7.4
T686								95.0 8.0	97.2 11.4	104.8 8.3	103.7 7.0	105.8 11.6
T702									94.0 7.6	105.8 11.5	100.0 8.7	97.8 9.1
T710										117.2 7.3	107.5 8.0	113.2 14.2
T896											112.7 8.7	111.8 11.8
T937												107.3 7.4

DAYS TO HEADING - WAITE

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	111.2 2.5	108.8 4.1	116.1 8.5	102.2 3.8	107.2 4.1	107.4 6.1	102.9 6.3	105.6 3.4	106.4 3.9	108.8 4.1	108.7 5.9	112.6 7.4
T31		110.4 3.4	110.8 7.0	105.6 3.4	105.6 3.4	110.6 5.5	106.4 3.9	100.4 4.6	107.2 4.1	109.0 6.1	106.5 7.2	116.7 11.2
T33			119.0 4.8	108.0 4.2	117.2 6.6	119.9 6.9	114.4 7.2	111.5 8.4	112.2 4.3	118.6 8.2	111.6 6.6	116.0 5.2
T34				103.9 4.0	105.6 3.4	109.8 9.9	106.3 5.6	103.1 2.8	104.8 2.5	110.0 7.3	101.3 4.3	111.6 6.6
T58					110.4 3.4	109.7 7.9	108.4 7.6	105.6 3.4	104.8 2.5	112.5 9.1	112.4 6.0	112.2 4.3
T106						121.7 4.1	122.1 6.2	106.4 3.9	112.7 9.5	121.6 6.8	113.6 7.9	118.2 6.5
T246							111.4 5.0	106.3 5.6	108.2 6.1	117.7 6.4	117.4 7.7	113.0 3.2
T686								104.0 0	105.6 3.4	105.6 3.4	105.6 3.4	114.2 5.9
T702									119.0 4.8	109.6 3.9	109.8 5.8	117.2 6.6
T710										118.0 5.2	106.4 3.9	119.0 4.8
T896											112.0 0	111.2 2.5
T937												120.0 4.2

DAYS TO ANTHESIS - WAITE

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	129.0 0	124.8 3.6	132.5 3.7	125.5 3.7	128.3 2.2	127.5 10.5	123.4 3.0	126.9 3.4	122.7 2.2	125.5 3.7	125.5 3.7	129.0 4.7
T31		129.0 0	130.4 3.0	124.8 3.6	126.2 3.6	128.3 4.0	126.2 4.9	122.7 2.2	124.1 3.4	129.0 3.3	126.2 4.9	132.8 6.6
T33			135.3 2.2	132.1 6.6	135.3 2.2	133.9 3.4	131.8 3.6	130.7 6.3	129.7 2.2	136.6 8.1	131.1 3.4	132.5 4.9
T34				122.7 2.2	126.9 3.4	127.6 6.4	126.2 3.6	123.4 3.0	126.2 3.6	128.3 4.0	124.8 3.6	130.4 6.4
T58					129.0 0	127.2 7.5	126.9 5.8	125.5 3.7	125.5 3.7	127.6 5.5	132.1 7.4	130.4 4.4
T106						132.5 3.7	136.9 7.7	126.2 4.9	129.7 4.0	137.3 5.1	132.5 3.7	136.0 0
T246							128.3 4.0	126.2 3.6	126.9 4.7	131.1 3.4	131.8 3.6	133.9 3.4
T686								126.2 3.6	126.2 3.6	125.5 3.7	125.5 3.7	132.5 3.7
T702									130.4 3.0	128.3 2.2	129.7 5.2	134.9 5.1
T710										134.6 3.0	125.5 3.7	134.6 3.0
T896											130.4 3.0	131.1 3.4
T937												136.0 0

Appendix IV

The mean and standard deviation values of the four observed characters in the F_4 diallel. Each site is presented individually. The mean values for all sites is also presented, additive site effects having been removed. All sites have been adjusted for field heterogeneity effects (Chapters Four and Five).

ADJUSTED YIELD - WAITE

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	360.5 135.1	393.3 176.8	632.3 222.8	352.3 141.0	488.3 191.2	360.3 179.0	572.9 96.7	384.5 91.3	489.0 126.1	443.1 84.8	225.9 202.8	350.5 171.2
T31		576.1 85.2	464.8 178.5	364.4 91.0	340.9 185.4	426.0 210.3	556.9 114.0	373.7 149.2	487.4 153.3	552.5 148.3	425.0 137.8	439.9 212.2
T33			470.2 149.9	492.3 227.0	564.1 163.4	486.0 186.6	576.1 177.9	580.3 170.1	491.1 203.5	298.9 136.3	413.5 170.2	731.5 132.4
T34				403.6 62.3	433.2 147.2	365.6 155.8	524.7 158.4	370.6 83.5	606.3 140.9	541.3 83.5	210.8 107.1	494.7 171.9
T58					378.2 125.1	371.8 184.9	506.1 204.9	377.9 110.0	398.1 174.2	396.6 100.8	252.6 145.1	525.7 179.1
T106						179.2 160.6	284.1 115.1	421.2 109.4	300.3 132.0	307.1 160.3	246.1 109.3	406.9 68.9
T246							474.5 110.5	492.3 131.4	552.1 166.9	501.6 117.2	315.6 184.8	542.8 163.3
T686								420.2 104.2	487.2 186.4	343.6 140.3	167.6 164.8	564.5 222.0
T702									494.7 157.3	460.6 149.5	296.6 196.8	592.2 178.7
T710										467.2 152.7	216.5 92.6	425.6 144.1
T896											264.0 151.2	328.4 181.4
T937												768.1 79.5

ADJUSTED YIELD - ROSEWORTHY

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	338.6 46.3	382.4 76.3	465.8 165.5	390.7 120.0	463.6 118.3	382.6 71.3	557.2 162.8	365.7 98.6	464.9 103.0	400.3 99.0	331.9 100.3	519.2 158.0
T31		485.2 91.4	401.6 119.6	416.1 92.4	378.5 94.7	418.0 99.7	493.3 80.3	334.8 77.7	512.4 200.7	456.5 152.3	394.2 114.1	451.4 126.0
T33			529.2 140.6	453.2 149.0	385.2 97.6	438.1 107.9	444.9 171.8	395.0 124.6	480.4 141.8	390.6 167.6	481.0 145.9	566.7 132.6
T34				397.8 77.6	402.8 67.5	443.9 123.6	372.6 66.4	384.7 88.6	588.0 168.7	434.0 78.6	336.4 125.5	436.7 110.4
T58					384.3 86.1	367.3 90.9	438.7 56.4	365.0 84.1	401.0 77.9	412.8 102.6	367.1 97.7	498.3 162.9
T106						413.5 78.4	341.0 66.0	378.9 72.0	408.6 90.1	330.9 118.2	398.0 80.2	511.3 81.7
T246							514.1 75.7	426.4 89.9	581.7 102.7	468.2 126.0	289.6 85.2	497.4 114.5
T686								393.4 73.4	379.4 94.4	374.3 65.0	327.9 114.9	395.7 142.9
T702									607.1 138.3	444.7 124.9	365.1 85.5	575.0 142.7
T710										476.9 71.0	377.8 153.9	440.5 149.9
T896											408.6 102.5	466.3 155.9
T937												674.6 63.9

ADJUSTED YIELD - STRATHALBYN

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	369.1 83.7	513.9 46.9	609.5 120.2	464.3 100.6	461.0 56.9	374.4 95.6	526.8 109.2	403.4 87.8	519.7 98.2	397.3 69.8	328.0 97.8	413.8 126.3
T31		436.1 54.2	395.1 150.5	392.7 50.1	408.7 81.0	318.4 65.0	449.6 92.8	375.4 120.1	425.6 104.9	538.7 106.0	539.6 89.0	420.5 150.1
T33			466.0 67.0	456.6 157.3	641.6 109.2	372.9 82.3	542.9 140.5	421.2 90.8	634.6 72.2	320.2 107.7	453.1 80.4	559.3 133.2
T34				320.6 29.8	443.5 73.5	393.4 48.6	343.6 105.3	416.1 90.2	608.6 171.8	506.7 81.5	349.8 94.4	393.3 67.1
T58					429.2 45.6	293.7 50.9	470.3 118.1	367.4 75.5	418.6 109.8	406.9 129.1	343.3 111.9	421.6 77.9
T106						263.0 51.6	350.9 98.3	403.5 90.2	481.8 60.4	373.2 79.9	290.6 72.1	435.6 86.4
T246							402.0 100.2	346.2 84.7	544.0 140.5	430.3 87.3	419.0 126.0	401.3 105.3
T686								416.0 78.0	465.4 131.2	422.0 64.9	308.1 77.2	399.3 77.8
T702									654.2 89.3	501.0 84.7	480.3 88.3	519.7 105.5
T710										470.5 70.3	353.4 86.9	423.3 92.8
T896											321.8 52.7	437.3 68.9
T937												471.8 99.3

ADJUSTED YIELD - ALL SITES

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	356.1 93.1	429.9 125.9	572.8 184.0	402.4 126.5	470.7 128.8	372.4 120.2	552.3 123.3	384.5 90.8	491.2 108.3	413.6 85.1	294.0 147.3	427.8 163.7
T31		499.1 96.1	420.5 149.6	392.0 79.8	376.0 127.6	387.5 143.5	499.9 103.5	361.3 116.7	471.9 153.9	515.9 139.2	461.0 126.3	437.3 161.4
T33			487.7 121.9	467.4 175.8	530.3 163.9	432.3 136.9	521.3 168.3	465.5 152.6	535.4 160.7	336.0 138.7	450.4 134.1	619.2 151.4
T34				374.0 69.5	426.5 100.6	401.0 118.7	413.6 138.3	390.5 86.6	601.0 155.7	492.4 90.4	297.7 123.3	439.7 124.7
T58					397.2 91.3	344.3 123.7	471.7 138.3	370.1 88.0	405.9 123.0	405.4 107.9	333.3 117.4	481.9 148.6
T106						285.2 143.0	325.3 96.7	401.2 90.3	394.0 122.2	337.1 122.7	311.6 107.3	451.3 88.7
T246							463.5 104.5	419.2 114.7	559.3 135.3	466.7 111.5	344.2 144.6	480.5 139.2
T686								409.9 84.1	443.3 145.8	380.0 99.0	267.9 140.2	453.2 173.0
T702									585.3 144.0	469.6 120.5	380.7 150.5	562.3 143.8
T710										471.7 99.4	315.9 132.5	429.8 127.1
T896											331.5 121.9	410.7 151.3
T937												636.9 150.7

ADJUSTED HEIGHT - WAITE

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	104.2 4.5	106.4 7.1	100.5 4.2	99.7 5.8	102.1 5.7	119.2 14.2	104.4 11.2	99.5 5.4	105.4 5.8	109.9 6.3	110.3 11.1	107.5 14.7
T31		113.1 5.2	105.9 11.0	104.0 7.3	104.7 6.1	111.4 11.6	103.7 7.8	99.3 6.4	108.0 11.3	116.6 3.8	97.8 7.9	101.7 9.8
T33			97.8 3.1	96.7 6.8	105.7 9.9	128.0 13.9	99.5 4.9	98.4 3.4	91.5 6.9	103.2 13.6	109.7 5.9	105.4 7.2
T34				99.9 3.1	106.6 5.8	118.3 10.4	96.7 4.1	97.6 8.3	93.5 5.4	114.1 8.3	97.3 6.0	108.1 12.5
T58					109.7 2.2	125.5 15.8	100.1 9.1	101.0 3.5	97.6 6.5	115.6 8.6	114.0 5.2	116.7 11.4
T106						141.7 5.7	132.9 13.1	119.1 14.1	116.8 8.7	131.6 13.7	134.9 10.1	129.4 7.9
T246							95.0 2.6	93.0 9.3	97.3 5.1	108.1 11.8	110.1 9.6	101.9 7.1
T686								93.2 4.5	87.2 4.7	103.4 7.8	100.8 5.6	106.8 7.1
T702									87.9 3.3	99.4 10.1	96.4 6.2	95.4 9.2
T710										119.7 4.6	107.1 4.9	113.5 13.5
T896											115.8 6.6	113.7 4.8
T937												106.7 4.7

ADJUSTED HEIGHT - ROSEWORTHY

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	103.9 7.5	105.8 4.9	100.6 6.2	103.1 7.6	98.7 5.3	111.4 12.4	108.9 8.3	101.7 9.9	99.3 6.2	107.1 7.9	114.2 14.3	115.5 13.4
T31		111.6 6.9	98.5 5.9	104.3 6.1	106.2 5.2	109.8 5.3	104.5 11.5	97.2 6.3	103.2 7.6	117.6 8.1	107.3 8.1	109.4 13.4
T33			100.3 7.8	102.2 7.1	104.7 9.6	121.3 6.2	97.9 11.3	94.9 8.3	96.1 9.0	103.9 14.0	111.3 6.5	106.0 10.3
T34				103.7 6.7	100.0 7.8	114.0 11.6	99.3 6.5	99.4 7.5	97.1 5.4	105.3 13.6	103.0 6.6	104.2 7.2
T58					107.1 10.3	120.3 11.5	105.8 9.4	95.7 5.1	106.1 6.7	110.5 3.8	104.4 12.9	109.9 10.5
T106						147.8 5.5	120.9 15.5	121.0 12.0	115.7 11.6	126.3 12.2	132.1 10.6	124.5 9.2
T246							97.1 2.8	94.2 6.3	93.3 4.8	116.5 9.1	102.1 8.6	104.7 5.4
T686								92.7 5.8	98.9 6.2	105.8 9.0	104.1 9.0	101.4 13.2
T702									91.6 4.6	111.3 10.9	97.7 7.6	94.7 6.0
T710										120.3 6.3	107.9 10.6	114.4 12.3
T896											113.4 7.1	114.2 11.6
T937												111.4 4.5

ADJUSTED HEIGHT - STRATHALBYN

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	98.3 8.4	103.7 11.6	106.5 9.6	101.3 6.7	103.2 8.5	112.5 15.5	113.3 8.8	105.8 10.4	105.8 12.6	106.2 12.9	105.9 9.2	109.3 12.5
T31		105.6 9.6	109.7 17.3	99.2 6.0	101.0 5.5	106.5 14.2	107.4 11.9	102.1 12.1	109.1 8.5	108.7 10.8	105.1 9.9	112.5 14.8
T33			108.1 18.1	102.3 13.2	105.7 18.4	118.8 19.8	106.4 5.9	102.8 14.3	96.7 10.2	109.7 14.0	110.5 7.7	110.0 8.8
T34				104.6 12.5	108.7 10.6	114.4 17.0	104.0 12.0	102.6 11.3	99.6 9.2	114.6 7.0	110.6 6.5	107.2 13.6
T58					104.0 6.0	111.4 15.8	102.4 8.8	107.5 11.1	102.5 12.8	108.5 14.1	107.8 12.5	104.7 17.7
T106						127.7 24.9	112.9 14.6	103.9 13.8	110.3 12.3	113.3 14.2	118.5 16.8	114.6 19.5
T246							101.6 15.3	98.3 12.0	102.5 12.0	107.4 6.5	109.5 12.6	103.9 10.0
T686								99.7 10.3	104.4 15.0	104.0 8.6	107.4 6.8	109.8 11.9
T702									101.9 7.3	106.5 9.2	106.1 7.2	102.7 9.4
T710										112.3 6.8	109.7 8.7	110.7 17.3
T896											109.2 11.7	107.9 14.2
T937												103.8 10.7

ADJUSTED HEIGHT - ALL SITES

	T28	T31	T33	T34	T58	T106	T246	T686	T702	T710	T896	T937
T28	102.1 7.3	105.3 8.1	102.5 7.3	101.4 6.7	101.3 6.7	114.4 14.0	108.9 9.9	102.3 8.9	103.5 9.0	107.7 9.3	110.1 11.8	110.8 13.6
T31		110.1 7.9	104.7 12.8	102.5 6.7	104.0 5.9	109.2 10.9	105.2 10.3	99.5 8.6	106.8 9.3	114.3 8.8	103.4 9.3	107.9 13.2
T33			102.1 12.0	100.4 9.5	105.4 12.8	122.7 14.5	101.3 8.5	98.7 10.0	94.8 8.8	105.6 13.7	110.5 6.6	107.1 8.8
T34				102.7 8.3	105.1 8.8	115.6 13.0	100.0 8.5	99.9 9.1	96.7 7.1	111.3 10.6	103.6 8.3	106.5 11.2
T58					106.9 7.1	119.1 15.2	102.8 9.1	101.4 8.6	102.1 9.5	111.5 9.9	108.7 11.2	110.4 14.0
T106						139.1 16.9	122.2 16.2	114.7 15.1	114.3 11.0	123.7 15.1	128.5 14.4	122.8 14.3
T246							97.9 9.2	95.2 9.5	97.7 8.6	110.7 10.0	107.2 10.7	103.5 7.5
T686								95.2 7.7	96.8 11.9	104.4 8.2	104.1 7.6	106.0 11.2
T702									93.8 7.9	105.7 11.0	100.1 8.1	97.6 8.8
T710										117.4 6.9	108.2 8.2	112.9 14.1
T896											112.8 8.9	111.9 11.0
T937												107.3 7.7

Appendix V

The PASCAL procedures used to obtain the least squares solution for the diallel analysis (at one site only).

```
PROCEDURE LSTBQ(Z,SITE:INTEGER);
```

```
VAR PT:PEDIGREE;
    D,F,F,XINC,TOL,S,SS,MU:REAL;
    J,K,L,COUNT,KK,LL,M,JD,KD:INTEGER;
    ALIAS,DD:ARRAY[1..Q] OF REAL;
    AIRRAY[1..Q,1..Q] OF REAL;
```

} variables are
declared

```
PROCEDURE PIVOT(IVAR:INTEGER);
```

```
VAR PYEC:ARRAY[1..Q] OF REAL;
    I,J,K:INTEGER;
    PIV,TEMP:REAL;
```

```
BEGIN
```

```
    PIV:=-1/A[IVAR,IVAR];
    FOR J:=1 TO Q DO
        IF IVAR<J THEN
```

```
            BEGIN
                PYEC[J]:=A[IVAR,J];
                A[IVAR,J]:=A[IVAR,J]*PIV;
```

```
            END
```

```
        ELSE
```

```
            BEGIN
```

```
                PYEC[J]:=A[J,IVAR];
                A[J,IVAR]:=A[J,IVAR]*PIV;
            END;
```

```
    A[IVAR,IVAR]:=PIV;
```

```
    FOR J:=1 TO Q DO
        IF J=IVAR THEN
```

```
            BEGIN
```

```
                IF J<IVAR THEN TEMP:=A[J,IVAR]
                ELSE TEMP:=A[IVAR,J];
```

```
                FOR I:=J TO Q DO
```

```
                    IF I=IVAR THEN
```

```
                        A[J,I]:=A[J,I]+TEMP*PYEC[I];
```

```
                END;
```

```
END (* PROCEDURE PIVOT *);
```

} Matrix
pivot
procedure

```
PROCEDURE CALCGCA;
```

```
VAR I,J,K:INTEGER;
```

```
BEGIN KK:=0;
      S:=0.0 ; SS:=0.0;COUNT:=0;
      TOL:=MEAN(Z,SITE)/1.0E6;
      MU:=MEAN(Z,SITE);
      FOR I:=1 TO Q DO FOR J:=1 TO Q DO
      IF I>J THEN A[I,J]:=-99
      ELSE A[I,J]:=0.0;
```

} Constants and
variables are
initialized

```
PT:=FIRST;
IF SITE=MAXSITES THEN FOR J:=1 TO P DO READ(PP[J,MAXSITES])
ELSE
      (If mean of all sites required output
      from GENSTAT program is read)
```

```
BEGIN
```

```
REPEAT
  WITH PT' DO
  IF INCLUDED(PT) THEN
```

} Check for inclusion
in I.P.D.

```
  BEGIN
    CASE HEAD OF
```

```
    DETAIL:IF CH1[Z,3,SITE]>0 THEN
      BEGIN
        D:=CH1[Z,1,SITE];
        E:=CH1[Z,2,SITE];
        F:=CH1[Z,3,SITE];
      END ELSE D:=-1;
```

```
    NODETS:IF Z<6 THEN
      IF CH2[Z,3,SITE]>0 THEN
      BEGIN
        D:=CH2[Z,1,SITE];
        E:=CH2[Z,2,SITE];
        F:=CH2[Z,3,SITE];
      END ELSE D:=-1 ELSE D:=-1;
    END (* CASE STATEMENT *)
```

} Data points
are obtained

```
  IF D>-1 THEN
```

```
  BEGIN
    IF NUMBER >P THEN
      BEGIN JD:=FP'.NUMBER+1; KD:=MP'.NUMBER+1; END
    ELSE
      BEGIN JD:=NUMBER+1; KD:=NUMBER+1; END)
    IF JD>KD THEN BEGIN I:=JD;JD:=KD;KD:=I END;
    COUNT:=COUNT+1;
    IF JD=KD THEN XINC:=2*F ELSE XINC:=F;
    S:=S+D; SS:=S+E; KK:=KK+TRUNC(F);
    A[JD,JD]:=A[JD,JD]+F;
    A[JD,KD]:=A[JD,KD]+XINC;
    A[KD,KD]:=A[KD,KD]+F;
    A[1,JD]:=A[1,JD]+F;
    A[1,KD]:=A[1,KD]+F;
    A[1,Q]:=A[1,Q]+D;
    A[JD,Q]:=A[JD,Q]+D;
    A[KD,Q]:=A[KD,Q]+D;
    A[Q,Q]:=A[Q,Q]+E;
    A[1,1]:=A[1,1]+F;
  END)
```

} Matrix is
initialized

```
  END;
  PT:=PT'.NEXT;
UNTIL PT=NIL;
```

```

MU:=S/KK)
FOR J:=1 TO Q DO DDE[J]:=SQRT(A[J,J])
FOR J:=1 TO Q DO FOR K:=J TO Q DO
A[J,K]:=A[J,K]/(DDE[J]*DD[K])
FOR K:=1 TO P+1 DO
IF A[K,K]<TOL THEN ALIAS[K]:=1
ELSE BEGIN PIVOT(K); ALIAS[K]:=0 END;
ALIAS[Q]:=1;
FOR J:=1 TO Q DO FOR K:=J TO Q DO
BEGIN
IF ALIAS[J]=0 THEN S:=1/DD[J] ELSE S:=DD[J];
IF ALIAS[K]=0 THEN SS:=1/DD[K] ELSE SS:=DD[K];
A[J,K]:=A[J,K]*S*SS;
END ;

D:=0.0 ;
FOR J:=1 TO P DO D:=D+A[J+1,Q]
D:=D/P ;
FOR J:=1 TO P DO PPC[J,SITE]:=(D-A[J+1,Q]);
END;

FOR J:=1 TO P DO
BEGIN
LL:=1;
FOR K:=1 TO P DO
IF PPC[J,SITE]<PPC[K,SITE] THEN LL:=LL+1;
PPRANK[J,SITE]:=LL;
END;
END (* PROCEDURE CALCGCA *)

BEGIN
CALCGCA;
LSTSQOUT;
LSTSQFTEST;
END (* PROCEDURE LSTSQ *)

```

} Optimization
is done

} gca values
are stored

} gca
procedure
called

Appendix VI

The GENSTAT program used to obtain the least squares solution for the diallel analysis (for all sites).

WAITE INSTITUTE, ADELAIDE UNIVERSITY CYBER 173 - GENSTAT VERSION 4.01

GENSTAT V MARK 4.01

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```
1  "REFE/NID=150" DIALLEL
2  "SCAL" P,DF,ROWNO,DUNROW,S,NSUBV :NOVAL=0 :MV=* :INTERM=1
3  "VALU" P=12 :DF=11 :DUNROW=26 :ROWNO=2 :SKIP=1
4  "SET" DFFINAL=NOVAL :FRSTROW=ROWNO :FDF=DF
5  "INTE" DIALEYS=1...12
6  "NAME" PNAME=T28,T31,T33,T34,T58,T106,T246,T686,T702,T710,T896,T937
7  "INTE" PARTIAL=1,2,3,4,5,9,10,11,12
8  "FACT" MALE $PNAME,100 :FEMALE $PNAME,100 :SITE $3,100
9      :DIAGNLS $DIALEYS,100
10 "VARI" YVAR,DIFPLUS1 $100
11 "DSSP" SSBPROD $YVAR+FEMALE+MALE+SITE
12 "INPUT" 2
13 "LABEL" L1
14 "READ/SEQ=S" FEMALE,MALE,SITE,YVAR $S ,1X,2,1X,1,SKIP(X),1,7
15 "CALC" DIFPLUS1=ABS(FLOAT(MALE)-FLOAT(FEMALE))+1
16 "CALC/ZDZ=MV" YVAR=YVAR*(YVAR.GT.0)/(YVAR.GT.0)
17 "GROU" DIAGNLS=INTPT(DIFPLUS1)
18 "REST/C" YVAR $DIAGNLS=PARTIAL :SUBSET
19 "CALC" NSUBV=NVAL(YVAR) "JUMP" L2*(NSUBV.LT.1)
20 "CALC" YVAR=MV
21 "LABE" L2
22 "REST" YVAR
23 "CALC" NOVAL=NOVAL+NVAL(YVAR)-NMV(YVAR)
24 "SSP/SEQ=S" SSBPROD
25 "JUMP" L1+(S.GT.0)
26 "CALC" NOVAL=NOVAL-1
27 "PRIN" NOVAL $10
28 "INPUT" 1
29 "DEVA" FEMALE,MALE,YVAR
30 "RUN"
```

```
31 "START"  
32 "MACRO" SSPCON #  
49 "MACR" CONDENSE #  
79 "SCAL" IPD  
80 "FACT" GCR #P  
81 "DSSP/DF=DFFINAL" DIAL #Y+GCR+SITE  
82 "USE/R" SSPCON #  
83 "REGR" DIAL  
84 "Y" Y  
85 "FIT" GCR  
86 "ADD" SITE ;COEF=COEFF  
87 "CALC" IPD=NVAL(PARTIAL)  
88 "OUTP" 2 #80  
89 "PRIN/LABC=1,LABR=1" IPD,COEFF #10,13(10.4)  
90 "OUTP" 1  
91 "RUN"
```

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