AN EIGHT-PARENT DIALLEL CROSS ANALYSIS FOR OIL AND PROTEIN PER CENT AND THEIR RELATION TO OTHER CHARACTERS IN OATS (AVENA SATIVA L.)

by

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Short title

DIALLEL CROSS ANALYSIS IN OATS

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DEDICATION

To the memory of my dearly beloved mother and father, whose lives will always remain exemplary, this work is humbly dedicated.

ABSTRACT

Ph.D. SAMIR EL-SEBAE AHMED Plant Science (Agronomy)

AN EIGHT-PARENT DIALLEL CROSS ANALYSIS FOR OIL AND PROTEIN PER CENT AND THEIR RELATION TO OTHER CHARACTERS IN OATS (*AVENA SATIVA* L.)

The genetic control involved in the inheritance of nine important quality and agronomic characters and the relationships among these characters were investigated in the F_1 and F_2 generations from an eight-parent diallel cross in oats. Three different diallel analysis techniques were used. These were (a) the Griffing's analysis, (b) the Jinks-Hayman analysis, and (c) the graphical analysis.

The results indicated partial failure of one or more of the assumptions required for the genetic analysis, including that of no epistasis and gene correlations, for some characters. Although both additive and dominance effects contribute to the genetic variation in all characters, additive genetic variance is more important in the genetic control of most characters. The degree and direction of dominance varied according to the character and generation. Gene correlation, the distribution of positive and negative as well as dominant and recessive alleles, and the number of effective genes or groups of genes controlling each character, were investigated. Heritability estimates and genetic advance from selection varied according to the method of calculation and the generation, but they had almost the same rank for all characters. Phenotypic, genetic and environmental correlations among all characters indicated no difficulty in selecting in the desirable direction for most characters. In this study, the use of diallel cross techniques in oat improvement has been discussed and breeding strategies suggested.

SOMMAIRE

Ph.D. SAMIR EL-SEBAI AHMED Plant Science (Agronomy)

UNE ANALYSE DIALLELE DE LA TENEUR EN HUILE ET DU CONTENU PROTEIQUE ET LES RELATIONS EXISTANT ENTRE CES DEUX CARACTERES ET PLUSIEURS AUTRES, CHEZ L'AVOINE (AVENA SATIVA L.)

Le contrôle génétique impliqué dans l'hérédité de neuf importants caractères qualitatifs et agronomiques de l'avoine, ainsi que les rapports existant entre ces caractères furent étudiés chez les générations F_1 et F_2 issues d'un croisement diallèle réunissant huit parents. L'analyse diallèle fut effectuée à l'aide de trois méthodes différentes, soit l'analyse de Griffing, l'analyse de Jinks-Hayman et l'analyse graphique.

Les résultats obtenus ont révélé que, pour certains caractères, une (ou plusieurs) des hypothèses posées pour l'analyse génétique, soit l'absence d'épistasie et de corrélations entre les gènes, n'était pas entièrement vérifiée. Bien que les effets additifs et les effets de dominance aient contribué à la variation génétique chez tous les caractères, la variance génétique additive a joué un rôle prépondérant dans le contrôle de la plupart des caractères. L'intensité et la direction de la dominance ont varié selon le caractère et la génération. Les corrélations entre les gènes, la distribution des allèles positifs et négatifs, aussi bien que des allèles dominants et récessifs, ainsi que le nombre de gènes ou groupes de gènes responsables du contrôle de chaque caractère furent étudiés. Les estimations d'héritabilité et l'amélioration génétique apportée par la sélection ont varié selon la génération et la méthode de calcul employée; toutefois, tous les caractères occupaient à peu près le même rang, quelle que soit la méthode de calcul utilisée. Les corrélations phénotypiques, génétiques et environnementales relevées entre tous les caractères indiquèrent que, pour la plupart d'entre eux, la sélection de la direction désirée ne posait aucun problème. Dans cette étude, l'emploi des techniques d'analyse diallèle pour l'amélioration de l'avoine est discuté et des stratégies concernant l'amélioration de cette plante sont présentées.

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CHAPTER I

INTRODUCTION

Recognition of a world nutrition and food crisis during the past few years has stimulated plant breeders to improve the quality and increase the quantity of their crops. Oats (Avena species) constitutes one of the five major cereal crops in the world. In addition to having more adequate levels of oil than other cereal crops, the upper limit of protein content in Avena species extends beyond that of the other cereals. On the other hand, the energy value of oats is lower than that of other cereals for livestock feed. Therefore, improving the nutritional quality of this crop would increase its energy value and make it more valuable for food and feeding purposes.

Quality evaluation in oats as well as in other cereals has many determinants to be considered, but for the purpose of this study attention will be focused on the protein, oil and hull content, since they are nutritionally the most important components of quality in oats. Klinck (1967) and Donefer (1976) suggested that cereal breeders should consider developing cultivars of oats that provide higher energy, since energy is the most limiting factor in the feeding of ruminant animals with cereal grains. Klinck (1967) concluded that it should be possible in oats to select for high values of both protein and oil.

Dudley and Moll (1969) divided plant breeding into three stages: (a) assembly or creation of a pool of variable germplasm, (b) selection of superior individuals from the pool, and (c) utilization of selected individuals to create a superior cultivar. Breeding for superior qualitative characters in oats has long enjoyed effective genetic guidance, but breeding of superior quantitative characters has been denied such guidance to a large extent. The difficulty with quantitative characters is that they tend to be continuous in their variation. This means indistinguishable phenotypic classes and difficult or impossible applicability of classical Mendelian analysis (Johnson, 1963).

Knowledge of the relative magnitude of the various genetic and environmental parameters for characters of economic importance is essential before more efficient breeding and selection procedures can be employed. Since economically important characters are largely, if not entirely, quantitative in inheritance, they are described in terms of first and second order statistics, i.e., means, variances, and covariances. The use of first and second order statistics permits the estimation of population genetic parameters such as means, genetic variances, heritabilities, genetic, environmental, and phenotypic correlation coefficients, and expected genetic advances from selection. Knowing the magnitude and the importance of such estimates would be of great value to a plant breeder as guidance rules to systematize selection of parents, to regulate the manipulation of progenies or to permit prediction and isolation of superior lines. For example, the heritability concept is useful in determining to what extent differences among phenotypes are due to genotypic causes, and knowledge of the correlation between complex characters of low heritability, such as yield, and less complex characters which may have much higher heritabilities, would benefit plant breeders. It may be easier to select for a complex character by practising selection on a highly heritable character correlated with it.

There are numerous reports in the literature dealing with studies of the relative magnitudes of the various genetic and environmental parameters in oats. The diallel cross techniques developed by Griffing (1956a, 1956b) and Jinks and Hayman (1953) seem to provide sufficient information about the genetic identity and relationships among a number of parents. In this study, these two methods of diallel analysis were used.

The present investigation was designed to estimate both general (GCA) and specific (SCA) combining ability variances and effects for nine quality and agronomic characters in oats by means of diallel analysis techniques. In addition, it was designed to estimate the variance components, heritability, expected genetic advances, the number of genes or groups of linked genes involved in the inheritance of these characters, and the phenotypic, genetic and environmental correlations among all characters under investigation. Other objectives were to predict, on the basis of genetical information, which crosses in our material would give the best chances of finding high manifestations of each character which subsequently could be fixed in pure lines. At the same time, an intensive evaluation of diallel analysis techniques as a tool for plant improvement was carried out.

CHAPTER II

REVIEW OF LITERATURE

The review of literature will include four main topics related to qualitative and quantitative characters in self-pollinated crops, especially the small grains. These topics are: (1) The importance of oats as a feed and food crop and the possibilities for improving their quality; (2) variance components, heritability and genetic advances from selection; (3) relationships between characters; and (4) diallel analysis techniques and their application in plant breeding.

1. Oats as a feed and food crop and the possibilities for improving their quality

Quality in cereals is usually judged by their suitability for a particular end use. Most cereals are used primarily for human food directly or as animal feed. Thus, cereal quality is largely a relative concept and is considered in relation to a particular class of food product. For animal feed, differences in the quality of the by-products are usually considered to be relatively unimportant with some cereal crops, whereas they become important in others.

On the average, man derives about 70 per cent of his required calories and 50 per cent of his protein from cereals and cereal-based products (Frey, 1976). Additionally, large quantities of cereal grains are used in the feeding of livestock, especially in the developed countries.

Prior to the mid-1960's, quantification of the nutritive value of oat (Avena species) grain lagged behind its realized value in human foods and animal feeds. The discovery by Murphy and co-workers (1968) that collections of the wild oat species A. sterilis L. contained high groat protein stimulated many new investigations. Recent studies have been mainly concerned with:

(a) oat protein quality and amino acid composition

(b) lipid content and fatty acid composition

(c) examining the genetics of groat yield and protein content and breeding for higher levels of these components.

With the recognition of a world food and protein crisis in recent years, plant breeders are attempting to improve the quantity and quality of cereal grains. Burrows (1974) stated that the oat crop could, and probably will play a very significant role in solving the food crisis problem. Oats will probably shift from being a feed grain to a new and updated food species. Burrow's statement is based on the fact that by breeding special oat cultivars for human use rather than for animal use, both types of crops (feed and food) can be grown essentially side by side, and the acreage in any area devoted to feed or food oats will be determined by domestic and world requirements.

Also, the genetic variation or the size of the gene pool in oats is as great as in any other of our major cereals and may be even greater than in most. Oats have not really been selected for quality even though several nutritionists rate their quality as excellent. Unexploited genes have been located in many of the diploid, tetraploid and hexaploid wild and cultivated species. There are many contrasting forms or types available in this species.

The nutritional quality of oat protein, with respect to its content of essential amino acids, is as good as, if not better than that of any other cereal crop (Burrows, 1974). The protein of oat grain has three unique features (Ohm and Patterson, 1973a, 1973b; Burrows, 1974; Frey, 1976):

(a) A high biological value relative to that of the other cereal grains. This is illustrated by feeding trials and by amino acid composition.

(b) The biological value of oats protein does not deteriorate as protein percentage in the grain increases. This could make it feasible to breed oat plants with higher protein levels without adversely affecting the nutritional quality of the grain. Burrows (1974) mentioned that in oats, cultivars can be bred that are rich in protein content because protein quality is essentially maintained.

(c) The protein percentage of oat grain probably can be elevated to very high levels by genetic means. In general, the protein content in whole grains of cultivated oats ranges from 9.0 to 16.0% (Frey and Watson, 1950) and the maximum protein in the groats of commercial cultivars is about 20% (Briggle, 1971).

Data from many researchers suggest that it should be possible to elevate the groat protein percentage above the 14.0 to 17.% normally found in commercial cultivars. Two new cultivars of oats, Dal and Goodland, were released from the Wisconsin Experiment Station in 1972 and 1973, respectively. These cultivars produce grain with 19-20% groat protein (Shands et al., 1974). Frey (1976), at Iowa State University, also reported the development of a new cultivar of oats with adequate levels of grain yield and protein. He reported the discovery of genes from A. sterilis that increased the yield of experimental lines of cultivated oats by 20-30%. These genes were designated as the "yield genes". The author found that the yield increases of these lines were accomplished without depressing groat-protein percentage. On the other hand, the Wisconsin researchers (Shands et al., 1974) discovered genes for high protein that have no effect on yield. Their genes were designated as the "protein genes".

Frey has research underway to determine whether the independency of the "yield genes" will be maintained when combined with "protein genes" from the Wisconsin cultivars.

If the high protein character is genetically controlled and heritable, the genetic incorporation of this high-protein character into high-yielding cultivars with desirable agronomic traits would greatly increase the protein yield of oats. Many workers have suggested that, in the short run, breeders can best achieve the goal of producing commercially acceptable oat cultivars with a significantly elevated groat-protein content by utilizing crosses within the A. sativa species.

On the other hand, Briggle et al. (1975) reported that several breeders have succeeded in selecting high protein segregates from A. sterilis x A. sativa crosses, but as yet none of these selections has met the requirements for release as an oat cultivar. Generally, these high protein cultivars are lower in yield than standard cultivars and produce slender kernels with less endosperm. Both conditions are usually associated with high protein concentration. The authors asked whether the high groat protein of A. sterilis parents was the function of a low grain yield and an adverse kernel type, or was it due to the expression of specific genes controlling the amount of protein deposited in the groats. They concluded that if this situation prevailed, it may be very difficult for a breeder to combine high protein, high yield and large, plump groats in one genotype. They hope that through more intensified breeding efforts A. sterilis genotypes can be identified which have specific genes for high protein concentration not associated with lower grain yield.

Sraon et al. (1975) agreed with Briggle et al. (1975) that the inverse relationship of protein and yield could present a problem of how to combine high protein and high yield in one cultivar. They rejected the idea of increasing protein content by sacrificing yield. Burrows (1974) pointed out some of the problems in breeding for high protein cultivars in oats. These problems are:

(a) The lower yield potential of high protein strains

(b) the apathy of food researchers and food processors to develop new recipes and new uses for oat in the human diet

(c) the many published reports of animal nutritionists minimizing the importance of protein in feed grain and stressing high energy content and high yields of energy per acre.

Burrows recommended that efforts must be made to break the negative association between yield and protein content and to understand why the negative association exists. He reported that it may not be possible to combine high protein and high grain yield directly because the developmental factors within the plant that ultimately lead to a higher protein content in the seed may also adversely affect the total accumulation, utilization and distribution of carbon fixed in photosynthesis during the early life of the plant. Burrows suggested the following strategies to increase grain and energy yields per acre:

(a) Conventional breeding programs

(b) improving the intrinsic energy content of the kernel by crossing high protein and high fat cultivars and selecting for high levels of both

(c) lengthening the time to differentiate large panicles with more kernels per culm

(d) utilizing seed dormancy to raise yield potential.

An early study by Black and Kempthorne (1954) showed that the seemingly universal negative association between grain yield and protein percentage is "phenotypically" real but not necessarily genetic in origin.

Recently, Frey (1973) tested oat cultivars and lines in field experiments where soil nitrogen was either very deficient or adequate for growth of oat plants. The author obtained a negative and significant genetic correlation coefficient (-0.26) between grain yield and groat protein under low soil nitrogen conditions, while under adequate soil nitrogen, his genetic correlation was not significant (0.04). He concluded that the negative correlation observed between these two traits is an artifact resulting from limited availability of soil nitrogen. In another study, Frey (1976) reported that negative correlations between grain yields and protein percentages of cereal species may be artifacts of past experimentation. Data from wheat and oats suggest that genes are present in these species that can cause independent quantum increases in either grain protein content or grain yield.

Because oats are used mostly for livestock feed, and have a great genetic diversity in oil content, breeders might wish to make the development of cultivars with desirable levels of oil a major objective in breeding programs. Oats have higher oil content than other cereals. Brown et al. (1966), and Brown and Craddock (1972) reported a range of 3-11% oil in the groats.

Klinck (1967) reported that since energy is the most limiting factor in the feeding of the ruminant animals with grains, cereal breeders should consider developing cultivars that provide higher energy levels. The author concluded that it should be possible to select for high values of both protein and oil content in oats. Brown and Craddock (1972) demonstrated from their unpublished data that oil content in oats is highly heritable. They concluded that oat breeders should have little difficulty in developing suitable cultivars with high or low oil content.

The same conclusion was drawn by Baker and McKenzie (1972). They concluded that it should be practical to select for oil content in oats. To achieve this goal, the authors suggested that high-oil parents should be used when breeding for oil content. They warned that one must be wary, however, in choosing parents to start a selection program. The choice of closely related cultivars would result in a cross that is essentially devoid of genetic variability and potential for improvement.

In general, three points are critical in deciding whether or not to develop a high oil content oat for feed or food purposes:

(a) The level of oil content that could be expected. Failure to identify parental genotypes in some of the wide crosses suggests that several genetic factors control oil content in oats. However, Baker and McKenzie (1972) stated that it may be possible to develop an oat cultivar with at least 10% oil.

(b) The problem of storage of high-oil oats. A lipase enzyme extracted with oat oil causes rapid rancidity and deterioration of oil quality. For this reason oats with 7% oil have been preferred by human food processors (Forsberg et al., 1974). Brown et al. (1970) showed that the content of free fatty acids, which cause rancidity, is reduced as the kernel matures but still constitutes a measurable portion of the lipid fraction. They recommended that studies on the effect of different harvest and storage conditions on the content of free fatty acids in high-oil cultivars are required before the potential of high-oil oats can be fully evaluated.

(c) The unfavorable association between oil and protein. This association might make it somewhat difficult to combine high levels of oil and protein. However, Brown et al. (1966) found some strains which possessed relatively high levels of oil and protein while others were low in both.

The success in incorporating the opaque-2-gene, producing high lysine content, into high-yielding lines of maize has indicated that yield and quality in cereals may not necessarily be irreconcilable (Frey, 1976).

Due to the high fiber content of the hull, the energy value of oat grains is inferior to that of wheat, barley and corn, for which reason oats is the grain least liked by the formulators of livestock feeds. However, there is a notable lack of information on the relative feeding values of different grains as measured through appropriate animals, and on the correlation of such data with chemical composition (Lawes, 1971).

From a feed quality standpoint, there is justification for contemplating the development of naked (hulless) oats. However, plant breeders have not succeeded in obtaining highly productive cultivars of naked oats. In addition, there are storage and other problems associated with this character. Klinck (1977) concluded that the common covered oat is the preferred type so long as the caryopsis percentage is high. He stated that selection for high caryopsis content or low hull can achieve results. Wesenberg and Shands (1973) suggested that it may be difficult to isolate segregates with more than 80% caryopsis.

Donefer (1976) reported that on the basis of his assumptions and experience he would recommend to plant breeders that minimizing cellulose (fiber) content appears to be one of the most effective ways of increasing the available energy content of oat grains. Also, he suggested that cellulose analysis is a simple chemical procedure for energy evaluation of grains.

Lawes (1971) summarized the difficulties encountered in producing good commercial naked-grain cultivars as follows:

(a) Intrinsic low grain-yielding ability associated with multiflorous spikelets and high proportion of small grains.

(b) Incomplete expression of the naked character. All cultivars produce a proportion of covered grains and mosaicism occurs within individual panicles.

(c) Liability to grain shedding. Morphologically the grain is held less securely in naked than in covered cultivars, though cultivar differences exist.

(d) Premature germination of unharvested grains.

(e) Poor germination of seed samples. The embryos are poorly protected and liable to suffer damage during threshing.

(f) Deterioration during storage, due to high oil content and susceptibility to damage by micro-organisms.

With such wide genetic variation in oats for protein, oil and hull per cent, oat breeders would be able to combine high levels of the three characters with desirable agronomic traits if these characters are genetically controlled and heritable, and if sufficient information about their genetic control is available.

2. Variance components, heritability and genetic advances from selection

Various authors have emphasized the utility of the estimates of variance components, and in particular, the genetic variance component, as a basis for predicting the response of quantitative characters to selection in plant breeding programs. Selection in a given population is based on the phenotype of individuals while only a portion of the phenotypic value is transmitted to the following generation. Thus, it is of primary importance to know the relative magnitudes of the different components of the phenotypic value.

The phenotypic expression of a character can be considered as the sum of a genetic effect and a deviation attributable to environment and interaction between the genotype and the environment involved. Wright (1921, 1935) considered the genotypic variance to consist of three components:

(a) additive genetic variance, σ^2_A

(b) variance due to dominance deviations from the additive scheme, σ^2_D

(c) variance due to epistatic deviations from the additive scheme, σ^2_I

Estimates of variances due to the different sources of variation contributing to differences between individuals as described above are important for plant breeders to develop their breeding programs. Comstock and Moll (1963) reported three advantages of knowing the true magnitudes of genetic variation:

(a) Over-estimation of genetic variation would in some cases lead to investment of time and effort not justified by the real potential for improvement of genetic stocks employed.

(b) Optimum procedures may vary significantly, depending on the magnitude of genetic variances.

(c) There is a danger that sound breeding programs may be abandoned prematurely or unwisely because of results that are disappointing relative to unwarranted expectations based on erroneous estimates of genetic variance.

In general, the different procedures suggested by plant breeders for partitioning the phenotypic variance of quantitative characters in a population carry the following biological assumptions: (1) normal diploid behavior at meiosis; (2) no maternal effects; (3) absence of multiple alleles; (4) linkage equilibrium; (5) random selection; (6) no epistasis. However, under certain circumstances, models are available in which one or more of these restrictions may be eliminated (Sprague, 1966). These procedures have been discussed by Anderson and Kempthorne (1954), Cockerham (1963), Crumpacker and Allard (1962), Dudley and Moll (1969), Gardner (1963), Griffing (1956a, 1956b), Hayman (1958, 1960), Kempthorne and Curnow (1961), Mather and Jinks (1971), Matzinger (1963), and Sprague (1966). Anderson and Kempthorne (1954) presented a model based on the factorial model to estimate genetic effects. Hayman's (1958, 1960) analysis is also used to separate epistatic and dominance variation in generation means. The author pointed out that no accurate estimate of the additive, or breeding, effects could be obtained if epistasis is present in a great magnitude.

Progress under selection in breeding programs depends on the magnitude of heritability for the trait being selected for. Estimates of genetic variance and its additive and dominance variance components as well as phenotypic variance are used by plant breeders to estimate heritability. Several reasons have been put forward for requiring an estimate of heritability. For example, Lush (1948) listed the following points: (a) when heritability in the narrow sense is high, reliance should be placed mainly on mass selection, and as heritability becomes lower, more emphasis should be placed on pedigrees, sib tests and progeny tests; (b) if the epistatic variance is relatively high, more reliance should be placed on selection between families, and line breeding; (c) if over-dominance is predominant, the breeding plan should turn toward inbreeding, with the object of producing hybrids for the commercial market; (d) if the variance due to interactions between heredity and environment is relatively large, the breeding plan tends more toward producing a separate cultivar for each ecological region; and (e) heritability may be used to estimate expected improvement due to selection.

For purposes of clarity, certain terms are defined here as introduced by different authors. Knight (1948) defined heritability as the portion of the observed variance for which differences in heredity are responsible, while Dudley and Moll (1969) defined heritability in the broad sense as the ratio of total genetic variance to phenotypic variance, and heritability in the narrow sense as the ratio of the additive genetic variance to the phenotypic variance. Phenotypic variance is the total variance among phenotypes when grown over the range of environments of interest to the breeder. The total genetic variance is the part of the phenotypic variance which can be attributed to genetic differences among the genotypes. The genotype-environment interaction variance is that part of the phenotypic variance attributable to the failure of differences between genotypes to be the same in different environments.

Discussion of heritability concept and its implications in plant breeding have been reported by several workers (Burton, 1952; Dudley and Moll, 1969; Falconer, 1967; Hanson, 1963; Robinson, 1963; Warner, 1952).

Robinson (1963) stated that heritability estimates must be treated with some caution because they depend so much on the choice of plot size, planting density, and number of replications. He asked that if an estimate of heritability is as restricted in its application and since a ratio is not as informative as a knowledge of its two components, is there any point in estimating heritability. However, he stated that a meaningful estimate of heritability is of use in estimating expected progress from adopting the program, and it is also a very useful concept in determining the relative importance of genetic effects which may be passed on to offspring, even in cases where it would be difficult to extrapolate to other populations.

The variance components method proposed by Comstock and Robinson (1948, 1952) has been used extensively in estimating heritabilities. This method could be applied to either genetically different cultivars or families from a given generation. The major problem encountered in using the variance components method to estimate heritability is that the estimate of additive variance so obtained is quite likely to contain fractions of epistatic variances and genotype-environment interactions which, if present, would inflate the estimate.

As soon as heritability is estimated for a quantitative trait in a population, the question is raised as to what level progress would be expected under selection in that population. The estimate of such progress is called the genetic advance. Falconer (1967) defined the expected genetic advance from selection (G_s) as the product of selection intensity, the estimate of phenotypic standard deviation and the heritability estimate. Expected genetic advance has been estimated by most authors who have investigated heritability of quantitative characters.

In an early study, Love and McRostie (1919) studied the inheritance of the hull percentage in crosses of _A. sativa nuda_ with

A. fatua and four cultivars of A. sativa. They noticed a great amount of variation in the percentage of covered and hulless kernels in the F_2 intermediate plants. The authors discussed the possibility that multiple factors might be involved where one primary factor determines the covered or hulless condition, while other factors influence the covered condition of those plants only that are heterozygous for the primary factors.

Lebedeff (1930) studied the inheritance of covered/hullessness in several crosses of oats. He found that the totals for all crosses showing a dihybrid segregation and several of the individual crosses, conform closely to the expected results from the author's assumption. Certain cases of deficiency of fully covered plants led to the assumption that the basal gene was not fully epistatic to the subsidiary genes where these were in the double recessive condition.

The inheritance of the hull character was investigated by Chou (1932) in a cross of A. sativa with A. nuda. The author reported that the F_1 appeared hulless but was actually genetically intermediate. In the F_2 he found that the covered group always comprised about one-fourth of the total and a ratio of 3:1 could always be obtained by combining the hulless and intermediate types. Chou explained his data on the basis of one pair of primary factors and secondary multiple factors, number unknown, which favor the production of more hulless grains when dominant, and favor production of more covered grains when recessive.

Sappenfield (1952), in his 15 possible crosses between six cultivars of oats, found that earliness was inherited as an incompletely dominant character to lateness and was due to a series of multiple factors which gave a cumulative effect. Estimates of the number of genes involved ranged from a minimum of 2 pairs in the very early x very early crosses, to a minimum of 4 pairs in the very early x very late crosses. Sappenfield noticed that as the difference in time of heading between any two parents increased, the number of gene differences between the parents became greater. He suggested that transgressive segregation for earliness may frequently be obtained in crosses between cultivars of similar maturity.

Heritability is a predictor of the success that a plant breeder can expect to attain from selection. Frey et al. (1954, 1955), from crosses among cultivated oat strains and cultivars, concluded that grain-protein percentage was inherited polygenically and that it usually showed dominance, but the direction of dominance was dependent upon the particular strains mated. They reported a mean of broad sense heritability for F_2 plants of 15% in one study and 88% in a second.

Wallace et al. (1954) studied genotypic variance and covariance of six quantitative characters in an oat cross. The characters were yield, seed weight, plant height, culm number, number of seeds per plant, and number of seeds per panicle. They suggested that breeders perhaps need to pay more attention to selection for number of seeds per panicle. However, they were unable to devise a selection index based on the combined use of the characters studied which was considered to be more effective than selection based on yield alone. The authors raised the question as to how much of the superiority evident in an oat can be transmitted to its progeny in a cross since the particular gene combinations, which provide favorable epistatic effects in the superior parent, might not be reconstituted in any of the progeny. The importance of epistatic effects is not well known and the situation is complex because of the polyploid nature of oats. The expected genetic advance from selection was 12.9% (of the mean) for yield, 12.8% for seed number per plant, and 13.4% for seed number per panicle. The genetic coefficients of variability among progenies ranged from about 5% for seed weight to about 18% for seeds per panicle.

Frey and Horner (1957) compared the two regression methods of calculating heritability, the conventional and standard units, for heading date in oat crosses. Heritability in standard units tended to eliminate those environmental effects of different years that increase or decrease the range of the progenies relative to that of their parents. They reported average heritability of 44% for F_3 on F_2 and 93% for F_4 on F_3 by the conventional method, in contrast to 62 and 63%, respectively, from the standard unit method. The mean gains from selection for heading date of oats were 1.5 days and 2.8 days for the corresponding actual value from the conventional method. However, both values of predicted and actual gains were the same when heritability was calculated by the standard units method.

Jones (1957), in a study of individual plants from the F_2 to F_5 of 20 oat crosses, found that heritability was high for heading date and plant height, intermediate for kernel weight and low for yield. The average degrees of dominance were 0.47, 0.91, 1.43, and 2.44 for heading date, plant height, kernel weight, and yield, respectively. He concluded that significant gains in genetic advance could be obtained by selecting for these four characters even in the F_2 generation. The author stated that by delaying selection until the F_5, the largest increase in efficiency was indicated for yield and the smallest for heading date, a relationship which would be indicated by the heritability rankings.

Frey (1959a) studied the relation between environmental and genetic variances for heading date and plant height in oat crosses. His results indicated that the environmental and genetic variances were related for heading date but were independent for plant height. For heading date he obtained heritability percentages of 82 from the regression of F_3 on F_2, 56 for F_4 on F_3, 63 for F_5 on F_4, and 78 for F_6 on F_5. For plant height the percentages were 87 for F_4 on F_3, 90 for F_5 on F_4, and 89 for F_6 on F_5.

Jones and Frey (1960) reported that delaying the selection until the later generations would increase the expected genetic gains over that in early generations. They found that delaying the selection until the F_5 would increase the percentages of the expected genetic gains in oats by approximately 150 for heading date, 150 for height, 160 for kernel weight and 200 for yield in comparison with selection in the F_2 generation.

Petr and Frey (1966) obtained broad sense heritability percentages in oat crosses of 33, 53, 61 and 87 for number of panicles per plant, grain yield, plant height and heading date, respectively. They reported that heritability percentages and high levels of dominance for yield and panicles per plant observed in the F_1 indicated that selection for yield and number of panicles per plant should be delayed until later generations, while selection for plant height and heading date should be feasible in early generations.

Johnson and Frey (1967) examined the reactions of several agronomic characters of oats to different degrees of environmental stress. Genotypic variances among oat cultivars were increased when environmental stress was reduced. However, heritabilities did not always increase with reduced environmental stress. They concluded that the environment which gave the highest heritability for a set of cultivars was the best for practising selection among them, assuming that genotype-environment interaction did not negate the gains when the selected genotypes were grown in other environments.

The expected genetic advances from three simulated selection schemes were studied in oats and barley. The expected genetic gains were 13.4, 8.1 and 3.0% for grain yield, plant height and heading date, respectively, in oats and 10.3, 8.2, and 6.0% in barley (Frey, 1968).

Baker and McKenzie (1972), using crosses between cultivars with low, medium, and high oil content, found that the heritability of oil percentage varied from 68 to 93%. Such heritability values suggest that selection for low or high oil percentage in oat seeds could be accomplished with ease.

Campbell and Frey (1972), using 10 crosses of A. sativa x A. sterilis, concluded that much genetic variability for protein concentration existed among progenies from these crosses. Inheritance of the trait was relatively simple, and heritabilities were high enough to expect progress toward breeding for high protein concentration in oats, but the authors reported that what appeared to be a small number of loci involved in protein-content inheritance actually may be due to a large number of loci linked in blocks on a small number of chromosomes, which would give the impression of simple inheritance.

Ohm and Patterson (1973a) obtained partial dominance for per cent groat protein in a study of six A. sterilis parents in a diallel experiment in oats. In another study Ohm and Patterson

(1973b) crossed each of the same six A. sterilis collections with five A. sativa cultivars. General combining ability was highly significant for groat-protein concentration and high per cent protein was recessive in all crosses. Groat protein concentration was highly heritable.

For hull percentage Wesenberg and Shands (1973) reported heritability values of 0.36-0.93 in oats, but suggested that it may be difficult to isolate segregates with more than 80% caryopsis. Likewise, heritability values of 0.34-0.72 for hull percentage were reported by Granger and Stuthman (1973).

Brown et al. (1974) analyzed F_1 and F_2 populations from crosses involving eight oat (Avena sativa L.) parents differing widely in oil content. They obtained broad sense heritability values above 70%. A large part of the phenotypic variation was associated with general combining ability, although significant specific combining ability occurred in several crosses. Polygenic control for this character was indicated. The authors suggested that considerable genetic gain would be expected from phenotypic selection for oil content in oat seeds. Frey et al. (1975) studied the inheritance of the same character in interspecific crosses between A. sativa L. x A. sterilis L. Their results showed that oil per cent was inherited polygenically, with high oil content being partially dominant.

Using the components of variance method, Sraon et al. (1975) investigated the gene action, heritability, and number of effective factors controlling protein content in oats (Avena species) in a four-parent diallel cross. They found that additive gene action for groat protein percentage constitutes the major part. Partial dominance for low protein percentage was observed. Narrow sense heritability was 41%. The number of effective factors controlling protein content varied from 1 to 25 depending upon the genetic diversity of the parents and direction of the cross.

In general, data from several researchers indicated that selection for groat-protein percentage should be quite successful, even when applied on the basis of data from single plants. But as Frey (1975) cautions, to obtain this level of success, available soil nitrogen in the test field cannot be limiting and oat plants must be kept as disease-free as possible.

Recently, Frey (1976) and Iwig and Ohm (1976) reported that the inheritance of grain-protein percentage in crosses among strains of cultivated oats seems to be polygenic with partial dominance for low protein content in the F_1, but largely additive gene action in the F_2 and later generations. Frey (1976) reported that heritability of groat protein percentage was quite high by all methods of calculation. He concluded that selection for groat protein content based on data from individual plants and nonreplicated microplots should be successful. Iwig and Ohm (1976) concluded that intermating adapted, high yielding, homozygous lines with intermediate levels of protein for one or more cycles may be useful in concentrating alleles for high protein in commercial cultivars.

From an eight-parent half diallel of oats, Sampson and Tarumoto (1976) found that additive genetic variance constituted most of the phenotypic variance of heading date, plant height, grain yield and four components of yield. The authors concluded that the generally high additive variance revealed by the Griffing analysis indicates that the usual practice of choosing parents phenotypically and mating the best with the best will continue to give substantial progress. However, the appreciable amount of epistatic variance suggested by the Hayman-Jinks analysis was unexpected and indicates that more complex breeding schemes, such as choosing parents by progeny testing, will be necessary to achieve maximum genetic advance in oats.

3. Relationships among quality and agronomic characters in oats

Knowledge of the magnitude and type of relationships between plant characters has theoretical and practical implications in plant breeding. Knowledge of the correlation between complex characters of low heritability, such as yield, and less complex characters which may have much higher heritabilities, would benefit the breeder to the extent that it may be easier to select for the complex character indirectly by practising selection on the highly heritable character. In fact, in some cases it might be possible to achieve more rapid progress under selection for a correlated response than from selection for the desired trait itself (Falconer, 1967).

The genetic relationship among quantitative characters is of considerable interest to plant breeders. Falconer (1967) stated three reasons for determining such relationships. These reasons were: (a) to determine the changes brought about in a given character when selection is practised on another character; (b) to study the genetic causes of correlation through the pleiotropic action of genes; and (c) to examine the relationship between a metric character and fitness of that character in a natural population.

The phenotypic correlation is a linear combination of genetic and environmental correlations. However, the proportion to which genetic and environmental correlations make up the phenotypic correlations is variable depending on the magnitude of the heritabilities of both characters.

The correlations between some quantitative traits in oats have been estimated. In general, correlations calculated between yield and such characters as tillering ability, number of panicles per plant, panicle length, number of spikelets per panicle, number of seeds per panicle and 1000-grain weight have often proved variable between crops and seasons. Nevertheless, positive correlations have usually been found between grain yield and plant height, heading date, panicle length and number of spikelets per panicle.

The early work of Kiesselbach et al. (1940) in oats, barley and wheat, indicated positive correlations between yield and test weight. However, no association occurred between yield and plant height. Many early reviews showed that, almost universally, grain yield and protein content in the grain are negatively correlated. Such data prompted Wilcox (1949) to postulate that there is a "universal nitrogen constant" of 283. By this Wilcox means that the maximum amount of nitrogen any species can absorb in a single growth cycle, if all conditions are optimum, is 283 kg/ha. Presumably, this ceiling would lead to negative correlations between yield and nitrogen content even under suboptimal conditions.

Ross (1953) found that time of panicle initiation was as good a measure of earliness as time of heading (but more difficult to determine). His studies showed significant correlations of 0.917 and 0.928 in 1950 and 1951, respectively, between the number of internodes and days to head, late maturing cultivars having more internodes than early ones. Also, he found that the peduncle was significantly shorter in the late maturing cultivars, and there were negative correlations of -0.843 and -0.849 between peduncle length and days to heading and number of internodes at maturity, respectively. Late maturing cultivars which have more internodes than early cultivars also have shorter peduncles.

Black and Kempthorne (1954) later showed the derivation of the universal nitrogen constant to be in error, and evidence is accumulating that seems to suggest that the seemingly universal negative association between grain yields and protein percentage is phenotypically real, but not necessarily genetic in origin.

In bulked families of F_3 and F_4 generations of an oat cross, Wallace et al. (1954) obtained highly significant and positive correlations between yield and each of plant height, number of seeds per plant, and number of seeds per panicle. The phenotypic correlation coefficients were 0.45, 0.91 and 0.71 for F_3 and 0.70, 0.96 and 0.82 for F_4, while the genotypic coefficients were 0.33, 0.77 and 0.65 for F_3 and 0.90, 0.95 and 0.90 for F_4, respectively. The correlations between yield and seed weight were not significant in either generation. Plant height was positively correlated with both number of seeds per plant and number of seeds per panicle.

Frey and Wiggans (1957) found the tillering capacity of oats to be relatively constant from season to season. Tillering capacity appeared not to be related to heading date of spring-sown cultivars. Winter cultivars were found to have a higher mean number of tillers but spring cultivars could be found which equalled winter cultivars showing the highest tiller numbers. In another study, Frey (1959b) obtained a correlation coefficient value of -0.48 between heads per plant and seeds per head, and -0.19 for seeds per plant and weight per seed in oats.

In the cross of Lemhi x Thatcher wheat, McNeal (1960) found that heads per plant and kernels per head were more highly correlated with plant yield (0.60 and 0.66) than was kernel weight (0.40). while the correlation between grains per plant and plant height was low (0.40).

Brown et al. (1966) studied the variation in oil content and its relation to other characters in spring and winter oats (*Avena sativa* L.). They observed significant negative correlations of -0.312 and -0.477 between oil content and protein per cent in spring and winter oats, respectively. A significant negative correlation between yield and protein content was observed in the spring oats. There also appeared to be a slight negative association between kernel weight and oil content, especially in the winter oats. The authors also observed that some strains possessed relatively high levels of oil and protein while others had low levels. Data from Canadian Western Cooperative oat tests indicated that oat fat content was under good genetic control, and that little relationship existed between fat and protein content (Klinck, 1967). Klinck concluded that it should be possible to select for high levels of both.

Petr and Frey (1966) studied the genetic relationships among plant height, panicle length, heading date, number of spikelets per panicle, number of panicles per plant and grain yield in 15 diallel crosses among 6 oat cultivars. They found that the genetic correlations between grain yield and either plant height, panicle length, number of panicles per plant and number of spikelets per panicle were positive, and most of them were relatively high.

Jenkins (1969a, 1969b) made crosses involving a wide genetic base to study heterosis, combining ability and grain quality, as well as the relationships between some quantitative characters in oats. He found a positive correlation between seed yield and protein yield. However, the high-yielding genotypes invariably had a low protein content.

In a 5-parent diallel cross of spring wheat cultivars, Hsu and Walton (1970) estimated the correlation coefficients between yield and its components, as well as the associations between yield and some morphological characters. They obtained a high positive correlation of 0.87 between yield and number of spikes per plant, and a correlation of 0.58 between yield and number of kernels per spike. Also, the correlation between yield and 1000-kernel weight was significant, while the correlation between number of kernels per spike and 1000-kernel weight was negative (-0.37). Likewise, Rasmusson and Cannell (1970) obtained similar results with barley. Their results indicated that selection for number of heads resulted in changes in yield that were similar to those observed when selection was for yield itself. Selection for kernel weight was highly effective in altering yield in one of two populations. They concluded that selection for yield through its components was very effective in certain situations, but it could not be recommended as a routine procedure.

Sampson (1971) in F_1's, F_2's and bulked F_3 progenies of oats, found that seed weight showed the least correlation with other traits. The author discussed his results from the practical viewpoint of combining strong straw with high grain yield. He concluded that the usefulness of selecting for seed weight and panicle yield to improve plot yield is underlined.

From 56 random F_4 lines of oats including high, medium, and low oil cultivars, Baker and McKenzie (1972) found that oil content was not significantly correlated with kernel weight, kernel density, or per cent hull. These results suggest that oil content can be changed without correlated response in these kernel characteristics. At the same time, none of these kernel characteristics can be used as an aid in selection for high oil content. On the other hand, Brown and Craddock (1972) observed a positive correlation coefficient of 0.11 between oil content and groat weight in more than 4,000 entries from the world oat (Avena species) collection. They concluded that while this was statistically significant, based on more than 4,000 d.f., it was considered too small to have practical importance in oat breeding.

Ohm and Patterson (1973b) studied the amount of hybrid vigor and type of genetic control for per cent protein and protein yield in crosses between A. sativa L. and A. sterilis L. genotypes. Their results indicated that the relationship between protein percentage and protein yield was generally not significant, but tended to be negative. In another study, Ohm and Patterson (1973a) found that per cent groat protein tended to be negatively correlated with seed yield, although the correlation was low and nonsignificant. The results indicated that high levels of seed yield and protein per cent can be obtained in breeding oats with little difficulty.

Correlations among several chemical and agronomic characters were studied for 10 Avena sativa L. cultivars and for 46 F_4-F_6 backcross "N" lines derived from complex interspecific crosses involving a 6x amphiploid (Forsberg et al., 1974). Groat protein percentage was significantly and negatively correlated with yield. A strong negative association existed between groat protein percentage and kernel weight (-0.71).

Kaufmann (1974) studied the correlations among kernel characteristics and maturity in five oat crosses. Kernel weight showed a consistently high positive correlation with per cent plump kernels. Maturity and per cent hull tended to have the lowest interseason correlations. No characteristics showed significant heterogeneity of interseason correlations.

From the F_3 generation of three crosses between A. sativa L. x A. sterilis L. cultivars, and samples from the parents, Frey et al. (1975) found no correlation between oil percentage and any of groat weight, heading date or plant height. In spring wheat, Pepe and Heiner (1975) studied the relationships between plant height, protein percentage and yield. Plant height did not influence grain yield or protein percentage. They found a negative relationship between yield and protein percentage but the authors stated that the tendency for high yielding lines to have lower grain protein percentage appears to result from a limited or diluted source for protein production. However, this protein-source limitation appears among all height classes because the source size remains relatively constant while the sink size is greatly increased. As a result, the plant no longer can adequately supply the energy or nitrogenous substances needed to produce high-protein lines. To remedy this situation, the authors suggested that the geneticist, plant breeder and physiologist must identify the source limitations and develop a more efficient plant.

Frey (1976) reported that, seemingly, many of the reported negative correlations between grain yields and protein percentages in cereal species may be artifacts of past experimentation. Data from wheat and oats suggest that genes are present in these species that can cause independent quantum increases in either grain-protein content or grain yield.

4. Diallel analysis techniques and plant breeding

In any plant breeding program, the aim of selection is to identify superior genotypes which will transmit their desirable characteristics to future generations. In respect to quantitative characters, the difficulty is that they tend to be continuous in their variation. This means indistinguishable phenotypic classes and difficult or impossible applicability of classical Mendelian analysis. Thus, although the diallel cross mating system had been discussed earlier, it is not surprising that the advent of the Fisher-Yates-Mather-Jinks-Hayman-Griffing diallel cross technique about the middle of the 20th century was used by plant breeders as a long-overdue methodology for rationalizing the genetic study of continuous variation. A great number of diallel crosses have been made since that time and the new technique has been used extensively in cereal breeding programs during the past few years.

Most plant breeders have at least a passing acquaintance with the general concept of diallel analysis. The word "diallel" is derived from the Greek and means twice the complementary, referring to the presence of the two reciprocals (Broadhurst, 1967). The diallel cross mating system was first discussed by Schmidt (1919), working in Copenhagen, Denmark to estimate (a) the genetic components of the yield variability in crosses and (b) the actual yielding ability of the crosses. The application of diallel-cross technique for evaluation of quantitative variability in self-pollinated crops was developed by Hayman (1954), Jinks (1954) and Griffing (1956a, b). Modifications of the diallel-cross technique were discussed by Kempthorne and Curnow (1961), Curnow (1963), and Fyfe and Gilbert (1963).

A diallel cross is the set of all possible matings between several genotypes which could be defined as individuals, clones, homozygous lines, etc. If there are P genotypes there are P^2 mating combinations in the case of a complete diallel. Griffing (1956b) stated that the proper interpretation of the genetical parameters from the diallel analysis depends on the particular diallel method, the assumptions regarding the experimental material, and the conditions imposed on the combining ability effects. In this respect, four different experimental methods of diallel cross were suggested by the author. These methods vary with inclusion or absence of parental inbreds and/or reciprocal F_1's and with sampling assumptions (models).

Following the classification of Griffing (1956b), the four possible diallel crossing methods are: (1) parents, one set of F_1's, and reciprocal F_1's are included (all P^2 combinations); (2) parents and one set of F_1's are included but reciprocal F_1's are not (1/2 P(P+1) combinations); (3) one set of F_1's and reciprocal F_1's are included but not the parents (P(P-1) combinations); and (4) one set of F_1's but neither parents nor reciprocal F_1's are included (1/2 P(P-1)). For each method, there are two alternative models depending on whether the genotypes are assumed to be (a) a chosen or fixed set and cannot be regarded as a random sample from any population (Model I), and (b) a random sample from a population about which inferences are to be made (Model II). These four different diallel crossing methods with two different models for each, result in eight different situations, each requiring different analysis. Griffing (1956b) pointed out that to obtain an unbiased estimate, diallel crossing methods 3 or 4 must be used (i.e., the parents must not be included in the combining ability analysis). However, it is advisable to include the parents in the experimental material grown in the experiment so that comparisons of hybrids with their parents can be made in other types of analysis. Computer programs have been developed for the analysis of these different methods (Schaffer and Usanis, 1969).

Several other methods of diallel cross analysis have been developed (Jinks and Hayman, 1953; Hayman, 1954; Jinks, 1954; Allard, 1956; Kempthorne and Curnow, 1961; Fyfe and Gilbert, 1963). In the early 1950's, Jinks and Hayman, from the Biometrical Genetics Unit of the University of Birmingham, published a series of papers on the analysis and interpretation of data from diallel crosses. Hayman extended the statistical analysis by subdividing the interaction term into three subcomponents. At the same time, he and Jinks were developing theory for interpreting diallel statistics in terms of gene frequencies and gene effects. The Jinks-Hayman (1953) diallel analysis of parental and F_1 generations from a set of diallel crosses appeared to provide a rapid evaluation of the genetic relationships among a number of parents. This method thus seemed to offer promise in identifying parents whose hybrids are most likely to respond to selection (Crumpacker and Allard, 1962). This analysis includes parents and one or both sets of F_1 crosses. Thus, with respect to Griffing's classification of diallel crossing techniques, it is applicable to both experimental methods I and II.

The diallel analysis procedures have been used to obtain information concerning the inheritance of quantitative traits, and for the prediction of segregation in the F_2 and later generations. In general, the genetic interpretation of data from a diallel experiment is valid only if certain assumptions about the parental material are true (Sokol and Baker, 1977). These assumptions are: (1) homozygous parents; (2) diploid segregation; (3) no reciprocal differences; (4) gene frequencies equal to 0.5 at all segregating loci; (5) genes independently distributed between the parents (no-linkage); (6) no epistasis (no non-allelic interaction); and (7) no multiple alleles.

Failure of any of these assumptions invalidates the analysis to some degree, so it is important to test the validity of these assumptions before proceeding with the genetic analysis. The validity of certain of these assumptions can be ascertained from inferences based on knowledge of the crop species and the particular parents entering the diallel cross. Judgement concerning other of the assumptions must be based on statistical tests. Assumptions 1, 2, and 3 are the usual ones and could be assured from the history of self-pollination of the parents, and from numerous reports in the literature. For example, oats (Avena sativa L.) and wheat (Triticum aestivum L. em. Thell.) not only regularly form 21 bivalents at meiosis but the inheritance in these species is also uniformly disomic. In all probability, these three assumptions apply. The last four assumptions are not so easily accepted and they are difficult to evaluate independently. They are tested by the analysis as the null hypothesis. Hayman (1954, 1957) developed two methods for testing some of the assumptions mentioned above. He stated that he can always detect epistasis, and multiple allelism in the absence of epistasis, and when both of these factors are absent gene correlation may be exposed.

The type of diallel analysis used depends on: (1) the material under investigation; (2) the genetic hypothesis postulated; and (3) the method of estimation (Le Clerg, 1966). Some researchers are interested in the properties of the particular set of parental lines (Jinks, 1954; Hayman, 1954), whereas others are concerned with the population of which the parents are considered a sample (Kempthorne, 1956). The analyses of Hayman and Jinks were based on Model I (fixed model) and those of Kempthorne on Model II (random model) of sampling theory.

No discussion of the value of predictions based on the analysis of the diallel cross technique can be complete without reference to the practical aspects of the work, and with particular reference to the considerable amount of labor, time and expense involved in the conduct of a series of experiments. On the one hand, it may be argued that if a complex series of trials is necessary for the identification of promising parental combinations, no expense should be spared in their conduct. At the other extreme, it may be claimed that trials of this sort are an unnecessary extravagance, and that the plant breeder should be able to select his crosses by detailed consideration of the parental material available to him without recourse to experimental hybridizations (Lupton, 1965). In practice, a compromise has to be reached between these extreme views.

Difficulties in satisfying the conditions and assumptions of the diallel analysis have led some authors to question the validity of the entire analysis. Hayman and Mather (1955) feel that gene frequencies other than 0.5 can confound the statistical estimates. Kempthorne (1956) criticized the technique on the grounds that the diallel cross must be interpreted in terms of some population which has given rise to the homozygous parents by inbreeding. If such a population does not exist, then the whole analysis is likely to lead nowhere. From quite another viewpoint, he questioned the value of estimating additive variance, dominance variance and so on, whatever they may be defined, unless the estimated quantities are measures of the characteristics of a definite population. Since the parents of primary interest to breeders of self-pollinated crops will usually not have been derived by breeding from some definite population, Kempthorne evidently considers that the Jinks-Hayman type of diallel cross analysis has little practical value as an aid in the improvement of self-pollinated crops. The author, also, is of the opinion that unless genes are independently distributed between the parents (assumption 5), a genetic analysis of the diallel cross will not provide any valid information.

Gilbert (1958) examined the assumptions required for a valid genetic interpretation of a diallel experiment. He reported that a set of diallel crosses is obviously of interest to the plant breeder, but the information obtained may not be worth the trouble of making the cross. Gilbert categorically criticized the basic genetical assumptions of the technique and stated that the polygenic analysis of a diallel cross suffers from several theoretical defects. In any case its results do not appear to be directly relevant to practical breeding work. The performance of the parental cultivars themselves gives valuable prediction of the relative behavior of the crosses, but the diallel cross does give further information. Whether or not it might be used for assessing long-term potentialities of row material at the beginning of a long breeding program is unknown. He concluded that certain assumptions would seldom be justified in self-pollinating crops, that the value of this technique is exaggerated, and that information gained from it is little more than that obtained from the parents themselves.

When considering self-pollinated crops, most of the plant material of interest to breeders has been highly selected for traits of economic importance. Eberhart and Gardner (1966) are of the opinion that the diallel parents selected from such material cannot be considered as a random sample. They concluded that estimation of genetic variance components in self-pollinated crops does not provide any useful information.

In a recent study, Sokol and Baker (1977) reported that since the parents used in diallel experiments are rarely a random sample of inbred lines from a random mating population with gene frequencies of 0.5, one can rarely assume that genes are independently distributed in the parents with frequencies of 0.5. Furthermore, one cannot assume that epistasis is absent unless one has empirical evidence to support that assumption. The authors concluded that since assumptions 4, 5, and 6 are critical to the genetic interpretation of diallel experiments, such experiments are of little value in studying the genetics of quantitative traits in self-pollinating species.

On the other hand, several authors (Hayman, 1954, 1957; Jinks, 1954; Whitehouse et al., 1958; Johnson, 1963; Johnson and Aksel, 1964; and many others) reported that the diallel cross technique is invaluable in identifying crosses with the best selection potential, particularly in early generations, in addition to many other advantages. For example, Johnson (1963) reported that many of the points raised by Gilbert are well taken, for the technique has many shortcomings. 'It appears, however, that Gilbert fails to appreciate fully that a statistical-genetic analysis must be based upon statistical assumptions and produce statistical results. This consideration, coupled with the fact that a polygenic system is involved, makes it rather unfair, or even naïve, to expect that the diallel analysis will give results anything like those obtainable from classical Mendelian analysis. Also, Gilbert fails to justify, genetically at least, his insistence on valid statistical inference. The author enumerated the advantages of the diallel cross technique in his study as follows:

(1) Compared to other methods available, the diallel-cross technique provides a more systematic approach to large-scale studies of continuous variation and a better-disciplined analysis of the resulting data.

(2) The over-all analysis provides reliable genetic information on dominance and recessiveness (averaged over all arrays) and on complementary non-allelic interaction (averaged over all crosses within an array).

(3) The analysis demonstrates the primary importance of the yield component, number of kernels per head; this character lends itself to practical selection techniques as a morphological reflection of yield capacity.

(4) The general analysis permits genetically-sound elimination of a high proportion of arrays and crosses of low selection potential.

(5) Scaling tests provide a more critical evaluation of the selection potential of individual crosses. Such tests detect crosses that

are superlative in both highness of yield and significance of non-allelic interaction. Such crosses should have, as a theoretical probability, the highest yielding lines among their segregates.

From a 15-parent diallel cross in barley, Johnson and Aksel (1959) found that their results provide additional points toward refuting Gilbert's statement that for the plant breeder the information gained from the analysis of a diallel cross is little more than that obtained from the parents themselves. The authors reported that the diallel analysis provided additional information on the genetic identity of several characters, on dominance-recessive relationships, on genetic interaction, and on probable linkage associations. This information, greatly outweighing that obtainable from parental observations, will provide invaluable guidance in the plant breeding aspects of an investigation.

Breese (1963) reported that the Jinks-Hayman diallel analysis was developed as a quick means of recognizing different types of gene action in sets of inbred lines. The method has been used by Jinks to survey a wide variety of crop plants. Thus the technique has contributed greatly to our wider understanding of the genetic basis for heterosis. He stated that the method is not suggested as a panacea for all plant breeding complaints, but it can provide a considerable amount of adjunct genetic information which could be of great value in formulating coherent plant breeding programs. This is especially so when the information can be related to the past selective history of the inbred lines.

Hayman (1963), in the evaluation of small diallel crosses, reported that when the number of parents (n) is less than 10, none of the components of variation, either statistical or genetical, in the diallel cross, can be significant estimates of population parameters. However, in this case, the individual parents and crosses are of the main interest, and no population to which inferences might be made is envisaged. He concluded that the information available from the small diallel cross is that there are certain differences between the parents, between the crosses, or between the general or specific combining abilities of the parents.

In a very recent paper, Baker (1977) questioned whether or not a statistical analysis of data from a fixed set of parents and their single cross progeny can, in the absence of genetic information of any sort, answer questions or provide information that will result in greater plant breeding efficiency. His answer to this question was positive, but with qualifications. Baker reported that the diallel analysis can be expected to give some information about the relative importance of general and specific combining ability, to give a measure of the relationship between hybrid performance and general combining ability and of the relationship between hybrid performance and the performance of inbred parents. Also, the comparison of inbreds and hybrids affords an estimate of overall heterosis. The author stated that only if these questions are critical to a plant breeding program and only if the answers are not available from some other source can the use of diallel analysis be recommended in plant breeding. Diallel crosses may be used as a systematic way of crossing parental lines but should be evaluated against other mating designs.

CHAPTER III

MATERIALS AND METHODS

1. Genetic materials, experimental procedure and data collection

The material included in this study was eight genotypes of oats (*Avena sativa* L.), widely diverse in their parentages and agronomic characters. The 28 possible crosses (P(P-1)/2) from a diallel cross (excluding reciprocals) among these eight genotypes were made in the winter of 1974 and the summer of 1975 in the Department of Plant Science, Macdonald College. These genotypes were Q.0.64.31, Q.0.58.22, Ajax, Clintland 64, O.T.184, P.I.269182, C.I.3387 and Hinoat. Seeds from each of the 28 F_1's were sown in a greenhouse in the winter of 1975 to produce F_2 seeds.

Due to the limited number of F_1 seeds and to insure the availability of uniform seedlings for early generation testing, individual seeds of each parental genotype and of each F_1 and F_2 progeny were sown in jiffy pots in the greenhouse on 26 April, 1976.

All plants were transplanted to the field at Macdonald College on 10 May, 1976, where they remained until maturity. All material was planted as spaced plants in a randomized complete block design with four replications. Each plot comprised a 2-m row containing 10 plants 13.0 cm apart. Three spring wheat (Triticum aestivum L. em. Thell.) plants, also started in jiffy pots and transplanted, were used at each end of each plot as borders (Figure 1). Plots were 25 cm apart.

Certain data were recorded on the F_1's, F_2's and their parents in the field, while others were measured in the laboratory. In the field, heading date was recorded for each plot as the number of days from seeding (in the greenhouse) to the time at which 50% of the panicles in a plot were completely emerged from the flag leaf sheath. Plant height was recorded in centimeters on a single-plant basis from the ground level to the tips of the main panicles at harvest. The number of panicles per plant was counted for each plant in a plot at harvest.

The plots were harvested as they ripened and moved to a drying room where they were kept for about a month to dry. Plants were threshed and cleaned individually; grain yield and the number of grains per panicle were measured on a single-plant basis. 1000-grain weight was determined for each plot, by counting two 100-grain samples, averaging the two weights, and calculating the weight per 1000 grains. On a plot basis, two samples of about two g each were dehulled and the ratio of the hull to the original weight was

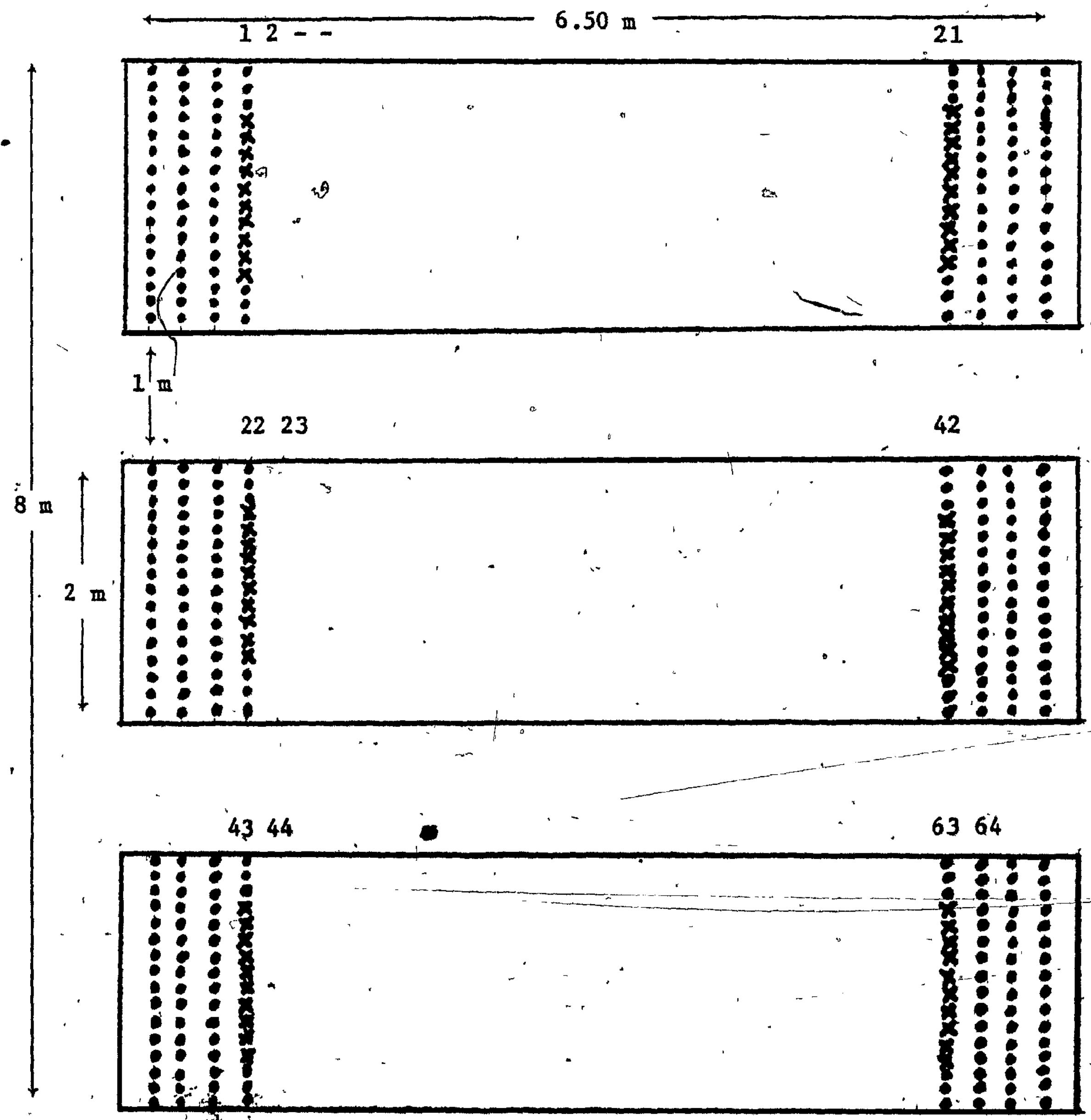

Figure 1. Field layout of one replicate of the design including the F_1's, F_2's and parents.

● Border rows

✖ 10 plants per row at 13.0 cm apart
Distance between rows = 25 cm.

calculated for each sample. The average of the two samples was considered as the hull per cent for the plot. To determine grain protein and oil per cent, about 20 g of grain from each plot was ground using a Wiley mill with a 40 mesh sieve. Percentages of protein and oil were measured using a Technicon, Infra-red Analyzer, based on the average of two ground samples per plot.

2. Statistical and genetic analysis

The plot mean for each character was used for statistical analysis. The analysis of variance was performed for each character in every generation. The linear model assumed for each of the parents, F_1 or F_2 populations was as follows:

$$Y_{ij} = U + R_i + G_j + E_{ij}$$

where

Y_{ij} = the mean observation of the j^{th} genotype in the i^{th} replicate

U = the effect due to the over-all mean

R_i = the effect due to the i^{th} replicate, $i = 1, 2, \ldots, r$

G_j = the effect of the j^{th} genotype, $j = 1, 2, \ldots, g$

E_{ij} = the effect due to random error associated with the j^{th} genotype in the i^{th} replicate.

Genotypes were considered fixed; differences between the genotypes were tested using the error mean squares.

When the analysis of variance showed significant differences between genotypes over replications, general combining ability (GCA) and specific combining ability (SCA) variances and effects for the eight parental genotypes and their crosses were estimated according to Griffing's (1956b) combining ability analysis method IV, model I (fixed model), using the computer program "Diall" (Schaffer and Usanis, 1969) for each of the F_1 and F_2 generations, separately.

Parameters representing genetic components of variation were estimated using the diallel cross analysis of Jinks and Hayman (1953) provided by Lee and Kaltsikes (1972). The Lee and Kaltsikes computer program was used to analyze the F_1 and F_2 generations with their respective parents separately for variance and covariance; it extracts components of genetic variance with their standard errors and provides ratios of components and statistics for graphical analysis. The statistical significance of the components given in this analysis indicates which estimates were greater than "t" times their standard errors, where $t(0.05) = 2.01$ and $t(0.01) = 2.68$ for 52 degrees of freedom in our 8-parent diallel cross. For 7, 6 or 5-parent diallel crosses, the degrees of freedom are 44, 36 and 28, respectively. The error component (E) provided by Lee and Kaltsikes' (1972) program is the error mean square of a conventional analysis of variance with $(g-1)(r-1)$ degrees of freedom, where g is the number of progenies (F_1's or F_2's) plus parents[1] and r is the number of replicates.

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[1] The number of progenies and parents (g) for F_1 or F_2 analysis = 36.

The analysis and interpretation of data from the F_2 generation follow the same general form as that of the F_1 data except that the contribution of h is halved by each generation of inbreeding. Thus, the coefficients of H_1 and H_2 for the F_2 generation are 1/4 of those of F_1 statistics and the coefficient of F for the F_2 generation is 1/2 of those of the F_1 statistics.[1]

The variance components were calculated from both the Griffing and the Jinks-Hayman diallel analyses. In the first one (Griffing), variance components were calculated according to the method described by Kempthorne and Curnow (1961), while in the second method (Jinks-Hayman), variance components were estimated according to the formula proposed by Crumpacker and Allard (1962). Assuming the model is adequate, the components of variance were calculated for the two methods of analysis from the expectation shown in Table 1.

Narrow sense (N.S.) and broad sense (B.S.) heritabilities were estimated from the two methods of analysis as follows:

1 - From the Griffing analysis (1956b) as described by Kempthorne and Curnow (1961)

a - N.S. heritability = $\hat{\sigma}^2_A/\hat{\sigma}^2_P = 2\,\hat{\sigma}^2_{gca}/[(2\hat{\sigma}^2_{gca} + \hat{\sigma}^2_{sca}) + \hat{\sigma}^2_E]$

b - B.S. heritability = $\hat{\sigma}^2_G/\hat{\sigma}^2_P = (2\,\hat{\sigma}^2_{gca} + \hat{\sigma}^2_{sca})/[(2\,\hat{\sigma}^2_{gca} + \hat{\sigma}^2_{sca}) + \hat{\sigma}^2_E]$

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[1] For further information and discussion concerning the analysis of F_2 and F_3 diallel data, see the papers of Johnson and Aksel (Can. J. Genet. Cytol. 1: 208-265, 1959; Can. J. Genet. Cytol. 6: 176-200, 1964).

TABLE 1. Expectations of the variance components from the Griffing and the Jinks-Hayman diallel analyses.

Variance component	Griffing analysis[a]	Jinks-Hayman analysis[b]
General combining ability variance $\hat{\sigma}^2_{gca}$	$\frac{\text{GCA.MS} - \text{Error MS}}{(\text{No. of parent lines} - 2)}$	-
Specific combining ability variance $\hat{\sigma}^2_{sca}$	SCA.MS - Error MS	-
Additive variance $\hat{\sigma}^2_A$	$2\ \hat{\sigma}^2_{gca}$	$1/4\ \hat{D}$
Non-additive variance $\hat{\sigma}^2_{NA}$	$\hat{\sigma}^2_{sca}$	$1/4\ (\hat{H}_1 - \hat{F})$
Genetic variance $\hat{\sigma}^2_G$	$\hat{\sigma}^2_A + \hat{\sigma}^2_{NA}$	$1/4\ (\hat{D} + \hat{H}_1 - \hat{F})$
Environmental variance $\hat{\sigma}^2_E$	Error MS	Error MS
Phenotypic variance $\hat{\sigma}^2_P$	$\hat{\sigma}^2_G + \hat{\sigma}^2_E$	$1/4\ (\hat{D} + \hat{H}_1 - \hat{F}) + E$

[a] Expectations of variance components for Method 4 Model 1 of the Griffing analysis according to Kempthorne and Curnow, 1961.

[b] Expectations of variance components from the Jinks-Hayman analysis as described by Crumpacker and Allard, 1962.

2 - From the Jinks-Hayman analysis (1953) as described by Crumpacker and Allard (1962)

a - N.S. heritability $= \hat{\sigma}^2_A/\hat{\sigma}^2_P = \dfrac{1/4\,\hat{D}}{1/4(\hat{D} + \hat{H}_1 - \hat{F}) + \hat{E}}$

b - B.S. heritability $= \hat{\sigma}^2_G/\hat{\sigma}^2_P = \dfrac{1/4(\hat{D} + \hat{H}_1 - \hat{F})}{1/4(\hat{D} + \hat{H}_1 - \hat{F}) + \hat{E}}$

The statistics $\hat{D}$, $\hat{H}_1$, $\hat{H}_2$, $\hat{F}$ and $\hat{E}$ are provided in the Lee and Kaltsikes (1972) computer diallel program, and the variance components of the general ($\hat{\sigma}^2_{gca}$) and specific ($\hat{\sigma}^2_{sca}$) combining ability as well as the error ($\hat{\sigma}^2_E$) component are provided in Schaffer and Usanis (1969) program.

The number of genes or blocks of genes (K) involved in the inheritance of each character was calculated from the Jinks-Hayman (1953) analysis only in both generations. This was designated as ($\hat{h}^2/\hat{H}_2$) in their diallel analysis.

Expected genetic advance from selection (G_s) and the relative expected genetic advance from selection (RG_s) were calculated using the formulas:

$G_s = K.\hat{\sigma}_P.H$ and

$RG_s = \dfrac{G_s}{\bar{x}} \times 100$

where

G_s is the expected genetic advance from selection; it measures the difference between the mean genotypic value of the q selected lines, that is $\bar{a}_s$, and the mean genotypic value of the n original lines, $\bar{a}$, thus $G_s = \bar{a}_s - \bar{a}$.

K is the selection differential; its value depends on the percentage of the population selected (e.g., for 5% K = 2.06 (Allard, 1960)).

$\hat{\sigma}_P$ is the phenotypic standard deviation of the character of the original lines.

H is the broad sense heritability coefficient.

Since characters differ widely in their mean values and the scales of measurement, the genetic coefficient of variation (GCV) was also measured for each character in each generation as follows:

$$GCV = \frac{\sqrt{\hat{\sigma}_G^2}}{\bar{x}} \times 100$$

where

GCV is the genetic coefficient of variation, and $\hat{\sigma}_G^2$ and $\bar{x}$ are the genetic variance component and the mean of the character in question, respectively.

Phenotypic, genetic and environmental correlation coefficients among all characters were calculated separately in the F_1 and F_2 generations. Phenotypic correlations (r_P) in the F_1 or F_2 generation were calculated as follows:

$$r_P = \frac{MP2(X, Y)}{\sqrt{MS2(X).MS2(Y)}}$$

where

MP2(X, Y) is the genotype mean product for characters X and Y, and MS2(X) and MS2(Y) are the genotype mean squares for characters X and Y, respectively. Covariance estimates were obtained by the analysis of covariance which is similar to the analysis of variance. The mean product of genotypes for characters X and Y, obtained from the analysis of covariance was considered to be an estimate of the phenotypic covariance of the two characters. MS2 obtained from the analysis of variance tables for each of the characters X and Y was taken as an estimate of the phenotypic variance. Environmental (r_E) and genetic (r_G) correlation coefficients for characters X and Y, based on the genotype means, were calculated in a similar manner using the formulas given by Anand and Torrie (1963). These formulas are:

$$r_E = \frac{MP1(X, Y)}{\sqrt{MS1(X).MS1(Y)}}$$

and

$$r_G = \frac{\hat{Cov}._b\ (X, Y)}{\sqrt{\sigma^2_{bX} \cdot \sigma^2_{bY}}}$$

where

$$\hat{Cov}._b\ (X, Y) = [MP2(X, Y) - MP1(X, Y)]/R$$

$$\hat{\sigma}^2_{bX} = [MS2(X) - MS1(X)]/R$$

$$\hat{\sigma}^2_{bY} = [MS2(Y) - MS1(Y)]/R$$

The analysis of variance and covariance in the F_1 or F_2 generation was of the form shown in Table 2.

TABLE 2. Analysis of variance and covariance table for genotype means of the F_1 or F_2 generation

Source	df	MS	MP(X,Y)	EMS*
Total	RG-1			
Replicates	R-1	MS3	MP3	$\sigma_e^2 + G\sigma^2$
Genotypes	G-1	MS2	MP2	$\sigma_e^2 + R\sigma^2$
Experimental error	(R-1)(G-1)	MS1	MP1	σ_e^2

* EMS is the expected mean squares.

CHAPTER IV

RESULTS AND DISCUSSION

1. Genetic analysis

As a preliminary to the genetic analysis of the F_1 and F_2 data, analyses of variance were made to determine significant differences between the different genotypes[1] for all characters. The analysis of variance was of the form shown in Table 2. In each case, F values were significant beyond the one per cent probability level, indicating that the genetic analysis could be carried forward. The genetic analysis in this study will include three different diallel analysis procedures, namely, (a) Combining ability analysis (Griffing's analysis), (b) Jinks-Hayman analysis, and (c) Graphical analysis. In order to determine the validity of the genetical parameters and interpretations, the assumptions of the genetic analysis will be tested before all analyses are carried forward.

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[1] By genotypes is meant the 8 parents and their 28 F_1 or F_2 crosses. The analysis of variance was also performed on the 28 F_1's and 28 F_2's separately to determine significant differences between crosses.

1.1 Validity of assumptions of the diallel analysis

Several assumptions are made when diallel analyses are used to evaluate the genetic and environmental variance components associated with quantitatively inherited characters and in the prediction of segregation in the F_2 and advanced generations (Crumpacker and Allard, 1962; Hayman, 1954; Sokol and Baker, 1977). These assumptions are: (1) homozygous parents; (2) diploid segregation; (3) no reciprocal differences; (4) gene frequencies equal to 0.5 at all segregating loci; (5) genes independently distributed between the parents (no linkage); (6) no epistasis (no nonallelic gene interaction; and (7) no multiple alleles.

Failure of one or more of these assumptions invalidates the genetic analysis to some extent. Therefore, it is important to test whether the data involved in the present study met the required assumptions for an additive-dominance model with additive environmental effects and independence of the genes in action and distribution (Mather and Jinks, 1971). In this study, assumptions 1 and 2 were valid since oat is a self-pollinated crop, and from numerous reports in the literature, not only that oats regularly form 21 bivalents at meiosis but also inheritance in this species is uniformly disomic. Assumption 3 is justified from the many reports in the literature which indicate the absence of reciprocal effects in oats (Campbell and Frey, 1972; Chae and Forsberg, 1975; Petr and Frey, 1966). Assumptions 4, 5, 6 and 7 are difficult to evaluate separately. They were tested with the other assumptions as a whole by two different tests. These were the analysis of variance for $W_r - V_r$ and the regression (b W_r/V_r) of the parent-offspring covariances (W_r) on the array variances (V_r). The nonsignificant differences of the $W_r - V_r$ over arrays (genotypes) and the value of b = 1 or close to unity indicate the adequacy of the model.

F values of the analysis of $W_r - V_r$ and the regression (b W_r/V_r) of the parent-offspring covariances on the array variances for the nine characters involved in the present study in both F_1 and F_2 generations are shown in Table 3.

In the first test of the assumptions (Table 3), the values of $W_r - V_r$ over arrays are expected to be consistent and the F value over arrays of the analysis of variance of $W_r - V_r$ is expected to be non-significant for an additive-dominance model with independent gene distribution. In the F_1 generation, the F value was not significant for all characters except heading date, number of panicles per plant and 1000-grain weight. These significant F values indicated failure of one or more of the basic assumptions underlying the analysis. In the F_2 generation, these assumptions were fulfilled for all characters except oil per cent, plant height, 1000-grain weight and heading date.

In the second test, the linear regression (b W_r/V_r) showed that the regression coefficient (b) did not differ significantly from unity

TABLE 3. Array F values of the analysis of variance of $W_r - V_r$ and the regression coefficients of W_r on V_r to test the adequacy of the model in the F_1 and F_2 generations[a]

Character	F value for the array (W_r-V_r) ANOVA				Regression coefficient b W_r/V_r			
	F_1	F_1†	F_2	F_2†	F_1	F_1†	F_2	F_2†
Protein %	1.96	1.71 (3)	1.06		0.65*	0.89 (3)	0.72	
Oil %	2.30		5.98**	3.38* (2)	1.11		0.92	0.85 (2)
Hull %	0.70		1.48		0.73		0.66	
Plant height	1.01		11.19**	0.53 (5,6)	0.97		0.87	1.13 (5,6)
Heading date	4.34**	2.63 (5)	2.17*	4.96** (3,7)	0.99	1.04 (5)	0.83*	0.84 (3,7)
Grain yield/plant	1.77		0.75		0.77		0.70	
No. of panicles/plant	3.43*	2.10 (6)	1.86	2.22 (1,7)	0.51	0.78 (6)	0.56*	1.15 (1,7)
No. of grains/panicle	2.21		1.23		0.78		1.17	
1000-grain weight	10.00**	4.05* (1,2,6)	2.36	0.21 (1,2,6)	0.01**	0.58 (1,2,6)	0.45*	0.61 (1,2,6)

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

[a] Any significant value indicates failure of one or more of the assumptions underlying the analysis for a particular character.

† Values in the F_1 and F_2 generations after eliminating the epistatic parent(s). Epistatic parents are in parenthesis.

for any character, except for protein per cent and 1000-grain weight in the F_1 generation and for heading date, number of panicles per plant, and 1000-grain weight in the F_2 generation. These characters, particularly heading date, number of panicles per plant and 1000-grain weight, appeared to suffer from failure of one or more of the basic assumptions required for the genetical analysis as shown from the two tests (Table 3). Hayman (1957, 1963) recommended that when such failure occurs it is desirable to eliminate separately the parent(s) corresponding to the maximum and minimum $W_r - V_r$ (the epistatic parent(s)), to restore the rectilinearity of the W_r/V_r graph. Jinks and Hayman (1953) have also used deviation from a linear regression of array covariances on array variances (W_r on V_r) as an indicator of the presence of epistasis and recommended that the array or arrays leading to the deviation be removed from the analysis and the data reanalyzed.

In the present study, both suggestions were used to determine and eliminate the epistatic parent(s). For protein per cent, the removal of "Ajax" in the F_1 generation (minimum $W_r - V_r$, Appendix Table 1), improved both the $W_r - V_r$ and b W_r/V_r tests and fulfilled the required assumptions for this character. With oil content, in the F_2 generation, the removal of "Q.0.58.22" (minimum $W_r - V_r$, Appendix Table 4), slightly improved the $W_r - V_r$ F value, but the regression coefficient (b) was decreased from 0.92 to 0.85. The exclusion of "Ajax" and "C.I.3387" in the case of heading date (F_2 generation), increased the ($W_r - V_r$) F value and slightly improved the regression coefficient. The failure of the genetic assumptions in such cases may not be due only to the presence of epistasis but could be due to one or more other factors, such as gene correlations or unequal distribution of positive and negative alleles at the loci under consideration. This conclusion is in agreement with those reported by Nassar (1965) and Feyt (1976). They pointed out that these tests, especially the regression of W_r on V_r, will be able to detect epistasis only in the absence of any correlation of gene frequencies in the parents of the diallel, and it is not possible to differentiate between the effects of epistasis and correlated genes. With the other characters showing failure of the assumptions required for the genetic analysis, removal of the epistatic parent(s) has succeeded in removing such failure without many complications (Table 3).

On the basis of the above analysis, it appears that one or more of the assumptions required for the diallel analysis in the present study, including that of "no epistasis," were not strictly valid for some characters such as heading date, number of panicles per plant and 1000-grain weight. But the fact that the regression coefficients were not significantly different from unity, particularly after eliminating the epistatic parent(s), indicates that the additive-dominance genetical model was satisfactory to explain the variation present in this study. However, with characters failing one or more of the above-mentioned assumptions, interpretation of their genetic parameters and ratios should be regarded with more caution and the genetical results from the corrected cases (after removing the epistatic parent(s)) would be more valuable in the genetical interpretation than those involving the epistatic effects.

1.2 Combining ability analysis (Griffing's diallel analysis)

Parentages and the actual mean values over four replications of the eight parents included in this study, pertaining to nine characters, are given in Table 4. The eight genotypes differed significantly for all characters. Parent "C.I.3387" ranked first for oil per cent, hull per cent, number of panicles per plant and 1000-grain weight, and was among the highest parents for all other characters except plant height. The high grain yield potential of this parent is due mainly to its superiority in the two yield components: number of panicles/plant and 1000-grain weight. The highest levels of protein content occurred with "Hinoat." This parent was also one of the early maturing cultivars. "O.T.184" is the shortest parent and would appear to be a valuable source in breeding for short-strawed cultivars if the genetic control of such a character in this parent were fully understood. Also, this parent was among the highest parents in grain yield. Other interesting genotypes in this study are "Q.O.58.22" and "Q.O.64.31." Q.O.58.22 ranked the highest parent for its grain yield and was one of the early maturing cultivars, while "Q.O.64.31" ranked

TABLE 4. Parental oat genotypes: parentage and the actual mean performance for 9 characters over replications at Macdonald College in the 1976 season*

Genotype	Parentage	Protein (%)	Oil (%)	Hull (%)	Plant height (cm)	Heading date (days)	Grain yield/ plant (g)	No. of pan-icles/ plant	No. of grains/ panicle	1000-grain weight (g)
1. Q.O.64.31	Harmon x W.B.16385	13.32d	6.40bc	23.49a	100.93d	59.75b	10.53a	5.10c	76.33a	27.63b
2. Q.O.58.22	Dorval x Yamaska	13.42d	6.60b	23.59a	102.43de	55.00a	11.45a	8.30ab	50.49b	27.70b
3. Ajax	Victory x Hajira	15.02c	5.97cd	26.42b	108.43f	58.75b	8.63a	6.58bc	51.32b	26.43b
4. Clintland 64	Clintland 5 x Limhja 3 x Clinton 59 6 x Grey Algerian 2 x Clintland	16.00b	4.72e	25.83b	83.58c	54.75a	4.29b	4.95c	40.14c	24.20c
5. O.T.184	Harmon^6 x (Rosens mutant x Rodney)	11.52e	6.19bc	26.01b	61.80a	62.25c	8.30a	6.05bc	54.94b	26.18b
6. P.I.269182	Originally from Turkey	12.92d	9.56a	26.75b	111.13f	72.50e	10.54a	8.51ab	50.29b	27.28b
7. C.I.3387	Lee x Victoria	13.10d	10.03a	23.10a	106.85ef	68.75d	11.43a	10.85a	36.94c	30.33a
8. Hinoat	Victory x *A. strigosa*	17.89a	5.56d	29.12c	77.88b	55.00a	4.12b	6.03bc	25.58d	27.68b
Grand mean		14.15	6.88	25.54	94.13	60.84	8.66	7.05	48.25	27.18

* Means within columns followed by the same letter are not significantly different at the 0.05 probability level according to Duncan's new multiple-range test.

first for number of grains/plant. "Ajax," "Clintland 64" and "P.I.269182" had adequate levels for some of the characters involved in the present study.

Although information of the kind given in Table 4 is of some help to plant breeders when choosing parents, it tells nothing about general (GCA) or specific (SCA) combining ability nor the extent to which characters highly expressed in different parents can be brought together in the offspring. If, for example, attempts are made to raise grain yield by combining the large grain of "C.I.3387" and the numerous grains per panicle of "Q.0.64.31", it is very likely that a biological limit would be reached so that some other character, perhaps number of panicles per plant, would be reduced. Because of these limitations, there is little prospect of discerning which pairs of cultivars will combine advantageously without actually making the crosses. However, if information could be obtained about the genetic systems controlling these characters it would be easier for the plant breeder to predict the potential performance of certain cultivars or crosses in later generations from their performance in the F_1 and F_2 generations.

Due to the use of one set of parents with both the F_1 and F_2 generations, and to insure independent estimates of general and specific combining abilities, Griffing's analysis (1956b) method IV, model 1, was used in the present study. Also, this method of analysis was preferably recommended by Griffing (1956b) to obtain unbiased estimates of general and specific combining ability. General (GCA) and specific (SCA) combining ability mean squares (Table 5) indicated highly significant differences among the eight parents of oats for all characters, except the specific combining ability (SCA) for oil per cent and number of panicles per plant in the F_1 generation and grain yield per plant in the F_2 generation. The GCA mean squares were considerably larger than those due to SCA mean squares for all characters in both generations, indicating the predominant role of additive gene action in the expression of these characters.

One is never sure how to assess the relative importance of specific combining ability. The standard method is to compare the average of the squares of SCA effects with the average of the squares of GCA effects. This is the procedure recommended by Griffing (1956b) and others. Unfortunately, many researchers have used comparisons of mean squares as a means of assessing the importance of different types of combining ability. It is not difficult to show that this practice always results in an under-estimation of the importance of SCA. In this regard, Baker (1977) recommended that one should always use components of the mean squares, not the mean squares themselves, when comparing SCA and GCA. In another paper, Sokol and Baker (1977) suggested the use of the ratio of SCA to GCA sums of squares as an indication of their relative importance. It should be remembered that significant variation due to SCA may act as a signal to isolate certain parents and perform a more thorough comparison of their performance and that of their hybrid progenies.

TABLE 5. Mean squares (MS) for combining ability analysis, general ($\hat{\sigma}^2_{gca}$) and specific ($\hat{\sigma}^2_{sca}$) combining ability variance components, the ratio of SCA to GCA sum of squares and the coefficient of determination (R^2) for 9 characters in an 8-parent diallel cross in oats (F_1 and F_2 generations)

		df	Protein %		Oil %		Hull %		Plant height		Heading date	
			F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
GCA$^{(a)}$	MS	7	8.94**	6.08**	4.26**	2.97**	7.49**	4.03**	1017.77**	737.87**	43.63**	46.36**
	$\hat{\sigma}^2_{gca}$		1.45	0.98	0.70	0.49	1.19	0.61	168.86	121.72	7.19	7.54
SCA$^{(b)}$	MS	20	0.48**	0.50**	0.08	0.26**	0.62*	0.67*	12.08**	26.71**	2.57**	6.85**
	$\hat{\sigma}^2_{sca}$		0.25	0.32	0.03	0.21	0.29	0.29	7.47	19.13	2.09	5.71
Error		81	0.22	0.18	0.05	0.04	0.33	0.38	4.61	7.57	0.48	1.13
$\frac{\text{SCA (SS)}}{\text{GCA (SS)}}$			0.15	0.24	0.05	0.25	0.23	0.47	0.03	0.10	0.17	0.42
R^2 †			0.87	0.81	0.95	0.80	0.81	0.68	0.97	0.91	0.86	0.70

(Table continued)

TABLE 5. (continued)

		df	Grain yield/ plant		No. of panicles/ plant		No. of grains/ panicle		1000-grain weight	
			F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
GCA[a]	MS	7	9.46**	7.91**	1.33**	6.18**	398.52**	148.29**	16.49**	8.92**
	$\hat{\sigma}^2_{gca}$		1.43	1.14	0.17	0.97	64.61	22.57	2.66	1.39
SCA[b]	MS	20	1.89**	1.64	0.45	0.77**	26.56**	41.80**	3.01**	1.84**
	$\hat{\sigma}^2_{sca}$		1.02	0.59	0.12	0.42	15.73	28.96	2.49	1.25
Error		81	0.87	1.05	0.34	0.35	10.83	12.84	0.51	0.59
$\frac{\text{SCA (SS)}}{\text{GCA (SS)}}$			0.57	0.59	0.97	0.36	0.19	0.81	0.52	0.59
R^2 †			0.64	0.63	0.51	0.74	0.84	0.55	0.66	0.63

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

(a) GCA is the mean performance of a line in hybrid combinations.

(b) SCA is the performance of a particular cross in comparison with the average combining ability of the parental lines.

† $R^2 = \frac{\text{GCA (SS)}}{\text{Total genetic (SS)}}$ is the ratio of the general combining ability sum of squares to the total sum of squares for genetic variation among the progeny in a diallel cross.

Gilbert (1958) suggested that the GCA of the parents may provide a good prediction of how hybrids will perform because the GCA effects may be less subject to environmental influence and thus provide a better indicator of a hybrid's long-term performance than the performance of that hybrid itself. An estimate of how well GCA estimates will predict hybrid performance is given by taking the GCA sum of squares as a per cent of the total sum of squares for genetic variation (additive and non-additive variation) among the progeny in a diallel cross (Baker, 1977). This ratio is equivalent to a coefficient of determination (R^2) corresponding to the correlation of hybrid performance with the average of parental GCA's. If this ratio approaches unity, a plant breeder can be fairly confident that the GCA's of the parents will give a fairly good prediction of hybrid performance.

In the present investigation, the GCA and SCA variance components, the ratio of SCA to GCA sum of squares and the ratio of the GCA sum of squares to the total genetic sum of squares (R^2) were calculated to determine the relative importance of both GCA and SCA (Table 5). In general, the GCA variance components ($\hat{\sigma}^2_{gca}$) were higher than those of SCA variance components ($\hat{\sigma}^2_{sca}$) for protein per cent, oil per cent, hull per cent, plant height, and heading date in both generations, indicating the predominant role of additive gene action in the genetic control of these characters. For grain yield and its three components, general and specific combining ability variance component estimates were close to each other in most cases indicating the relative importance of both in the genetic control of these characters. In the F_2 generation, $\hat{\sigma}^2_{sca}$ was greater than $\hat{\sigma}^2_{gca}$ for number of grains per panicle, indicating that oat breeding should be directed toward the development of hybrid cultivars (if the purpose is to increase the number of grains per panicle), in order to capitalize on the observation that certain hybrids perform much differently than could be expected from their parental performance.

In general, the low values of the ratio of SCA to GCA sum of squares and the high values (close to 1) of the coefficient of determination for combining ability indicate the importance of GCA effects. These two ratios support the above conclusion that the GCA or the additive gene action was very important in the genetic control of the first five characters, while specific combining ability or non additive gene action was as important as additive gene action in the control of grain yield and its components. It should be emphasized here that, since the parents of this diallel cross were not randomly selected, the above conclusions can be drawn about only the eight parental lines and their crosses used in the present investigation.

1.3 Jinks-Hayman (1953) diallel analysis

Based on a statement by Sampson and Tarumoto (1976) that the genetic system of A. sativa L. is not as simple as one might conclude from Griffing's (1956b) analysis, the use of another type of diallel analysis, such as that described by Jinks and Hayman (1953), in addition to Griffing's analysis, would serve oat breeders in providing additional genetic information which could be used in oat improvement programs.

Since the method of analysis was described in detail by Jinks and Hayman (1953), a summary with a brief interpretation of the estimates of genetic and environmental parameters and ratios is given in Table 6. The use of second-degree statistics allowed estimates of genetic and environmental variance components to be made for each character in the present study (Table 7). In this table, all estimators relate to general character responses over all crosses. The statistical significance of the components given in Table 7 indicate which estimates were greater than (t) times their standard errors. The t value depends on the number of parents involved in the diallel cross. In the present study, due to the exclusion of some epistatic parents, the diallel analyses were performed on the bases of 8, 7, 6, and 5 parent diallels. The t values and the degrees of freedom associated with each diallel analysis were as follows:

TABLE 6. Jinks-Hayman's (1953) diallel analysis parameters and ratios and their interpretation

Parameter or ratio	Interpretation
$\hat{D}$	The component attributable to additive gene effects
$\hat{H}_1$	The component attributable to dominance effects (in the absence of dominance $\hat{H}_1 = 0$)
$\hat{H}_2$	The estimated value of $\hat{H}_2$ should be the same as $\hat{H}_1$ when $\mu = v = 0.5$ and the interpretation is the same as $\hat{H}_1$
$\hat{h}^2$	This statistic indicates the square difference of mean performance between hybrids and parents (if it is large and significant it indicates the existence of differences between hybrids and parents)
$\hat{F}$	The sign and magnitude of $\hat{F}$ is an indicator of the relative frequencies of dominant and recessive alleles in the parents. A positive value of $\hat{F}$ indicates an excess of dominant alleles and a negative value indicates an excess of recessive alleles.
$\hat{E}$	The conventional experimental error from the analysis of variance
$(\hat{H}_1/\hat{D})^{1/2}$	An estimate of the mean degree of dominance over all loci in the diallel cross.
$\hat{H}_2/4\ \hat{H}_1$	This ratio has a maximum of 0.25 when $\mu = v = 0.5$. An unequal distribution of positive and negative alleles causes this ratio to be less than 0.25
$\frac{(4\ \hat{D}\hat{H}_1)^{1/2} + \hat{F}}{(4\hat{D}\hat{H}_1)^{1/2} - \hat{F}}$	The ratio of the total number of dominant to recessive alleles in the parents.
$\hat{h}^2/\hat{H}_2$	This ratio provides an estimate of the number of genes or groups of genes controlling the character in the diallel cross.

TABLE 7. Mean estimates and standard errors of genetic and environmental statistics and their ratios for 9 characters from an 8-parent diallel cross in oats

Statistics or ratio	Protein %			Oil %			Hull %	
	F_1	F_1† (3)	F_2	F_1	F_2	F_2† (2)	F_1	F_2
$\hat{D}$	3.61** ±0.29	4.15** ±0.30	3.73** ±0.25	3.46** ±0.11	3.49** ±0.12	4.07** ±0.15	3.47** ±0.37	3.36** ±0.37
$\hat{H}_1$	1.49* ±0.66	0.88 ±0.72	4.27** ±0.56	0.10 ±0.24	4.46** ±0.28	3.95** ±0.35	2.99** ±0.85	9.70** ±0.86
$\hat{H}_2$	1.17* ±0.57	0.60 ±0.64	3.88** ±0.49	0.12 ±0.21	3.73** ±0.24	3.30** ±0.31	2.05** ±0.74	6.38** ±0.75
$\hat{h}^2$	-0.08 ±0.38	-0.20 ±0.43	2.44** ±0.33	0.04 ±0.14	3.54** ±0.16	3.29** ±0.21	1.18* ±0.50	1.72** ±0.50
$\hat{F}$	-1.32 ±0.68	-1.42 ±0.72	0.46 ±0.58	0.44 ±0.25	2.74** ±0.28	2.13** ±0.35	0.60 ±0.88	3.29** ±0.88
$\hat{E}$	0.78** ±0.09	0.82** ±0.11	0.67** ±0.08	0.18** ±0.04	0.14** ±0.04	0.14** ±0.05	1.31** ±0.12	1.41** ±0.12
$(\hat{H}_1/\hat{D})^{1/2}$	0.64	0.46	1.07	0.17	1.13	0.99	0.93	1.70
$\hat{H}_2/4\hat{H}_1$	0.20	0.17	0.23	0.25	0.21	0.21	0.17	0.16
K_D/K_R ‡	0.56	0.46	1.12	2.23	2.06	1.72	1.20	1.81
$\hat{h}^2/\hat{H}_2$	-0.07	-0.33	0.63	0.39	0.95	1.00	0.57	0.27

(table continued)

TABLE 7. (continued)

Statistics or ratio	Plant height			Heading date				Grain yield/plant	
	F_1	F_2	F_2 † (5,6)	F_1	F_1 † (5)	F_2	F_2 † (3,7)	F_1	F_2
$\hat{D}$	304.08**	294.30**	147.59**	43.91**	51.31**	41.92**	45.91**	8.92**	8.29**
	±8.81	±12.59	±11.13	±1.64	±1.99	±2.05	±3.12	±1.24	±1.41
$\hat{H}_1$	150.13**	658.71**	262.83**	25.39**	28.10**	130.01**	116.41**	3.99	13.99**
	±20.25	±28.95	±28.25	±3.76	±4.78	±4.71	±7.92	±2.84	±3.23
$\hat{H}_2$	78.08**	429.96**	217.26**	16.23**	21.30**	110.35**	85.39**	2.42	10.70**
	±17.62	±25.19	±25.24	±3.27	±4.21	±4.10	±7.08	±2.47	±2.81
$\hat{h}^2$	37.15**	103.50**	27.46	28.69**	45.77**	165.46**	113.96**	2.07	4.50*
	±11.82	±16.89	±16.99	±2.19	±2.83	±2.75	±4.76	±1.66	±1.89
$\hat{F}$	-195.99**	-139.09**	173.45**	23.35**	32.39**	29.72**	49.86**	3.97	8.47*
	±20.81	±29.76	±27.19	±3.86	±4.76	±4.84	±7.62	±2.92	±3.32
$\hat{E}$	17.03**	26.80**	23.00**	1.95**	1.72*	3.94**	3.51**	3.69**	4.32**
	±2.94	±4.20	±4.21	±0.55	±0.70	±0.68	±1.18	±0.41	±0.47
$(\hat{H}_1/\hat{D})^{1/2}$	0.70	1.50	1.33	0.76	0.74	1.76	1.59	0.67	1.30
$\hat{H}_2/4\hat{H}_1$	0.13	0.16	0.21	0.16	0.19	0.21	0.18	0.15	0.19
K_D/K_R ‡	0.37	0.73	2.57	2.07	2.49	1.50	2.03	2.00	2.30
$\hat{h}^2/\hat{H}_2$	0.48	0.24	0.13	1.77	2.15	1.50	1.33	0.85	0.42

(table continued)

TABLE 7. (continued)

Statistics or ratio	No.of panicles/plant				No.of grains/panicle		1000-grain weight			
	F_1	F_1† (6)	F_2	F_2†(1,7)	F_1	F_2	F_1	F_1†(1,2,6)	F_2	F_2†(1,2,6)
$\hat{D}$	4.59** ±0.48	4.22** ±0.56	4.52** ±0.55	2.52** ±0.77	204.84** ±13.60	198.90** ±24.01	4.83** ±1.68	10.09** ±2.93	5.39** ±1.39	9.82** ±3.03
$\hat{H}_1$	1.43 ±1.10	0.04 ±1.35	6.95** ±1.27	2.91 ±1.95	95.20** ±31.26	608.79** ±55.19	12.79** ±3.87	0.60 ±7.91	23.19** ±3.20	21.10* ±8.19
$\hat{H}_2$	0.54 ±0.96	-0.06 ±1.19	3.33** ±1.11	-1.56 ±1.74	64.20* ±27.20	495.58** ±48.01	9.48** ±3.36	0.07 ±7.17	14.82** ±2.78	8.44 ±7.43
$\hat{h}^2$	0.32 ±0.64	0.11 ±0.80	-2.43* ±1.09	-2.36 ±1.17	47.31* ±18.24	118.52** ±32.20	9.82** ±2.26	0.09 ±4.84	0.12 ±1.87	-5.08 ±5.02
$\hat{F}$	4.41** ±1.13	1.39 ±1.34	3.45* ±1.31	4.02* ±1.87	-10.34 ±32.14	235.99** ±56.72	-0.08 ±3.97	2.03 ±7.31	5.04 ±3.29	10.15 ±7.58
$\hat{E}$	1.60** ±0.16	1.28** ±0.20	1.67** ±0.18	1.68** ±0.29	40.19** ±4.53	46.12** ±8.00	3.16** ±0.56	2.72* ±1.20	2.60** ±0.46	2.99* ±1.24
$(\hat{H}_1/\hat{D})^{1/2}$	0.56	0.09	1.24	1.07	0.68	1.75	1.63	0.24	2.07	1.47
$\hat{H}_2/4\,\hat{H}_1$	0.09	-0.38	0.12	-0.13	0.17	0.20	0.19	0.03	0.16	0.10
K_D/K_R ‡	13.26	-3.64	1.89	6.80	0.93	2.03	0.99	2.40	1.58	2.09
$\hat{h}^2/\hat{H}_2$	0.59	1.90	0.17	1.51	0.74	0.24	1.04	1.26	0.01	-0.60

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

† Estimates in the F_1 or F_2 generation after eliminating the epistatic parent(s), epistatic parent(s) are in parentheses.

‡ $K_D/K_R = [(4\,\hat{D}\,\hat{H}_1)^{1/2} + \hat{F}] \,/\, [(4\,\hat{D}\,\hat{H}_1)^{1/2} - \hat{F}]$ is the ratio of total number of dominant to recessive alleles in the parents.

No. of parents included	dF	t value 0.05	t value 0.01
8	52	2.01	2.68
7	44	2.02	2.70
6	36	2.03	2.73
5	28	2.05	2.76

Estimates of the additive genetic variance ($\hat{D}$) were highly significant and higher in magnitude than those due to the dominance variance ($\hat{H}_1$ and $\hat{H}_2$) in the F_1 generation for all characters (Table 7), except 1000-grain weight where the additive variance component was significant but less than the dominance variance. It is clear that this deviation was mainly due to the presence of non-allelic interaction and/or gene correlation which inflated the dominance variance components. The removal of the epistatic parents (parents 1, 2 and 6) removed the effects due to non-allelic interaction and the values of $\hat{D}$ became higher than those of $\hat{H}_1$ or $\hat{H}_2$. Exclusion of the epistatic parents did not succeed in correcting the failure of the assumptions underlying the genetic analysis due to unequal gene frequency for this character as indicated from the low $\hat{H}_2/4\ \hat{H}_1$ value. This will be discussed further later on. In general, the ~~high~~ and significant values of $\hat{D}$ indicate the importance of additive gene action in the genetic control of these characters. This was in agreement with results from the Griffing's analysis.

In the F_2 generation, although the estimates of $\hat{D}$ were highly significant, they were lower in magnitude than those due to $\hat{H}_1$ and $\hat{H}_2$.

These results agreed with those of other workers (Chae and Forsberg, 1975; Iwig and Ohm, 1976; Sampson and Tarumoto, 1976). Generally, $\hat{H}_1$ and $\hat{H}_2$ were significantly different in the F_1 generation, except for protein per cent (excluding epistatic parent no.3), oil per cent, grain yield per plant, number of panicles per plant, and 1000-grain weight (excluding parents 1, 2 and 6). In the F_2 generation, dominance effects were significant for all characters except number of panicles per plant (excluding parents 1 and 7). The fact that the $\hat{H}_1$ and $\hat{H}_2$ were not equal and $\hat{F} \neq 0$ implies presence of gene correlation in this study for most characters, except protein, oil and hull per cent where $\hat{H}_1$ was close to $\hat{H}_2$ in most cases, indicating that $u = v = 0.5$. Heterosis was indicated by the sign and value of $\hat{h}^2$. For protein and oil per cent, $\hat{h}^2$ was low in magnitude, indicating no heterosis in the F_1 while it was positive and significant in the F_2 generation. Significant heterosis was indicated for hull per cent in both generations. Heterosis was in the direction of tall and late-maturing plants for plant height and heading date (positive and significant $\hat{h}^2$). In the F_2 generation, hybrid means were lower than parental means for number of panicles per plant and 1000-grain weight (as indicated from their negative values of $\hat{h}^2$). An excess of dominant alleles was shown from the positive values of $\hat{F}$ for all characters in both generations except for protein per cent, plant height, number of grains per panicle and 1000-grain weight in the F_1 generation, where more recessive alleles were involved in the control of these characters. The environmental components ($\hat{E}$) were significant for all characters in both generations.

The estimated genetic and environmental components were combined into ratios to estimate additional genetic characteristics of the population in this investigation (Table 7). The value of $(\hat{H}_1/\hat{D})^{1/2}$ is an estimate of the mean degree of dominance over all loci. With no dominance this value is expected to equal 0; with average partial dominance the value is expected to fall within the range of 0 to <1; with complete dominance this value should equal 1, and with over-dominance it should be >1. In the present study, the degree of dominance was inconsistent from one generation to the other. In the F_1 generation, all characters except 1000-grain weight showed partial dominance $(\hat{H}_1/\hat{D})^{1/2} < 1$, while in the F_2 over-dominance was observed for all characters $(\hat{H}_1/\hat{D})^{1/2} > 1$. Hayman (1957) reported that the measure of degree of dominance $(\hat{H}_1/\hat{D})^{1/2}$ may be either increased or decreased; the particular combination of dispersion and unidirectional dominance as well as the existence of epistatic effects inflates $(\hat{H}_1/\hat{D})^{1/2}$ seriously and may easily turn partial dominance into apparent over-dominance. In this study this was true, and the removal of epistatic parents (1, 2 and 6) for 1000-grain weight in the F_1 generation changed the degree of dominance from over-dominance to partial dominance. The same situation occurred with oil per cent in the F_2 generation. This illustrates the extent to which non-allelic genic interaction can inflate this estimate of degree of dominance and emphasizes the importance of a preliminary test with the V_r, W_r graph. Hayman (1957) reported that $(\hat{H}_1/\hat{D})^{1/2}$ can also be computed from epistatic diallels, but it is not certain what it measures and it must be called the apparent degree of dominance.

The ratio $\hat{H}_2/4\hat{H}_1$ provides an estimate of the average frequency of negative (u) versus positive (v) alleles (at loci exhibiting dominance) in the parents with a maximum value of 0.25 when the positive and negative alleles are equally distributed in the parents. Estimates of uv in the present study showed that for protein per cent, oil per cent, hull per cent and number of grains per panicle the parents generally had an equal distribution of alleles at those loci that exhibit dominance, while for the other characters the parents probably had an unequal distribution of alleles. These results agree with the previously discussed situation of the relatively close $\hat{H}_1$ and $\hat{H}_2$ values and the low $\hat{F}$ estimates for the characters protein per cent, oil per cent, hull per cent and number of grains per panicle, which indicates an equal distribution of alleles in the parents. Also, these results of gene correlation could explain part of the failure of the additive-dominance model showed by the analysis of $W_r - V_r$ and the regression of W_r on V_r for some characters in this study (Table 3).

Another parameter that gives a fairly good indication of the equality of distribution among the parental cultivars of dominant versus recessive genes is the ratio $[(4\hat{D}\hat{H}_1)^{1/2} + \hat{F}]/[(4\hat{D}\hat{H}_1)^{1/2} - \hat{F}]$. The value of this ratio was greater than 1 for all characters in both generations, except protein per cent, plant height and number of grains per panicle in the F_1 generation, where their values were less than 1. These results indicate more dominant than recessive genes among the parents for all characters except protein per cent, plant height and number of grains per panicle in the F_1 generation where more recessive than dominant alleles were observed in the parents. The negative values of the $\hat{F}$ component (Table 7) for these three characters in the F_1 generation and the positive values of the $\hat{F}$ component for the other characters support this conclusion. Since the $\hat{F}$ components for protein content and number of grains per panicle in the F_1 generation were statistically non significant, one can perhaps conclude also that the dominant and recessive alleles for these characters are equal in the parents.

The ratio $\hat{h}_2/\hat{H}_2$ estimates the number of genes (K) or groups of linked genes showing some degree of dominance. This estimate will be under-estimated if the dominance effects of the genes affecting the character are not equal in size and direction, or if the distribution of the genes is correlated. In the present investigation, two genes or groups of linked genes controlled heading date, number of panicles per plant and 1000-grain weight, and at least one gene or group of linked genes appeared to control the other characters, since the assumptions associated with the formula of gene number are several (Wright, 1968). Many of these assumptions do not hold in most cases, which results in a downward bias in the gene number estimate. One feels that what appeared to be a small number of genes involved in the inheritance of these characters, particularly grain yield, actually may be due to a large number of genes linked in blocks on a small number of chromosomes, which would give the impression of simple inheritance. Similar results were obtained by several workers in oats (Campbell and Frey, 1972; Sampson and Tarumoto, 1976).

In general, results from this analysis indicated that the genetic variation for all characters was mainly additive with a minor and unstable role of dominance effects. The generally high additive variance revealed by both the Griffing and Jinks-Hayman analyses indicates that the usual practice of choosing parents phenotypically and mating the best with the best will continue to give substantial progress. However, with characters such as heading date, numbers of panicles per plant and 1000-grain weight, which appear to be affected by epistasis or gene correlation or both, a more complex breeding scheme, such as choosing parents by progeny testing, will be necessary to achieve maximum genetic advance in oats.

Finally, we should emphasize here again that throughout this study we were investigating a given set of genotypes. The $\hat{D}$, $\hat{H}_1$, $\hat{H}_2$, etc., from this experiment characterize only those genotypes involved in the present study. We do not try, nor intend to try, to infer properties of any population from which these genotypes might have been selected. Furthermore, the standard errors of the genetical components in the present study arise from sampling the environment and also from sampling the segregation in the F_2 families. These errors do not measure possible variation due to sampling the genotypes from any hypothetical genetical population pool.

1.4 Graphical analysis

The adequacy of a simple additive-dominance model with additive environmental effects was tested by two different tests: the heterogeneity of $W_r - V_r$ and the regression of W_r on V_r (b W_r/V_r). The graphical analysis, in general, provides information on three main points (Mather and Jinks, 1971).

1.--It supplies a test of adequacy of the genetical model. In the absence of non-allelic interaction and with independent distribution of the genes among the parental inbreds, W_r is related to V_r by a straight regression line of unit slope (b $W_r/V_r = 1$). As the regression of W_r on V_r agrees with a slope of one, the gene system can be deduced to be additive without the complication of gene interaction.

2.--Given that the model is adequate, a measure of the average degree of dominance is provided by the departure from the origin of the point where the regression line cuts the W_r axis. With complete dominance, the regression line of slope b = 1 would pass through the origin. In the case of over-dominance, the regression line would cut the W_r axis below the origin and with partial (incomplete) dominance the line would cut the W_r axis above the origin. If dominance is absent, the points would cluster about the position where the slope of the parabola is +1.[a]

3.--The relative order of points along the regression line indicates the distribution of dominant and recessive genes among the parents. The points nearest the origin stem from the arrays derived from parents with the most dominant genes and the points farthest from the origin stem from arrays derived from parents with the fewest dominant genes.

Another two points should be mentioned concerning information that can be obtained from the V_r, W_r values. Firstly, the direction of dominance; the relative values of $W_r + V_r$ over arrays indicate the relative number of dominant to recessive alleles in the common parents of the arrays. By comparing the $W_r + V_r$ value for each array with the mean of the common parent, i.e., comparing $W_{ri} + V_{ri}$ with $\overline{P}_i$, we can see whether the distribution of dominant to recessive alleles is correlated with the phenotypes of the common parent. This correlation will be negative if the parents with a high score, i.e., those containing the most increasing genes, have the lowest values of $W_{ri} + V_{ri}$, i.e., contain most dominant genes, and positive if the reverse is true. Hence, we can deduce whether or not the increasing or decreasing alleles are dominant alleles. Secondly, the V_r, W_r

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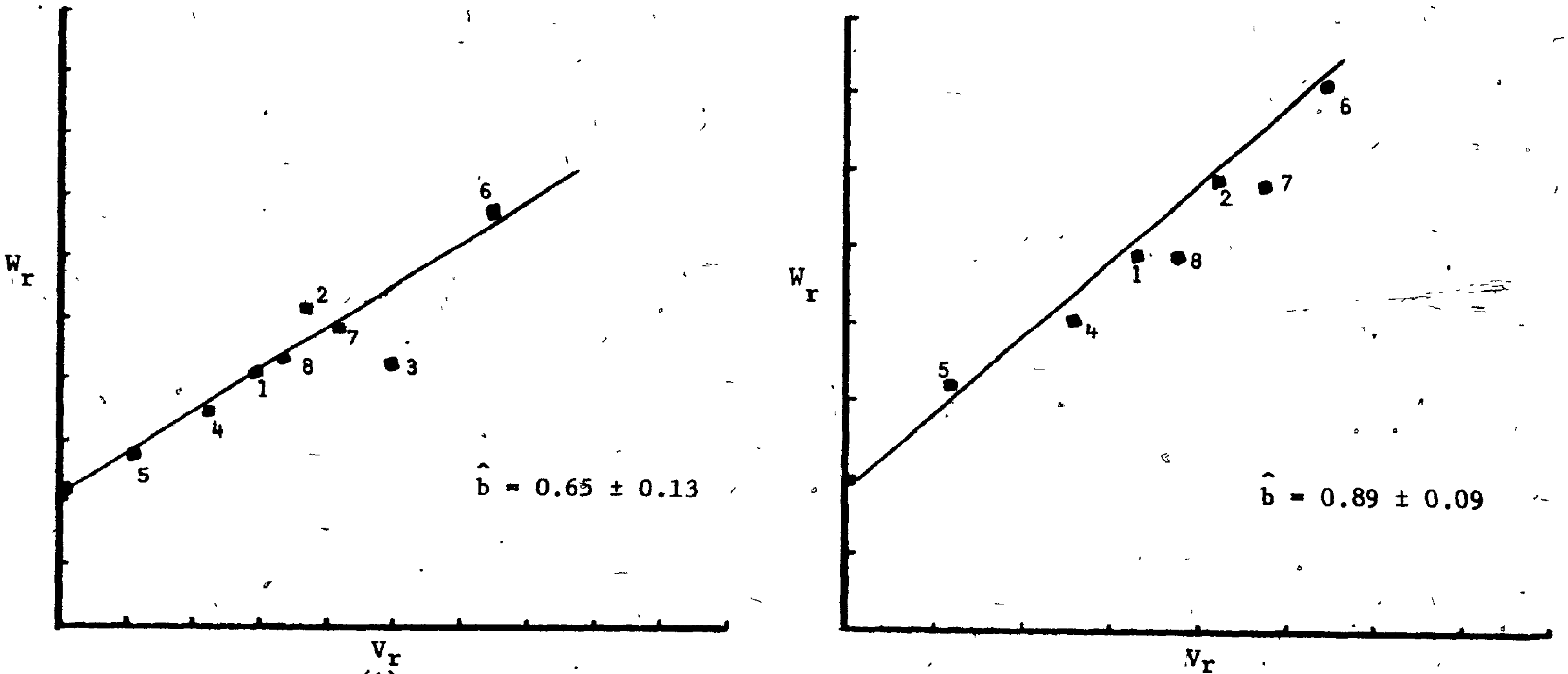
[a] For a detailed explanation of graphical analysis see Hayman (1954), Jinks (1954) and/or Jinks (1955).

graph could be used to detect the residual heterozygosity in the parents. The regression V_r, W_r graph is a scatter about a line of unit slope, points above the line corresponding to heterozygous parents and those below the line to inbred parents (Hayman, 1954).

The graphical analysis for per cent protein in the F_1 generation (Figure 2A) shows that the regression line is significantly below the unit slope (b = 0.65), indicating epistasis and/or genetic correlation effects. Thus, the additive variance should be considered somewhat less than the values presented in Table 7, since the deviation of the regression from unity could be due, at least partly, to epistasis. The same applies to variance components and heritability estimates presented later on. Excluding parent 3 (Ajax), which contributes to non-allelic interaction (the lowest $W_r - V_r$ value, Appendix Table 1), removed such effect and the regression line (Figure 2B) became non-significantly different from 1 (b = 0.89). The regression lines in Figure 2A and B intercept the W_r axis above the origin, indicating partial dominance. Parent 5 appears to carry the most dominant genes, while parent 6 carries the most recessive genes on the average in this group of genotypes. In the F_2 generation, the slope of the regression line did not differ significantly from unity, indicating adequacy of the model (Figure 3A). Although b W_r/V_r did not differ significantly from 1, the position of parent 2 in Figure 3 as well as its value of $W_r - V_r$ (Appendix Table 2), indicated that such a parent would contribute some epistatic effects to the genetic



(A)

(B)

Figure 2. V_r, W_r graphs for protein per cent in the F_1 generation from a diallel cross in *Avena sativa* L. (A) all parents are included. (B) epistatic parent 3 is excluded.

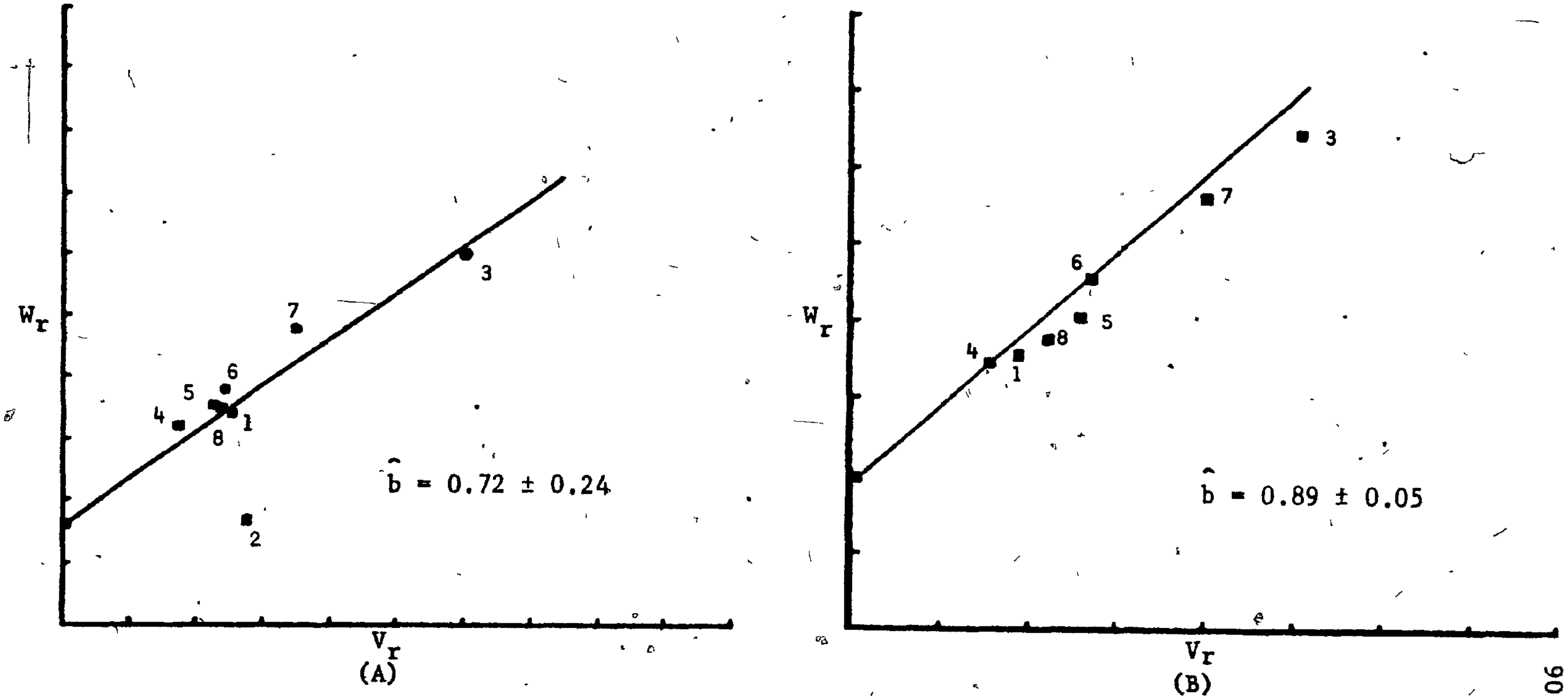


Figure 3. V_r, W_r graphs for protein per cent in the F_2 generation from a diallel cross in *Avena sativa* L. (A) all parents are included. (B) epistatic parent 2 is excluded.

analysis. Removal of this parent increased the regression coefficient from 0.72 to 0.89 (Figure 3B). Partial dominance is also indicated from the position of the regression line on the W_r axis. The degree of dominance from the graphical analysis for the F_2 generation does not agree with that reported earlier from the Jinks-Hayman analysis (Table 7). However, such a conflict could be due to the effect of non-allelic interaction and/or gene correlation. Parents 3 and 7 possess the most recessive alleles, while the other parents carry more dominant than recessive alleles in the F_2 generation. Parents 1 and 8 seem to have dominant and recessive genes more or less in equal proportions in the two generations. The direction of dominance for all characters will be discussed later in the section dealing with predictions concerning future generations.

The regression line in the V_r, W_r graph for oil per cent in the F_1 generation (Figure 4) is approximately of unit slope (b = 1.11), indicating no epistasis. The position of the regression line is above the origin, indicating partial dominance. Array 4, with its small W_r, V_r value, has the greatest excess of dominant alleles, while arrays 6 and 7 seem to carry most of the recessive alleles. In the F_2 generation, although the regression line in the V_r, W_r graph is close to unity (b = 0.92) and does not differ significantly from the unit slope, the analysis of $W_r - V_r$ (Table 3) indicated failure of some of the assumptions required for the genetic analysis. The epistatic parent or parents in the present case are not easy to define

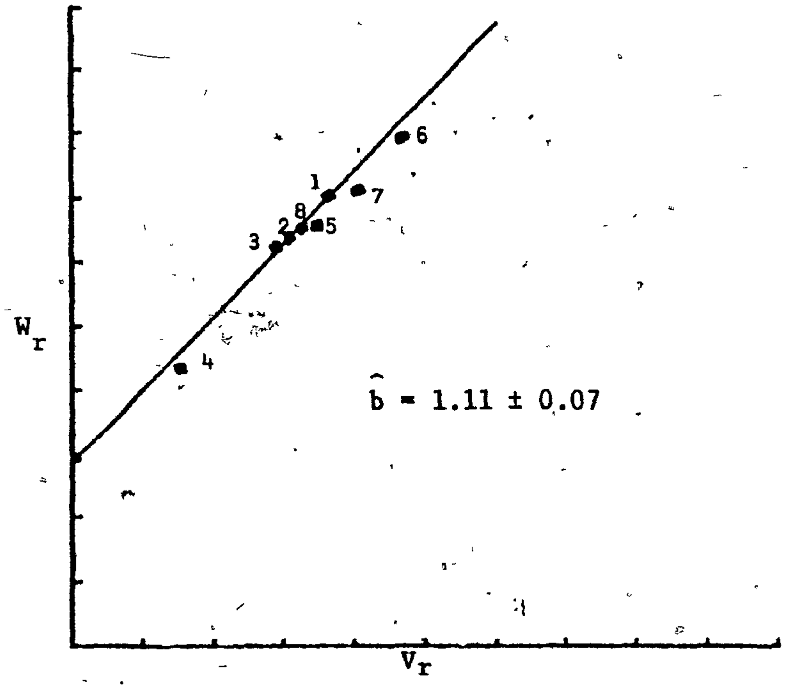


Figure 4. V_r, W_r graph for oil per cent in the F_1 generation from a diallel cross in *Avena sativa* L.

since all parents lie along the regression line (Figure 5A) and their W_r - V_r values (Appendix Table 4) are close to each other. We tried all possible combinations of analysis to define the epistatic parents. The results indicated that excluding parent 7 improved b W_r/V_r from 0.92 to 0.98 (not shown) but did not correct the failure indicated by the W_r - V_r test. Also, eliminating this parent resulted in lower additive genetic variance and increased the dominance variance. Such a situation is hard to accept because the W_r/V_r test cannot detect epistasis in the presence of gene correlation (Hayman, 1954; Sokol and Baker, 1977) and elimination of the epistatic parent(s) should result in increasing the additive genetic variance, a situation which does not exist in this case. Although the elimination of parent 2 reduced the W_r, V_r regression coefficient from 0.92 to 0.85 (Figure 5B), and this value was not significantly different from b = 1, it improved the W_r-V_r test (Table 3) slightly (0.05) and increased the additive genetic variance. One strongly believes that such failure of the assumptions of the genetical model is due not only to epistasis, but also to other factors such as gene correlation or unequal gene distribution in the parents. Partial dominance was indicated from the graphical analysis by the position of the regression line above the origin. These results confirmed those indicated earlier from $(\hat{H}_1/\hat{D})^{1/2}$ in Table 7, especially after eliminating parent 2. Parents 4 and 7 maintained their positions in the two graphs (Figure 5A, B) with parent 4 carrying most of the dominant alleles and parent 7 carrying the most recessive ones. This trend was almost the same in the F_1 generation.

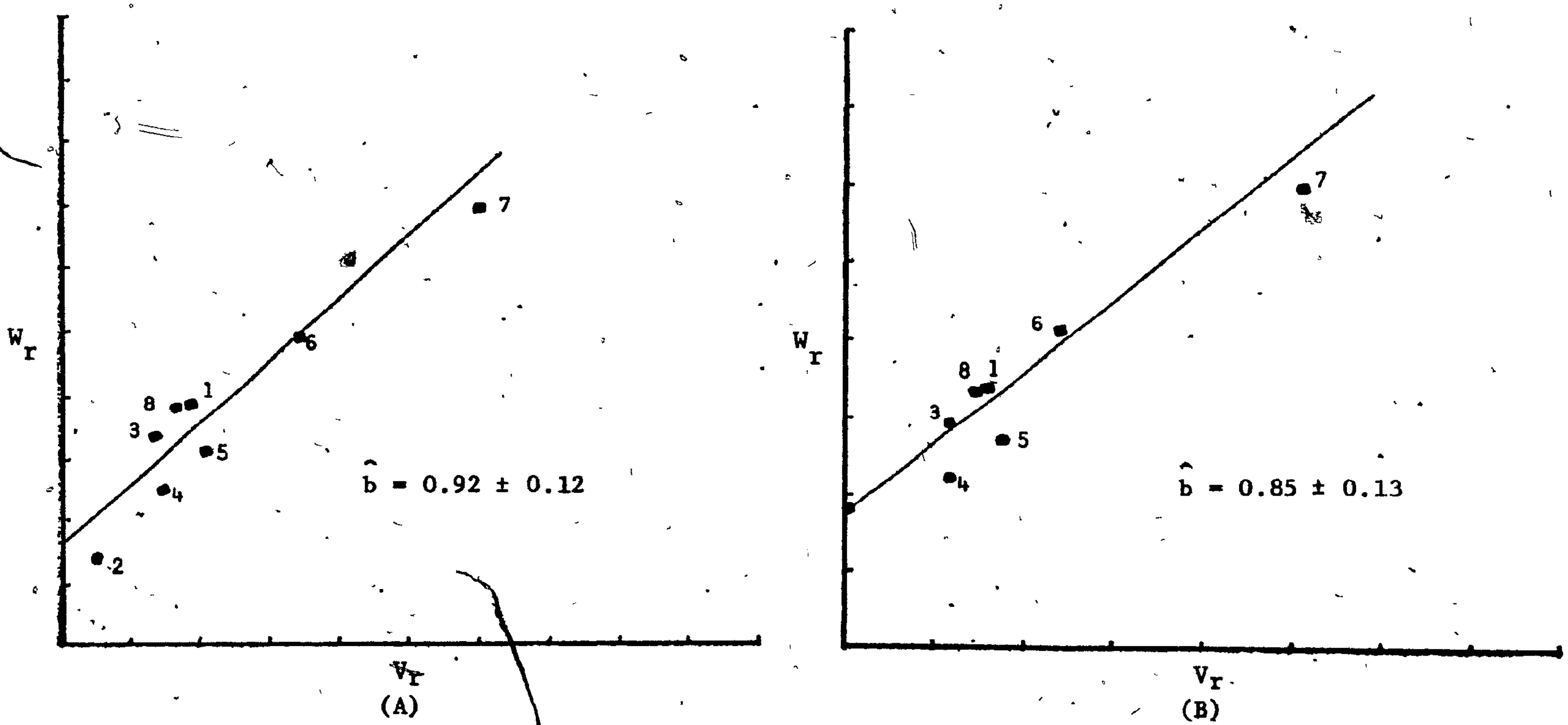


Figure 5. V_r, W_r graphs for oil per cent in the F_2 generation from a diallel cross in *Avena sativa* L. (A) all parents are included. (B) epistatic parent 2 is excluded.

Figure 6A and B shows a graphical analysis of the F_1 and F_2 data for hull per cent, based on an 8 x 8 diallel (28 crosses + 8 parents). The regression lines in the F_1 data ($b = 0.73$) and F_2 data (0.66) did not differ significantly from 1, indicating no epistasis. Both regression lines (Figure 6A and B) showed partial dominance and confirmed the result of $(\hat{H}_1/\hat{D})^{1/2}$ in Table 7 for the F_1 generation but not for the F_2. From the low b W_r/V_r value in the F_2 and from the distribution of the parents along the regression line (Figure 6B), one may predict that parent 7 contributes some epistatic effects. This is clear also from the value of $W_r - V_r$ for that parent shown in Appendix Table 5. Because the two tests of assumptions (Table 3) for this character did not show failure of the genetic assumptions, one might accept the present results, albeit with some caution. Parent 5 appeared to carry most of the dominant alleles in both generations, while parent 8 carried most of the recessive genes in both generations. The others, except parent 4, carry more or less equal numbers of dominant and recessive alleles.

The plant height V_r, W_r regression line in the F_1 generation is approximately of unit slope (Figure 7) and provides a good linear example from which to discuss the order of dominance. Array 5, with its small W_r, V_r value, has the greatest excess of dominant alleles, while arrays 3, 1 and 4 carry the most recessive ones. The other arrays (2, 6, 7 and 8) lie close to each other and are quite far from the origin, indicating more recessive than dominant alleles in these

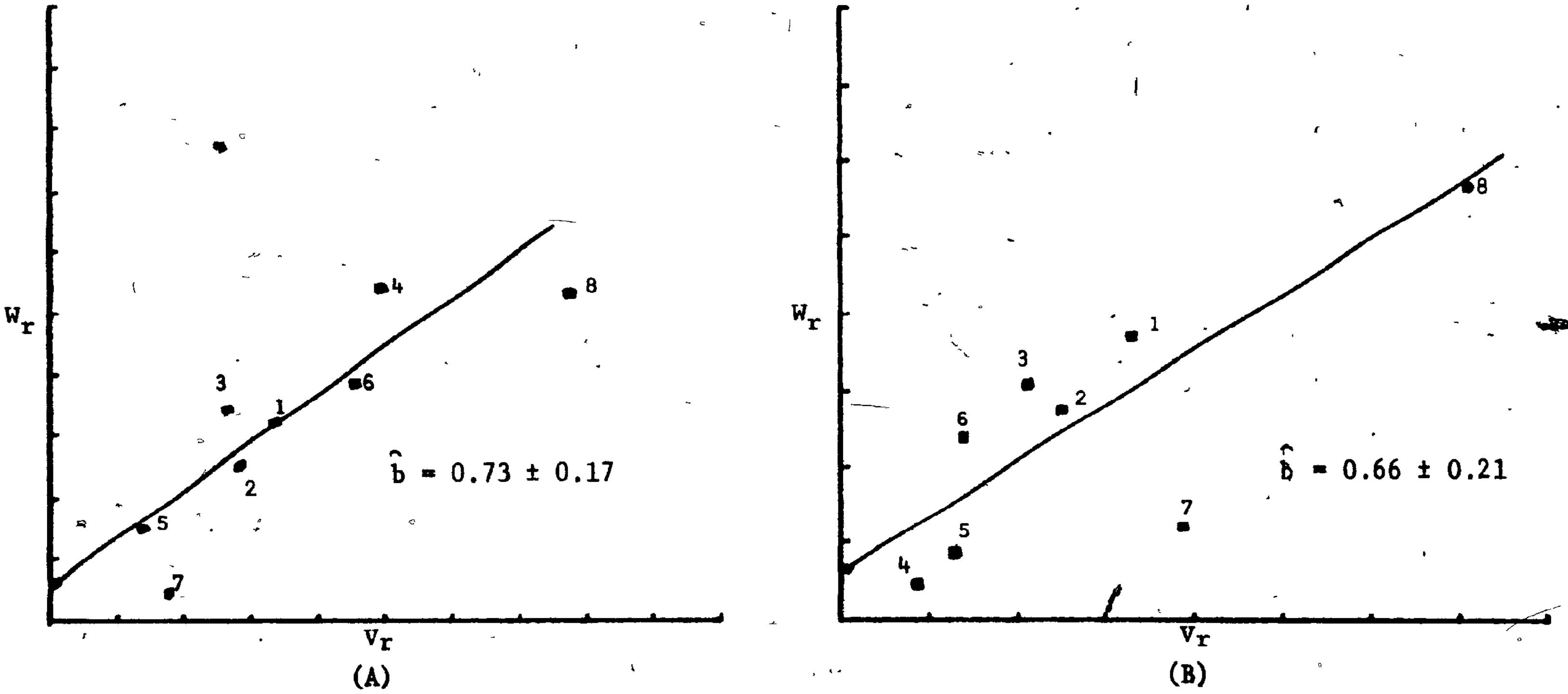


Figure 6. V_r, W_r graphs for hull per cent in the F_1 (A) and F_2 (B) generations from a diallel cross in Avena sativa L.

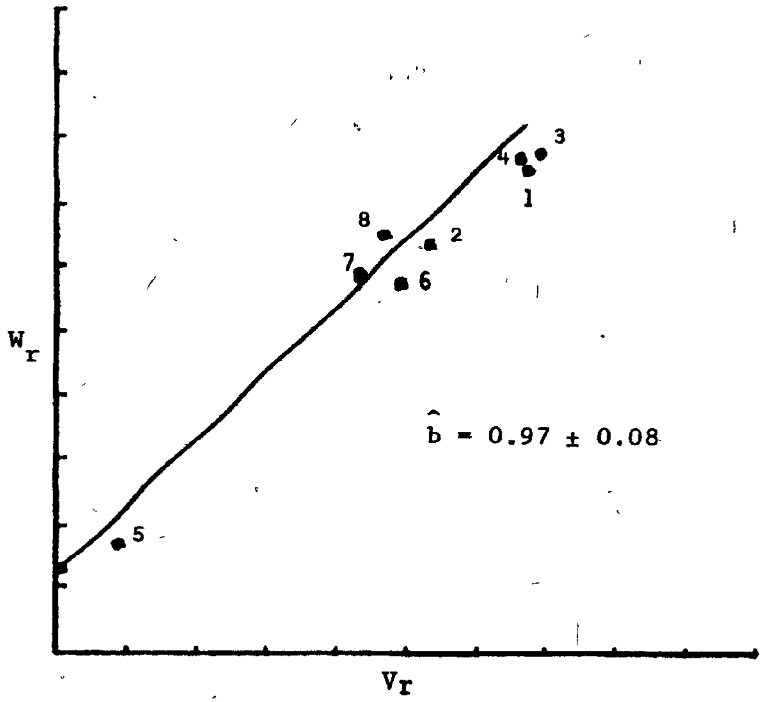
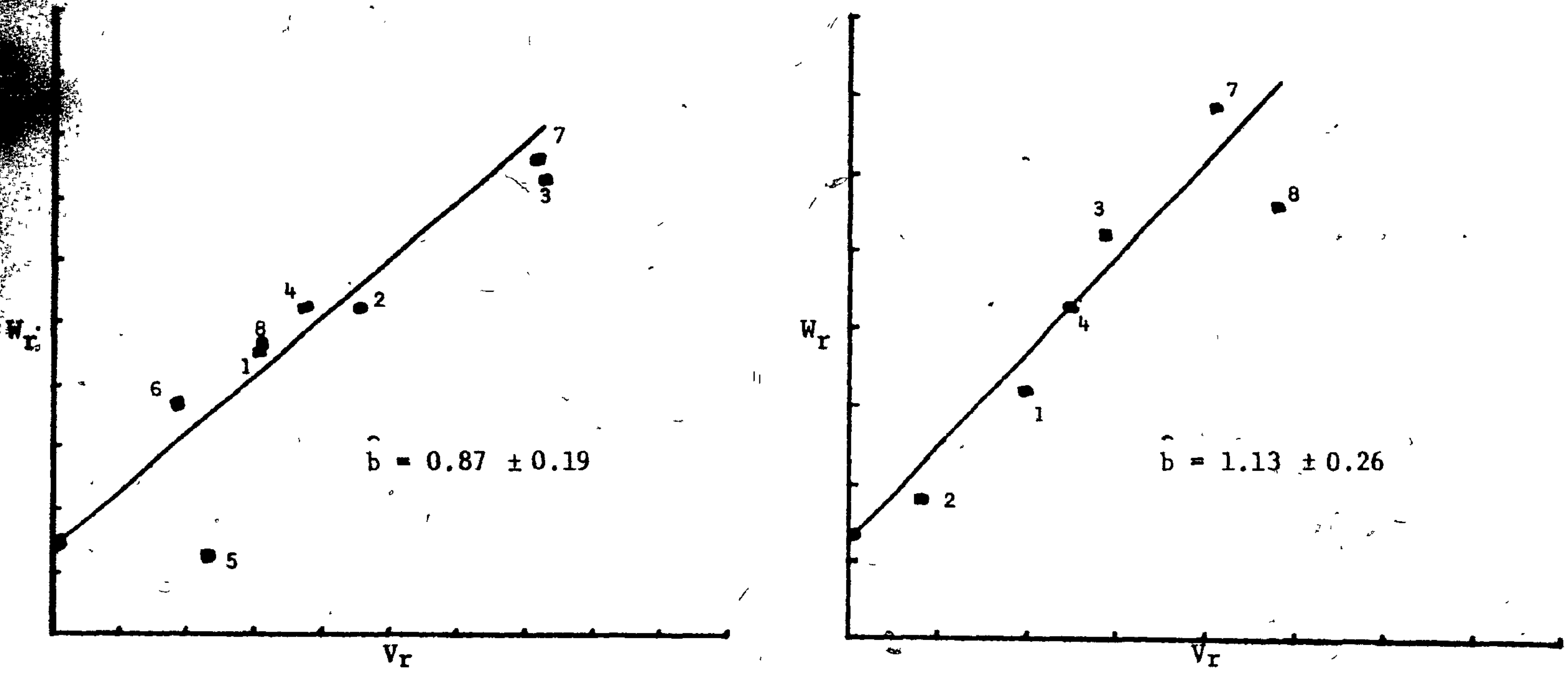


Figure 7. V_r, W_r graph for plant height in the F_1 generation from a diallel cross in *Avena sativa* L.

parents. Partial dominance was also indicated and these agree with those obtained from the Jinks-Hayman (1953) analysis (Table 7). Arrays 5 and 6 had the lowest and highest $W_r - V_r$ values (Appendix Table 7) and deviated significantly from the regression line in the F_2 generation (Figure 8A and B), but the regression line did not differ significantly from unit slope (b = 0.87), while the $W_r - V_r$ test indicated failure of some of the underlying assumptions (Table 3). Exclusion of these two arrays from the analysis improved the b W_r/V_r value (Figure 8B) and corrected the failure which appeared in the $W_r - V_r$ test. This suggests that two such parents contribute to non-allelic interaction, probably of the complementary type. Such interaction tends to move the regression line to the right (as in increasing dominance) and to drop its slope below the expected value of unity. Partial dominance was indicated in both graphs but these results disagree with those reported earlier in Table 7. Parent 7 occupied the far end of the regression line in both graphs (Figure 8A and B), indicating more recessive alleles, while the epistatic parents 5 and 6 carried the most dominant genes in Figure 8A, and parents 2 and 1 had the most dominant genes after eliminating the epistatic parents (Figure 8B).

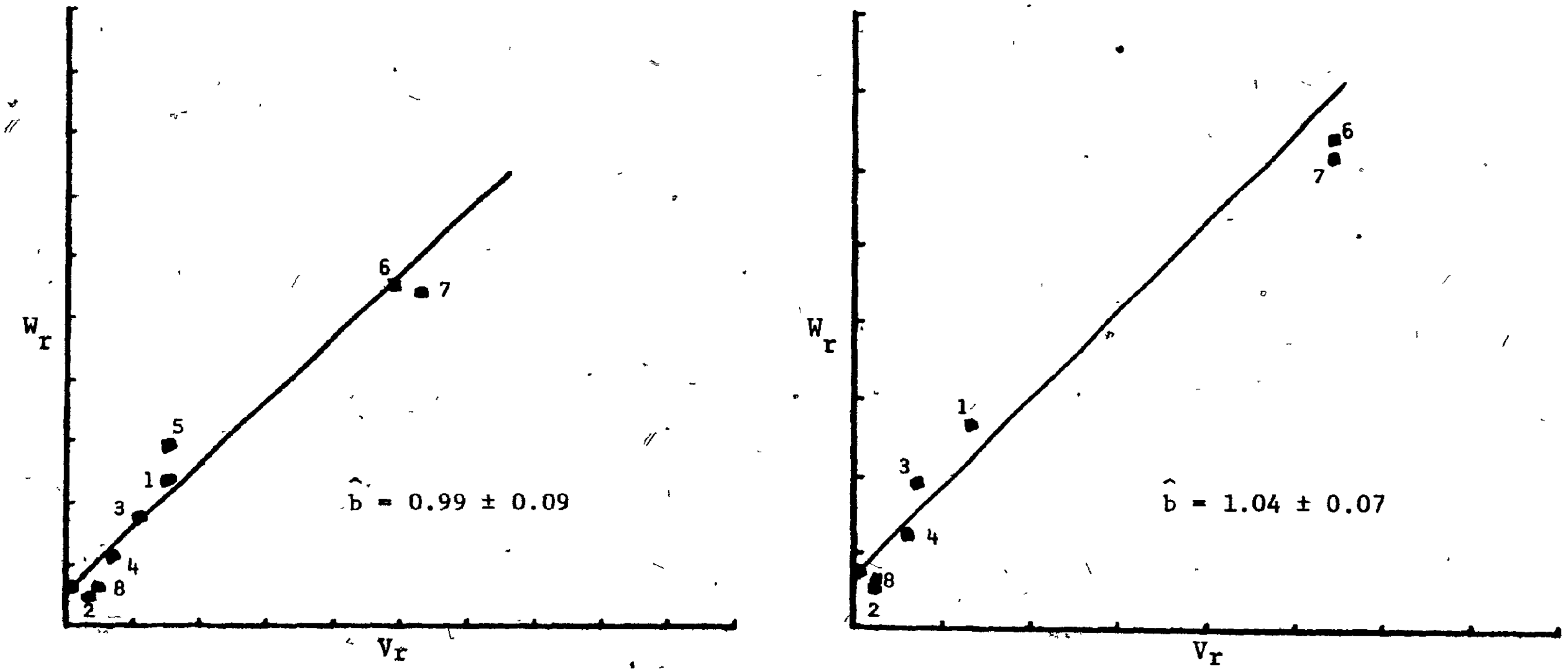
Heading date showed significant deviation of the assumptions underlying the genetic analysis in the F_1 and F_2 generations, as indicated from their significant $W_r - V_r$ arrays F values (Table 3). Although the regression line for the F_1 generation (Figure 9A) was



(A)

(B)

Figure 8. V_r, W_r graphs for plant height in the F_2 generation from a diallel cross in *Avena sativa* L. (A) all parents are included. (B) epistatic parents 5 and 6 are excluded.



(A) (B)

Figure 9. V_r, W_r graphs for heading date in the F_1 generation from a diallel cross in *Avena sativa* L. (A) all parents are included. (B) epistatic parent 5 is excluded.

almost of unit slope (b = 0.99), the analysis of $W_r - V_r$ test did not agree with that from the regression line. Hayman (1963) reported that if $W_r - V_r$ is not consistent, a situation occurring in the present study for heading date, at least one of the assumptions of the model must be relaxed. He defined the epistatic array as that which causes inconsistency in the quantity $W_r - V_r$. Parent 5 had a relatively high $W_r - V_r$ value (Appendix Table 8), suggesting non-allelic interaction. Exclusion of this array (Figure 9B) from the analysis improved both the regression line (b = 1.04) and the $W_r - V_r$ test, and the simple model became adequate. The regression lines in Figure 9A and B cut the W_r axis above the origin, indicating partial dominance and supported results obtained from the Jinks-Hayman analysis (Table 7). Parents 2 and 8 appear to have the most dominant alleles, while parents 6 and 7 have the most recessive alleles on the average in the present group of genotypes. Other parents have more dominant than recessive genes and lie near the origin. In the F_2 generation, both tests of assumptions required for the genetic analysis indicated lack of one or more of these assumptions (Table 3). Eliminating parents 3 and 7, which had the highest and lowest $W_r - V_r$ values respectively (Appendix Table 9), improved only the regression line (b = 0.84), but not the $W_r - V_r$ test. In such a case, one might conclude that such a character in the F_2 generation is influenced not only by the effect of epistasis, but also by other factors such as gene correlation. This was indicated from the low values of $\hat{H}_2/4\,\hat{H}_1$ in Table 7, suggesting the presence of gene correlation. The regression lines

(Figure 10 A and B) indicated partial dominance for this character in the F_2 generation. Parent 2 had the most dominant alleles, while parent 5 had the most recessive ones.

Figure 11 shows a graphical analysis of the F_1 (A) and F_2 (B) for grain yield per plant from an 8-parent diallel cross. Regression coefficients differed significantly from zero, but not from unity, indicating validity of the genetic assumptions in both generations. Partial dominance was indicated in the two generations from the position of the regression lines on the W_r axis. Array 5 had the lowest V_r, W_r values in both generations, indicating more dominant alleles, while array 1 had the most recessive alleles in the F_1 and ranked the second highest parent carrying recessive genes in the F_2, preceded by array 7. Other parents lay between the two extreme points on the regression lines, having dominant and recessive genes more or less in equal proportions.

The slope of the regression line for the yield component, number of panicles per plant in the F_1 generation, is significantly below unit slope ($b = 0.51$), suggesting that significant interactions of some arrays (epistasis) and/or major environmental components of variation are present. Also, the parents vary considerably about the regression line (Figure 12A), particularly parent 6. Exclusion of this parent, which also had the lowest $W_r - V_r$ value (Appendix Table 11), from the analysis improved b W_r/V_r (Figure 12B), and a simple model became adequate. The regression lines passed above the origin,

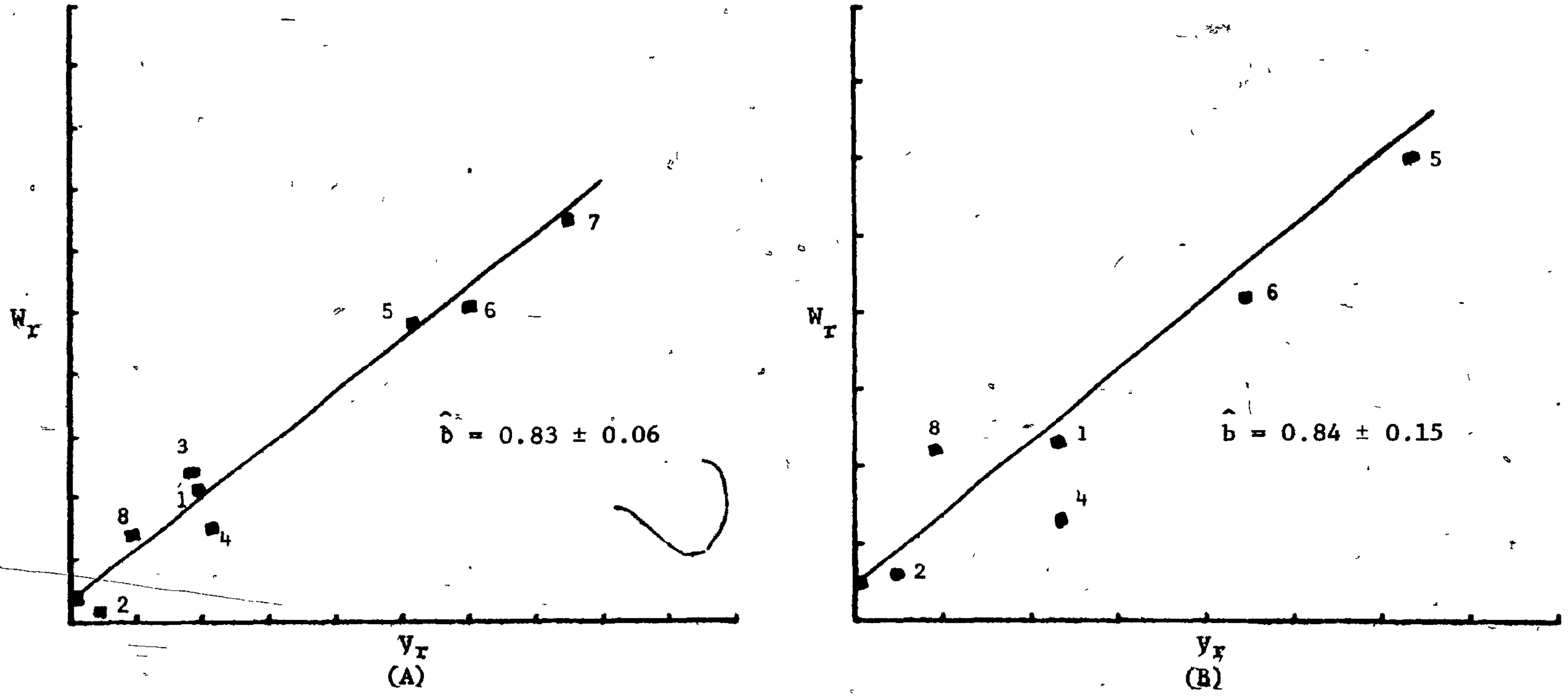


Figure 10. V_r, W_r graphs for heading date in the F_2 generation from a diallel cross in Avena sativa L. (A) all parents are included. (B) epistatic parents 3 and 7 are excluded.

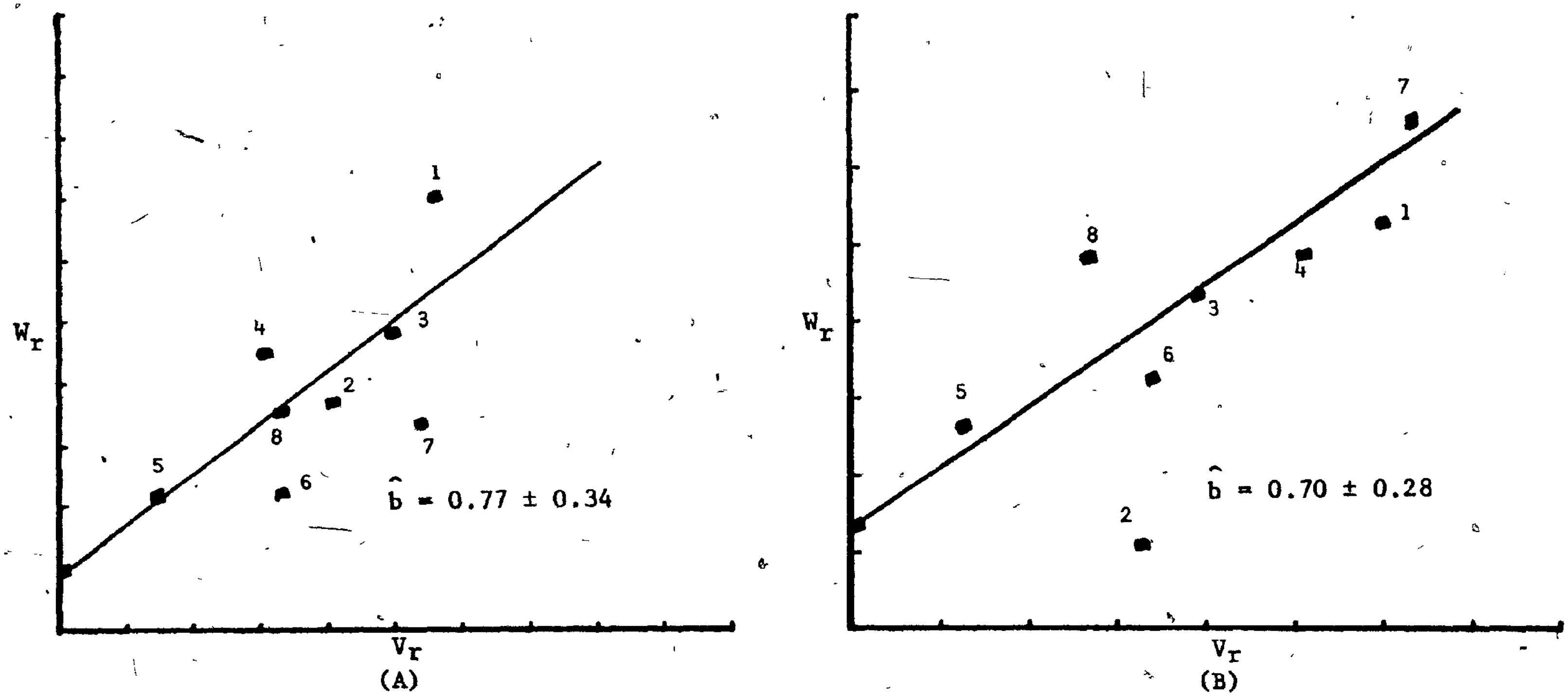


Figure 11. V_r, W_r graphs for grain yield per plant in the F_1 (A) and F_2 (B) generations from a diallel cross in Avena sativa L.

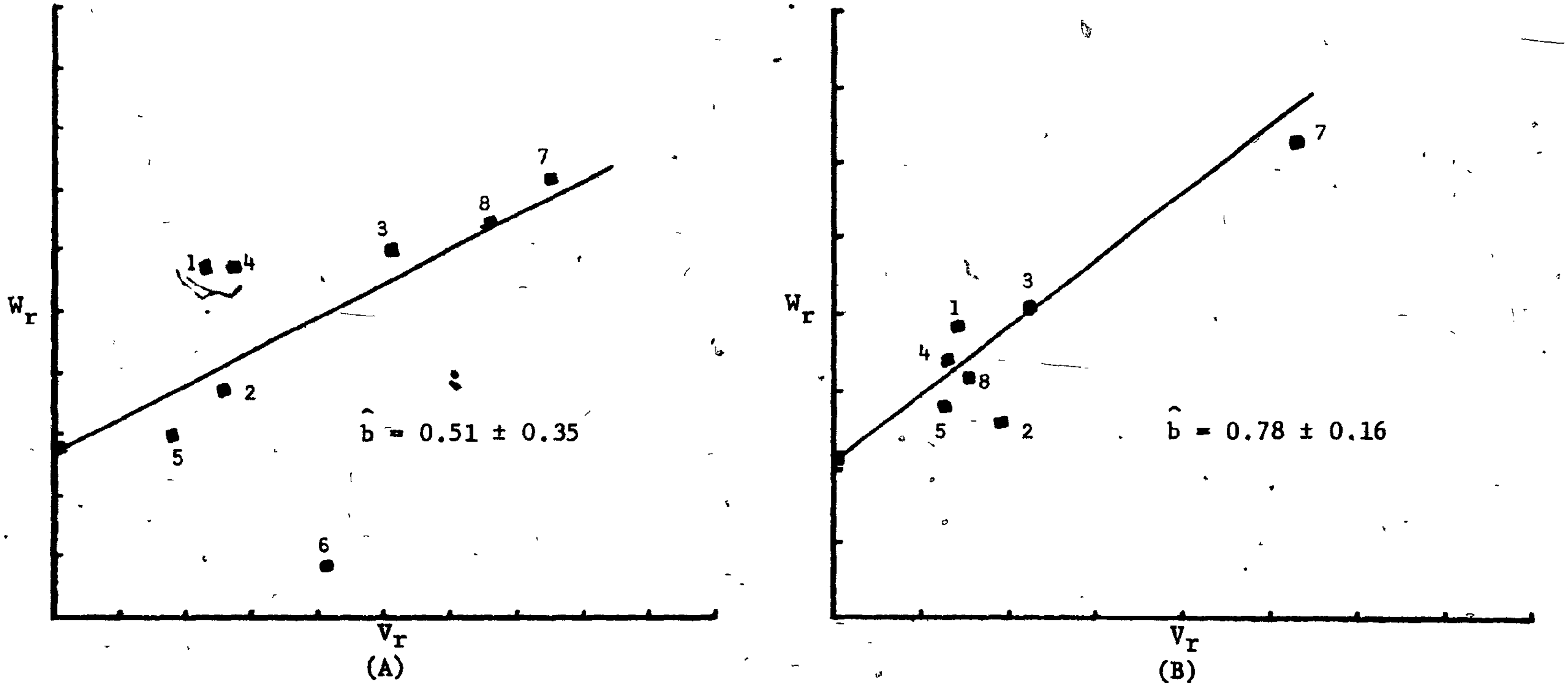
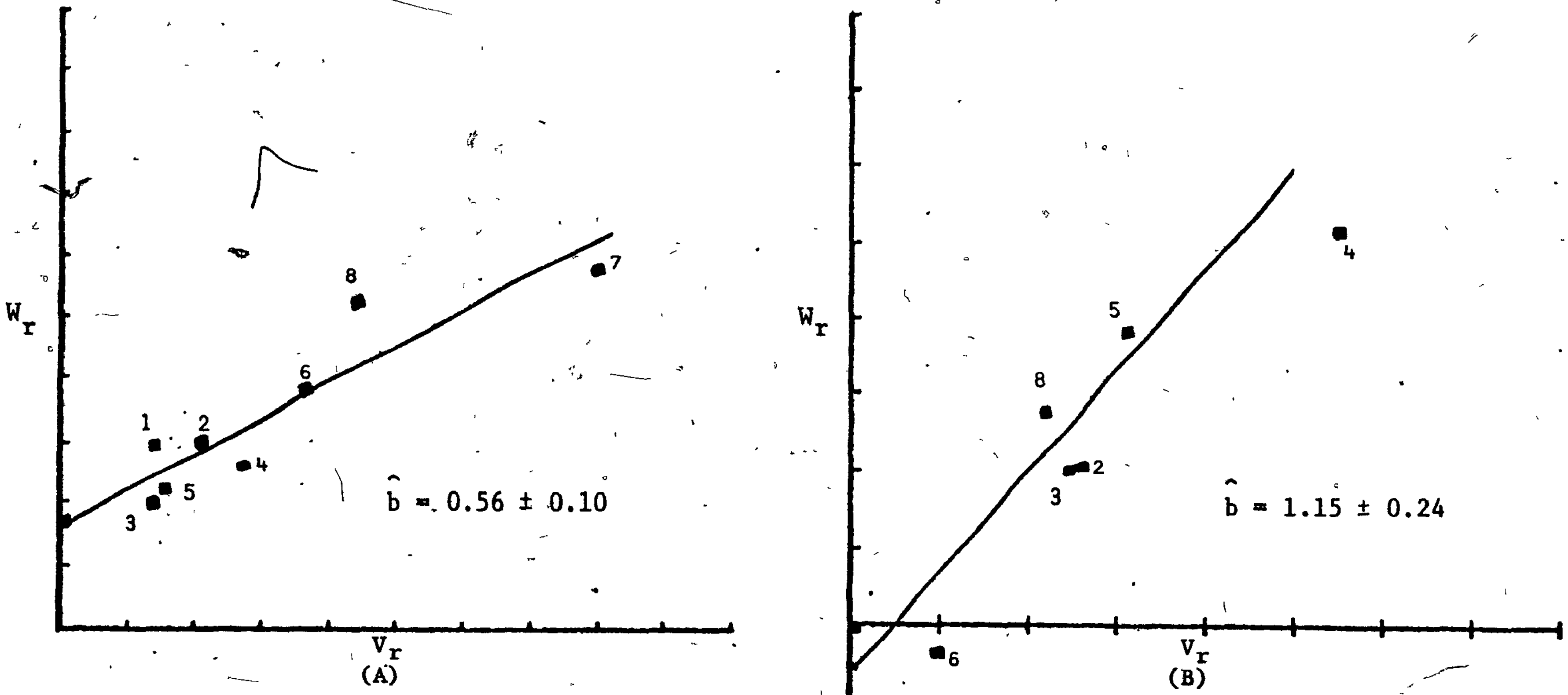


Figure 12. V_r, W_r graphs for number of panicles per plant in the F_1 generation from a diallel cross in *Avena sativa* L. (A) all parents are included. (B) epistatic parent 6 is excluded.

indicating partial dominance and these results were in agreement with those reported earlier (Table 7). Parents 5 and 7 maintained their positions in both graphs, with parent 5 carrying the most dominant alleles and parent 7 carrying the most recessive ones. Other ~~parents,~~ particularly after correcting for the epistatic effect (Figure 12B), had more dominant than recessive genes. In the F_2 generation (Figure 13A), the regression coefficient differed significantly from unit slope (b = 0.56), as shown in Figure 13A. Although all parents were close to the regression line, parents 1 and 7 showed the highest and lowest $W_r - V_r$ values (Appendix Table 12), suggesting non-allelic interaction. Omitting these two parents improved the graphical relationship (b = 1.15, Figure 13B), and removed the failure of the assumptions required for the genetic analysis. Over-dominance is shown in Figure 13B, from the negative intercept of the regression line with the W_r axis. These results are ~~also~~ in full agreement with those reported earlier from the Jinks-Hayman analysis (Table 7). The order of points along the regression line differs in Figure 13A and B; although parent 3 maintained its position, parents 4 and 6 changed places in the two graphs. This difference of order may be a reflection of the epistatic effects of parents 1 and 7, or it may be that too much importance cannot be attached to the finer details of order of points along the line.

The second yield component, number of grains per panicle, appeared to satisfy all the genetical assumptions in both generations



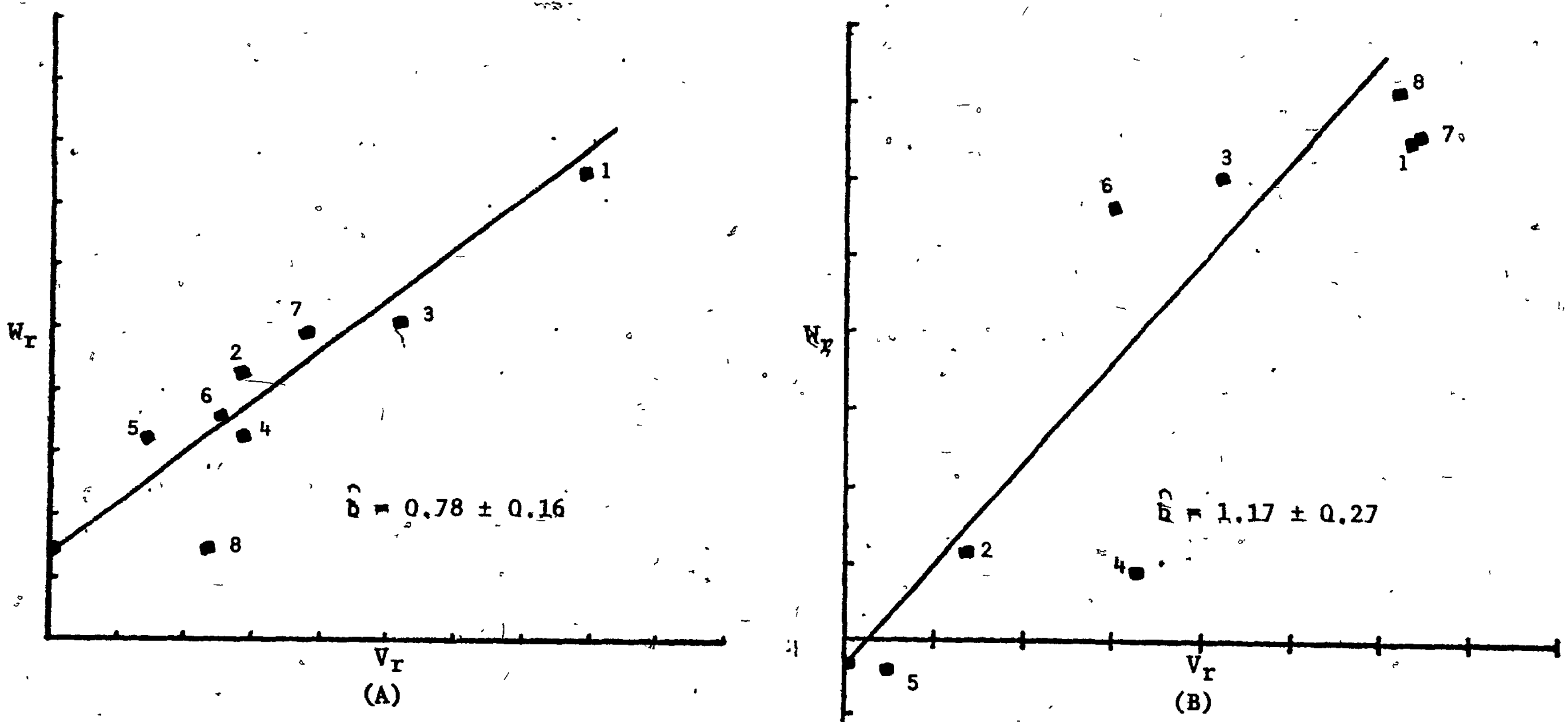
(A)

(B)

Figure 13. V_r, W_r graphs for number of panicles per plant in the F_2 generation from a diallel cross in Avena sativa L. (A) all parents are included. (B) epistatic parents 1 and 7 are excluded.

without the complications of the non-allelic interaction. The V_r, W_r graphs show regression lines with a slope not significantly different from 1 (Figure 14A, B). The regression line intercepts the W_r axis above the origin in the F_1 generation, suggesting partial dominance, while it intercepts the W_r axis below the origin, indicating overdominance in the F_2 generation. Results from the graphical analysis were in full agreement with that found earlier from the Jinks-Hayman analysis (Table 7), for both generations. The order of parents along the regression lines differs from the F_1 to the F_2 generation. Such differences in order may be due, in part, to genetic segregation and/or gene linkage in the F_2 generation. Although parents 5 and 1 had almost the same order in both generations, with parent 5 carrying most of the dominant alleles and parent 1 carrying most of the recessive alleles, parents 8 and 6 changed their order along the regression line according to the generation involved.

The slope of the regression line (Figure 15A) for the third yield component, 1000-grain weight in the F_1 generation, is significantly below unit slope ($b = 0.01$), indicating epistasis and/or gene correlation. Excluding the parents contributing to non-allelic interaction (parents 1, 2 and 6) improved the b W_r/V_r value (Figure 15B). Partial dominance is indicated from the position of the regression line above the origin, and it is clear that parent 7 with its low V_r, W_r carries most dominant alleles, while parent 3 (after correcting for epistatic effects) had the most recessive



(A)

(B)

Figure 14. V_r, W_r graphs for number of grains per panicle in the F_1 (A) and F_2 (B) generations from a diallel cross in *Avena sativa* L.

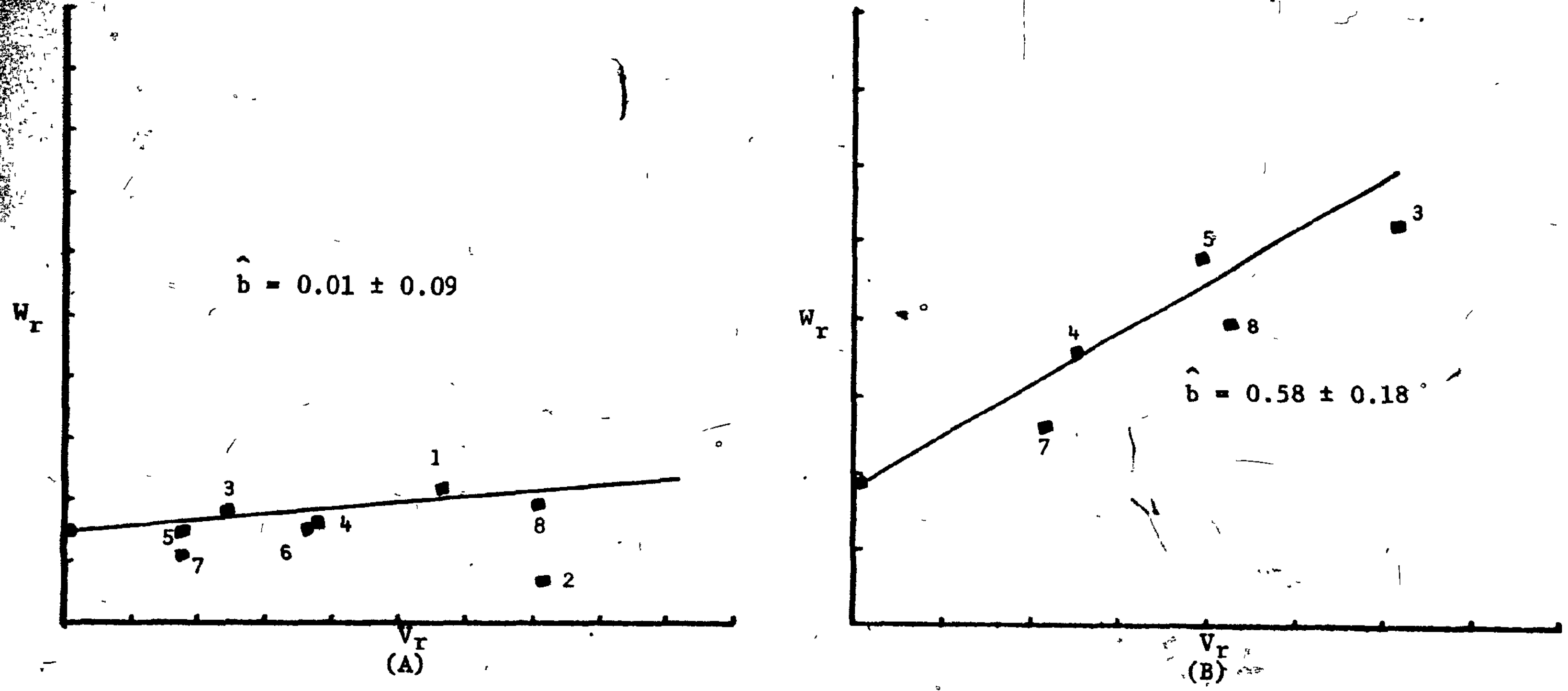


Figure 15. V_r, W_r graphs for 1000-grain weight in the F_1 generation from a diallel cross in *Avena sativa* L. (A) all parents are included. (B) epistatic parents 1, 2 and 6 are excluded.

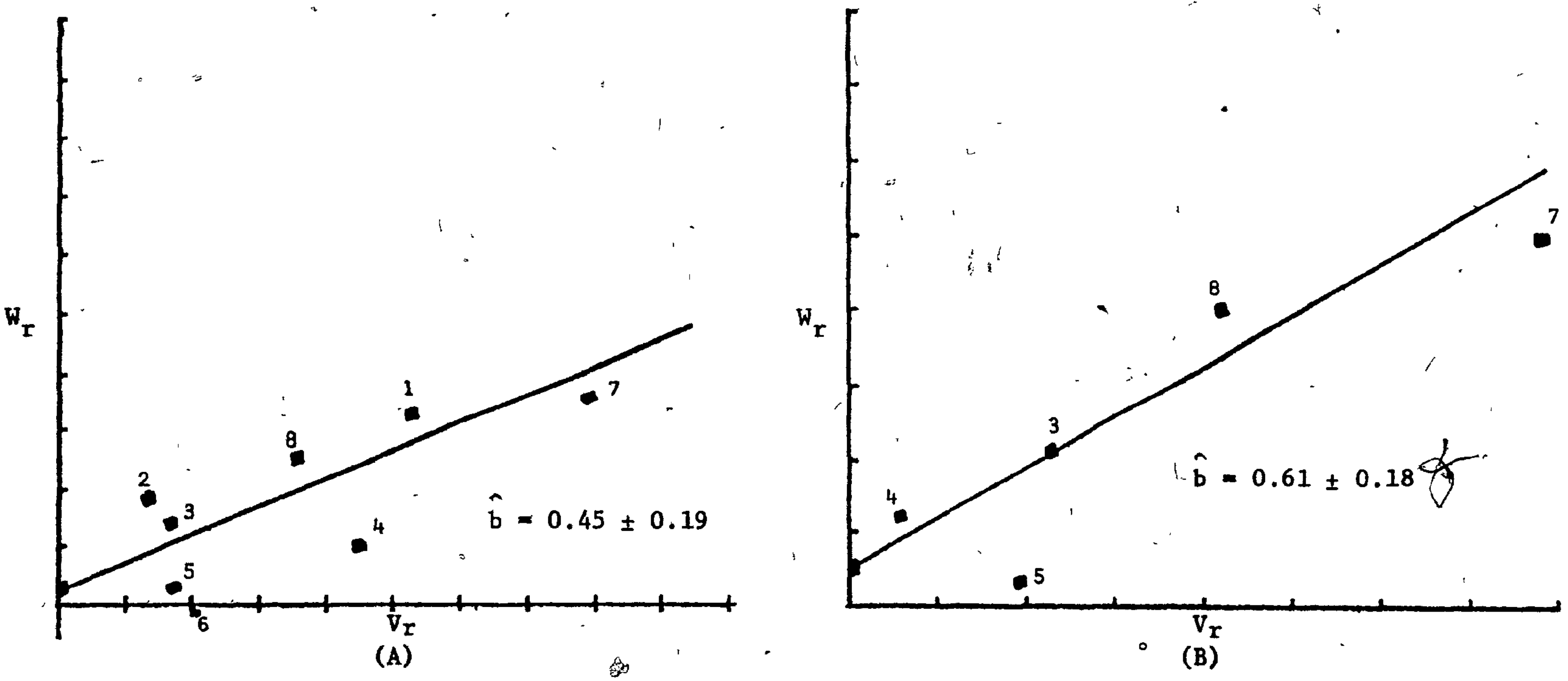


Figure 16.. V_r, W_r graphs for 1000-grain weight in the F_2 generation from a diallel cross in *Avena sativa* L. (A) all parents are included. (B) epistatic parents 1, 2 and 6 are excluded.

alleles. The same failure of the assumptions required for the genetical model was observed in the F_2 generation (Figure 16A). The regression line differed significantly from unit slope (b = 0.45), and eliminating the epistatic parents (1, 2 and 6) resulted in a regression line not significantly different from 1 (Figure 16B). The regression line cuts the W_r axis near the origin, indicating partial or near complete dominance. The order of parents along the regression line differed significantly from that in the F_1 generation and was almost in complete contrast. Because 1000-grain weight was the character in the present study most affected by non-allelic interaction and/or gene correlation, as indicated in Tables 3 and 7, and because of the high environmental influence on this character, one might conclude that too much importance cannot be attached to the finer details of order of dominance along the regression line. Also, the interpretation of the genetic components and/or ratios for this character should be treated with care, at least with the genotypes involved in the present study. Such a conclusion is in full agreement with that reported by Sampson and Tarumoto (1976) in oats.

2. Variance components, heritability and genetic advances

Quantitative characters are controlled by both genetic and environmental effects. The genetic effects are due to breeding value (additive), dominance, and epistatic effects. The breeding value of an individual for a given trait is the sum of the average effects of the genes it carries, the summation being made over the pair of alleles at each locus and over all loci (Falconer, 1967). Dominance deviation, or the intra-allelic interaction, is the interaction between alleles at the same locus while epistatic deviation, or the inter-allelic interaction, is the interaction between alleles at different loci.

Selection in a given population is based on the phenotype of individuals, while only a portion of the phenotypic value is transmitted to the following generation. A phenotype results from a pattern of development directed by a genotype and conditioned by environment. Thus, it is of primary importance for the plant breeder to know the relative magnitudes of the different components of the phenotypic value. Additive and non-additive variance estimates, together with genetic, environmental, and phenotypic variance estimates, calculated in the F_1 and F_2 generations for nine characters in the present study, are shown in Tables 8 and 9, respectively. These estimates were calculated by two different methods as described earlier: from the Griffing's (1956b) analysis as described by Kempthorne and Curnow (1961), and from the Jinks-Hayman (1953) analysis as described by Crumpacker and Allard (1962). These two methods of calculation are designated as method A and method B, respectively, in Tables 8 and 9. Estimates of the additive genetic variance calculated by the Griffing's analysis (Method A) were higher than the corresponding non-additive genetic variance for all

TABLE 8. Estimates of the variance components for 9 characters in oats based on two different methods of calculation in the F_1 generation

Character	Base§	σ^2_A	σ^2_A †	σ^2_{NA}	σ^2_{NA} †	σ^2_G	σ^2_G †	σ^2_E	σ^2_E †	σ^2_P	σ^2_P †
Protein per cent	(A)	2.90	–	0.25	–	3.15	–	0.22	–	3.37	–
	(B)	0.90	1.04	0.70	0.57	1.60	1.61	0.78	0.82	2.38	2.43
Oil per cent	(A)	1.40		0.03		1.43		0.05		1.48	
	(B)	0.87		−0.09=0		0.87		0.18		1.06	
Hull per cent	(A)	2.38		0.29		2.67		0.33		3.00	
	(B)	0.87		0.60		1.47		1.31		2.78	
Plant height	(A)	337.72		7.47		345.19		4.61		349.80	
	(B)	76.02		86.53		162.55		17.03		179.58	
Heading date	(A)	14.38	–	2.09	–	16.47	–	0.48	–	16.95	–
	(B)	10.98	12.83	0.51	−1.07=0	11.49	12.83	1.94	1.72	13.43	14.55
Grain yield/plant	(A)	2.86		1.02		3.88		0.87		4.75	
	(B)	2.23		0.01		2.24		3.69		5.93	
No.of panicles/plant	(A)	0.38	–	0.12	–	0.50	–	0.34	–	0.84	–
	(B)	1.15	1.06	−0.74=0	−0.47=0	1.15	1.06	1.60	1.28	2.75	2.34
No.of grains/panicle	(A)	129.22		15.73		144.95		10.83		155.78	
	(B)	51.21		26.39		77.60		40.19		117.79	
1000-grain weight	(A)	5.32	–	2.49	–	7.81	–	0.51	–	8.32	–
	(B)	1.21	2.52	3.22	−0.36=0	4.43	2.52	3.16	2.72	7.59	5.24

§ A and B are the variance components estimates calculated from Griffing's and Jinks-Hayman diallel analyses, respectively.

† Estimates after omitting the epistatic parent(s).

– Not calculated.

TABLE 9. Estimates of the variance components for 9 characters in oats based on two different methods of calculation in the F_2 generation

Character	Base§	σ^2_A	σ^2_A †	σ^2_{NA}	σ^2_{NA} †	σ^2_G	σ^2_G †	σ^2_E	σ^2_E †	σ^2_P	σ^2_P †
Protein per cent	(A)	1.96		0.32		2.28		0.18		2.46	
	(B)	0.93		0.95		1.88		0.67		2.55	
Oil per cent	(A)	0.98	-	0.21	-	1.19	-	0.04	-	1.23	-
	(B)	0.87	1.02	0.43	0.45	1.30	1.47	0.14	0.14	1.44	1.61
Hull per cent	(A)	1.22		0.29		1.51		0.38		1.89	
	(B)	0.84		1.60		2.44		1.41		3.85	
Plant height	(A)	243.44	-	19.13	-	262.57	-	7.57	-	270.14	-
	(B)	73.58	36.90	199.45	22.34	273.03	59.24	26.80	23.00	299.83	82.24
Heading date	(A)	15.08	-	5.71	-	20.79	-	1.13	-	21.92	-
	(B)	10.48	11.48	25.07	16.64	35.55	28.12	3.94	3.51	39.49	31.63
Grain yield/plant	(A)	2.28		0.59		2.87		1.05		3.92	
	(B)	2.07		1.38		3.45		4.32		7.77	
No.of panicles/plant	(A)	1.94	-	0.42	-	2.36	-	0.35	-	2.71	-
	(B)	1.13	0.63	0.88	-0.28=0	2.01	0.63	1.67	1.68	3.68	1.31
No.of grains/panicle	(A)	45.14		28.96		74.10		12.84		86.94	
	(B)	49.73		93.20		142.93		46.12		189.05	
1000-grain weight	(A)	2.78	-	1.25	-	4.03	-	0.59	-	4.62	-
	(B)	1.35	2.46	4.54	2.74	5.89	5.20	2.60	2.99	8.49	8.19

§ A and B are the variance component estimates calculated from Griffing's and Jinks-Hayman diallel analyses, respectively.

† Estimates after omitting the epistatic parent(s).

\- Not calculated.

characters in both generations. The same trend was observed with the Jinks-Hayman analysis (method B) for all characters, except for plant height and 1000-grain weight in the F_1 generation, and for hull per cent, plant height, heading date, number of grains per panicle, and 1000-grain weight in the F_2 generation.

It should be emphasized that the components in Tables 8 and 9 were calculated assuming no epistatic effects. In the presence of epistasis, the expectation for $\hat{\sigma}^2_{gca}$ would be (Matzinger and Kempthorne, 1956):

$$\hat{\sigma}^2_{gca} = 1/2\ \hat{\sigma}^2_{A} + 1/4\ \hat{\sigma}^2_{AA} + 1/8\ \hat{\sigma}^2_{AAA} \ \ldots$$

and such a situation would result in different variance component estimates from those mentioned in Table 1. The validity of this assumption was tested roughly through the graphical analysis, bearing in mind its limitations. Nassar (1965) showed through computer simulation that correlated gene distribution results in the regression of W_r on V_r being almost consistently less than unity and the intercept on the W_r axis predominantly below the origin, thus simulating the presence of epistasis and overdominance, respectively. The seriousness of such a situation increases with a decreasing number of parents. Elimination of the parent(s) contributing to non-allelic interaction resulted in higher additive genetic values than non-additive in both generations (Tables 8 and 9). Moreover, elimination of the epistatic parents resulted in negative estimates of the non-additive variance components for heading date, number of panicles per plant and 1000-grain weight in the F_1 generation, and for number of panicles per plant in the F_2 generation. These negative estimates of the non-additive genetic variance were reasonably considered to be zero.

Genetic variance estimates in the F_1 and F_2 generation were higher than the environmental estimates for all characters based on the two methods of calculation, except for grain yield in the F_2 generation. This indicates that the genetic variance component comprises the major proportion of the phenotypic variance component for all characters involved in the present investigation, and suggests that a genetic improvement for these characters in early generations should be effective. However, for characters showing epistatic effects, such a conclusion should be taken with more caution.

Phenotypic variance estimates, as well as genetic and environmental variance estimates, varied according to the method of estimation and the generation involved. In the F_1 generation, phenotypic variance components calculated by the Griffing's analysis (method A) were relatively higher than those calculated by the Jinks-Hayman analysis (method B) for all characters, except for grain yield per plant and number of panicles per plant. In the F_2 generation, the second method resulted in higher phenotypic variance estimates than the first one with all characters. Although such differences existed between the two methods of variance component estimates in the F_1 and F_2 generations, they had, in general, the same order for all characters in both generations, with plant height having the highest estimates and oil per cent and number of panicles per plant having the lowest estimates.

Progress under selection breeding programs depends on: (a) the magnitude of the genetic variation in the population, and (b) the extent to which this variation is responsible for the phenotypic variation. It would be interesting for the plant breeder to compare the characters with respect to (a) and (b), as well as to (c) the resulting expected genetic advance from selection, and (d) the sensitivity to environmental changes. These are usually estimated by: σ^2_G, $H = \sigma^2_G/\sigma^2_P$, $G_s = K.\sigma_P H$, and σ^2_{GE}, respectively. H refers to heritability in the broad sense,[1] and describes the proportion of phenotypic variance caused by genetic differences. σ^2_P represents the sum of σ^2_G and σ^2_E. G_s is referred to as expected genetic advance from selection, with K assuming different values, depending on the percentage of the population selected (e.g., for 5% $K = 2.06$). Since characters differ in their mean values and scales of measurement, (a) and (c) will be expressed as:

$$\frac{\sqrt{\sigma^2_G}}{\bar{X}} \times 100 \quad \text{and} \quad \frac{G_s}{\bar{X}} \times 100$$

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[1] This applies only to selection among sexually propagated clones or homozygous genotypes. In the case of segregating populations, the advance from selection as well as the choice of the breeding schemes depends on the relative magnitude of the components of σ^2_G to one another and to σ^2_P.

prior to comparisons and referred to here, for convenience, as "genetic coefficient of variation" (GCV) (Burton, 1952; Johnson et al., 1955) and "relative genetic advance from selection" (RG_s).

Estimates of heritability percentages, G_s, RG_s, and GCV for nine characters in oats in the F_1 and F_2 generations are presented in Tables 10 and 11, respectively. In general, heritability estimates calculated from the Griffing's analysis are higher than those from the Jinks-Hayman analysis. Broad sense heritability estimates are also higher than the corresponding narrow sense estimates for all characters in both generations, except for oil per cent, grain yield, and number of panicles per plant in the F_1 generation where broad and narrow sense heritability estimates were equal, as calculated from method B. This is due to the high additive genetic variance or the very low non-additive genetic variance involved in the inheritance of these characters as shown in Table 8. Although the two methods of calculation differed in their heritability estimates, a regular pattern was observed for all characters. In general, oil per cent, plant height, heading date, and number of grains per panicle showed the highest heritability estimates, while 1000-grain weight and grain yield had the lowest values in both generations.

Heritability is useful for comparing traits as to their usefulness as aids to selection. Situations often arise when a plant breeder selecting for a character such as grain yield has to pick a limited number of plants from his population for further progeny tests.

TABLE 10. Estimates of narrow (N.S.) and broad sense (B.S.) heritabilities, expected genetic advance from selection (G_s), relative expected genetic advance from selection (RG_s) and genetic coefficient of variation (GCV) for 9 characters in oats based on two different methods of calculation in the F_1 generation

Character	Base§	Heritability				G_s		RG_s		GCV	
		N.S.		B.S.							
			†		†		†		†		†
Protein per cent	(A)	86	–	93	–	3.52	–	25.85	–	12.54	–
	(B)	38	43	67	66	2.13	2.12	15.14	15.24	8.99	9.12
Oil per cent	(A)	95		97		2.43		35.33		17.38	
	(B)	82		82		1.74		25.30		13.56	
Hull per cent	(A)	79		89		3.18		12.43		6.39	
	(B)	31		53		1.82		7.12		4.74	
Plant height	(A)	96		98		37.51		39.84		19.73	
	(B)	42		91		25.12		27.19		13.80	
Heading date	(A)	85	–	97	–	8.23	–	13.52	–	6.67	–
	(B)	82	88	86	88	6.49	6.91	10.94	12.18	5.71	6.31
Grain yield/plant	(A)	60		81		3.64		41.99		22.74	
	(B)	38		38		1.90		23.38		18.42	
No.of panicles/plant	(A)	45	–	59	–	1.11	–	15.80	–	10.02	–
	(B)	42	45	42	45	1.43	1.42	21.24	22.27	15.93	16.15
No.of grains/panicle	(A)	83		93		23.91		49.55		24.95	
	(B)	43		66		14.76		32.04		19.12	
1000-grain weight	(A)	64	–	94	–	5.58	–	20.54	–	10.28	–
	(B)	16	48	58	48	3.29	2.26	11.69	8.08	7.48	5.68

§ A and B are the estimates calculated from Griffing's and Jinks-Hayman diallel analyses, respectively.

† Estimates after omitting the epistatic parent(s).

– Not calculated.

TABLE 11. Estimates of narrow (N.S.) and broad sense (B.S.) heritabilities, expected genetic advance from selection (G_s), relative expected genetic advance from selection (RG_s) and genetic coefficient of variation (GCV) for 9 characters in oats based on two different methods of calculation in the F_2 generation

Character	Base§	Heritability				G_s		RG_s		GCV	
		N.S.		B.S.							
			†		†		†		†		†
Protein per cent	(A)	80		93		3.00		21.23		10.67	
	(B)	36		74		2.43		17.03		9.61	
Oil per cent	(A)	80	-	97	-	2.22	-	32.21	-	15.85	-
	(B)	60	63	90	91	2.22	2.78	33.61	43.56	17.26	19.00
Hull per cent	(A)	65		80		2.27		8.87		4.81	
	(B)	22		63		2.55		9.95		6.09	
Plant height	(A)	90	-	97	-	32.84	-	34.89	-	17.21	-
	(B)	25	45	91	72	32.46	13.45	34.92	13.88	17.77	7.94
Heading date	(A)	69	-	95	-	9.16	-	15.05	-	7.49	-
	(B)	27	36	90	89	11.65	10.31	19.75	18.21	10.10	9.36
Grain yield/plant	(A)	58		73		2.98		34.38		19.56	
	(B)	27		44		2.53		30.62		22.48	
No.of panicles/plant	(A)	71	-	87	-	2.95	-	41.84	-	21.79	-
	(B)	31	48	55	48	2.17	1.13	30.67	17.36	20.03	12.19
No.of grains/panicle	(A)	52		85		16.33		33.83		17.84	
	(B)	26		76		21.53		46.38		25.75	
1000-grain weight	(A)	60	-	87	-	3.85	-	14.17	-	7.38	-
	(B)	16	30	69	63	4.14	3.71	15.03	13.77	8.81	8.46

§ A and B are the estimates calculated from Griffing's and Jinks-Hayman diallel analyses, respectively.

† Estimates after omitting the epistatic parent(s).

- Not calculated.

For example, if grain yield happens to be correlated with another character the breeder can pick his plants with respect to this character rather than purely at random, thus increasing the probability of picking superior genotypes. The character with high heritability[1] would be more useful in this respect. Results from the present study agree with those of many other reports in oats (Brown et al., 1974; Chae and Forsberg, 1975; Johnson and Frey, 1967; Ohm and Patterson, 1975; Petr and Frey, 1966; Sampson and Tarumoto, 1976).

The genetic advance from selection depends on the heritability estimate, the magnitude of phenotypic variance in the population, and the proportion selected. Consequently, high heritability estimates do not imply pronounced progress from selection if the phenotypic variance is small. In order to determine the validity of selection, expected genetic advance should be obtained. Expected genetic advance (G_s) and its per cent of the mean (RG_s), based on selecting the best 5 per cent for nine characters in the F_1 and F_2 generations in oats are shown in Tables 10 and 11.

Regardless of the method of estimation, G_s and RG_s were, in general, higher for all characters in both generations when calculated by Griffing's analysis than by the Jinks-Hayman analysis. Plant

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[1] An H value near 100 indicates that the phenotype is a good index of genotypic merit and that genetic gains can be made easily by selection, but an H value near zero indicates that the phenotype is a poor index of genotypic merit and that genetic gains from selection will be difficult (Johnson and Frey, 1967).

height and number of grains per panicle showed the highest G_s values, while oil per cent and number of panicles per plant had relatively the lowest values in both generations. This does not directly imply that selection for plant height and number of grains per panicle would be more efficient than for other characters in early generations, due to the fact that such characters differ widely in their mean values and scales of measurement. It is clear from Tables 10 and 11 that characters such as oil per cent, grain yield and number of panicles per plant, which have a relatively low G_s, have high RG_s values in both generations. This is due, as mentioned above, to the lower mean values for these characters and higher heritability and/or phenotypic variance.

The genetic coefficient of variation (Tables 10 and 11) differed according to the method of calculation and, in general, oil per cent, plant height, grain yield, number of panicles per plant and number of grains per panicle had a relatively high GCV. Protein per cent, hull per cent, heading date, and 1000-grain weight showed a relatively low GCV. On the basis of the relatively high H, RG_s and GCV, one might conclude that pronounced progress should be expected from selection for oil per cent, plant height, number of panicles per plant and number of grains per panicle in early generations. Moderate progress from selection in early generations should be expected with protein per cent, hull per cent, heading date and grain yield. Less genetic advance should be expected from selection in early generations for 1000-grain weight. However, such a conclusion will not hold for a character that is highly affected by the presence of non-allelic interaction, and more complex breeding procedures such as a progeny test are needed for more efficient gain from selection.

In conclusion, one can say that on the basis of the high additive variance revealed by both the Griffing and the Jinks-Hayman analysis, as well as the high heritability and genetic coefficients of variation, pronounced genetic improvement in oats could be obtained with little or no difficulty by using the most simple breeding programs, such as choosing parents phenotypically and mating the best with the best. However, with the characters affected seriously by epistasis, such as heading date, number of panicles per plant and 1000-grain weight, a more complex breeding program, such as choosing parents by progeny testing, will be necessary to achieve maximum genetic advance in oats.

It must be emphasized that this analysis gives information only about those genes which control the nine characters involved in the present investigation, and which are segregating in this group of crosses. It provides no information about the genes in entirely different parents which could be brought in to affect these characters, nor about any of the other characters which may be of importance in a breeding program.

3. Phenotypic, genetic and environmental correlations

Associations between plant characters are of considerable value in breeding programs. When two characters are linearly covariated, the underlying genetic system causing such association may be due to linkage or pleiotropy (Mode and Robinson, 1959). The phenotypic correlation is a linear combination of genetic and environmental correlations. However, the proportion to which genetic and environmental correlations make up the phenotypic correlations is of considerable interest to the breeder, and is variable depending on the magnitude of the heritabilities of both traits.

Estimates of the phenotypic, genetic, and environmental correlation coefficients for nine characters in the F_1 and F_2 generations are shown in Tables 12 and 13, respectively. In the F_1 or F_2 generations, the degrees of freedom required for testing the non-existence of phenotypic and environmental correlations were determined by subtracting one from each of the genotypes and the experimental error degrees of freedom, respectively. Although accurate tests of significance of the genetic correlations have not yet been developed, a rough test was used as described by Dyck and Baker (1975). In this method, standard deviations of genetic correlations were calculated by methods described by Mode and Robinson (1959), and a genetic correlation was considered to be significant if its absolute value exceeded twice its standard deviation.

TABLE 12. Phenotypic (r_P), genetic (r_G), and environmental (r_E) correlation coefficients among 9 characters in the F_1 generation of an 8-parent diallel cross in oats

Character		Oil%	Hull%	Plant height	Heading date	Grain yield/ plant	No.of panicles/ plant	No.of grains/ panicle	1000-grain weight
Protein %	r_P (a)	-0.34	0.29	0.27	-0.57**	-0.73**	-0.15	-0.75**	0.15
	r_G (b)	-0.35	0.32	0.28	$\underline{-0.59}$	$\underline{-0.87}$	-0.17	$\underline{-0.78}$	0.18
	r_E (c)	-0.32**	-0.03	-0.16	-0.24*	-0.25*	-0.10	-0.24*	-0.20
Oil %	r_P		-0.59**	0.46*	0.65**	0.51**	0.72**	-0.02	0.46*
	r_G		$\underline{-0.63}$	$\underline{0.46}$	$\underline{0.66}$	$\underline{0.59}$	$\underline{0.86}$	-0.02	$\underline{0.49}$
	r_E		-0.10	0.28**	0.35**	-0.01	0.01	0.03	0.13
Hull %	r_P			-0.54**	-0.15	-0.53**	-0.41*	-0.21	-0.46*
	r_G			$\underline{-0.56}$	-0.16	$\underline{-0.56}$	$\underline{-0.46}$	-0.21	$\underline{-0.48}$
	r_E			-0.32**	-0.04	-0.36**	-0.25*	-0.22*	-0.24*
Plant height	r_P				-0.01	0.21	0.39*	-0.19	0.56**
	r_G				-0.01	0.21	$\underline{0.46}$	-0.19	$\underline{0.58}$
	r_E				0.49**	0.32**	0.11	0.25*	0.11
Heading date	r_P					0.53**	0.40*	0.37*	-0.06
	r_G					$\underline{0.61}$	$\underline{0.51}$	$\underline{0.39}$	-0.06
	r_E					-0.08	-0.25*	0.03	0.03
Grain yield/ plant	r_P						0.55**	0.71**	0.14
	r_G						$\underline{0.49}$	$\underline{0.74}$	0.12
	r_E						0.75**	0.53**	0.27*
No.of panicles/ plant	r_P							-0.14	0.32
	r_G							-0.18	0.36
	r_E							0.02	0.19
No.of grains panicle	r_P								-0.27
	r_G								-0.30
	r_E								0.16

*, ** Significant at the .05 and 0.01 probability levels, respectively.

(a) Significant values are 0.37 and 0.48 for the 0.05 and 0.01 probability levels, respectively, for 26 dF.

(b) The underlined genetic correlation coefficients differ significantly from zero.

(c) Significant values are 0.22 and 0.28 for the 0.05 and 0.01 probability levels, respectively, for 81 dF.

TABLE 13. Phenotypic (r_P), genetic (r_G), and environmental (r_E) correlation coefficients among 9 characters in the F_2 generation of an 8-parent diallel cross in oats

Character		Oil %	Hull %	Plant height	Heading date	Grain yield/ plant	No.of panicles/ plant	No.of grains/ panicle	1000-grain weight
Protein %	r_P (a)	-0.31	0.35	0.18	-0.52**	-0.55**	-0.04	-0.65**	0.11
	r_G (b)	-0.32	0.40	0.20	-0.53	-0.63	-0.06	-0.68	0.12
	r_E (c)	-0.19	-0.05	-0.26*	-0.30**	-0.21	-0.09	-0.43**	0.02
Oil %	r_P		-0.52**	0.48**	0.72**	0.72**	0.84**	-0.05	0.33
	r_G		-0.57	0.48	0.74	0.84	0.93	-0.06	0.36
	r_E		-0.06	0.25*	0.24*	0.08	0.01	0.01	0.08
Hull %	r_P			-0.38*	-0.14	-0.64**	-0.57**	-0.14	-0.45*
	r_G			-0.42	-0.15	-0.83	-0.69	-0.20	-0.48
	r_E			0.08	-0.10	0.10	0.04	0.18	-0.32**
Plant height	r_P				0.05	0.45*	0.47*	-0.10	0.49**
	r_G				0.04	0.49	0.51	-0.13	0.53
	r_E				0.19	0.32**	0.11	0.32**	0.15
Heading date	r_P					0.59**	0.43*	0.32	0.04
	r_G					0.70	0.51	0.34	0.05
	r_E					-0.02	-0.18	0.06	-0.04
Grain yield/ plant	r_P						0.62**	0.47*	0.45*
	r_G						0.62	0.47	0.57
	r_E						0.65**	0.53**	-0.04
No.of panicles/ plant	r_P							-0.35	0.58**
	r_G							-0.42	0.72
	r_E							0.12	-0.12
No.of grains/ panicle	r_P								-0.24
	r_G								-0.25
	r_E								-0.15

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

(a) Significant values are 0.37 and 0.48 for the 0.05 and 0.01 probability levels, respectively for 26 dF.

(b) The underlined genetic correlation coefficients differ significantly from zero.

(c) Significant values are 0.22 and 0.28 for the 0.05 and 0.01 probability levels, respectively for 81 dF.

In general, correlations in the F_1 generation agreed with those found in the F_2 and genetic correlation coefficients were higher than the corresponding phenotypic coefficients in most cases, but the two types of correlation were similar in sign in all cases, indicating that significant phenotypic correlations were due to genetic causes in most associations. The environmental correlations in the present study were, in most cases, lower in magnitude than either phenotypic or genetic correlations, but were similar in sign in most cases, indicating that the associated characters were influenced by environmental conditions in the same direction. Many reports from different crops provide evidence of the comparatively higher value of genotypic than phenotypic correlations (Wallace et al., 1954, in oats; Dyck and Baker, 1975, in wheat; Johnson and Aksel, 1964, in barley; Weber and Moorthy, 1952, in soybeans).

Protein percentage was negatively and significantly correlated with heading date, grain yield per plant, and number of grains per panicle, while the correlation coefficients between protein percentage and the other characters were low in magnitude and non-significant in both generations (Tables 12 and 13). In the F_2 generation, a significant but low genetic correlation coefficient (0.40) was found between protein percentage and hull per cent. Such a relationship is unreasonable and data from the F_1 generation are more indicative. The negative correlation between protein percentage and heading date is of importance to oat breeders and indicates that it should be possible to breed for an early maturing cultivar with a high level of grain protein, but since both characters are highly influenced by environmental conditions, and in the opposite direction, one might conclude that to obtain such improvement in protein per cent and heading date optimum environmental conditions are required. Frey (1976) found that most correlations reported for groat-protein percentage with heading date, in oats, have been small and non-significant, and in wheat, Stuber et al. (1962) reported that phenotypic correlations between heading date and grain protein content were highly significant but were also too low for prediction purposes. The very high negative and significant correlations between protein percentage and both grain yield and its component, number of grains per panicle, in both generations, indicate that selection for higher levels of these characters might not be that easy to attain. Several reports in oats agreed with these results (Briggle et al., 1975; Brown et al., 1966; Burrows, 1974; Forsberg et al., 1974; Sraon et al., 1975), while Ohm and Patterson (1973b) reported that high levels of seed yield and protein per cent can be obtained with little difficulty in breeding oats.

The non-significant correlations between protein per cent and oil per cent, hull per cent, plant height, number of panicles per plant, or 1000-grain weight, are also very important in oat breeding programs, and indicate that the genetic and/or environmental factors determining the relationships between protein per cent and any of these characters are independent from one another. These results also suggest that it should be possible to obtain good quality oat cultivars (high in both protein and oil percentages, and low in hull per cent) with short stems and plump grains; both are desirable characters in most oat breeding programs. Environmental correlation coefficients between protein per cent and oil per cent, heading date, grain yield, and number of grains per panicle in the F_1 generation were significant but low in magnitude. In the F_2 generation, protein per cent showed significant environmental correlations with plant height, heading date and number of grains per panicle. The negative and significant environmental associations between protein per cent and any of the characters mentioned above in the F_1 or F_2 generations indicate that the two characters were influenced by the same environmental conditions, but in the opposite direction.

Phenotypic and genetic correlation coefficients between oil per cent and all other characters, except protein per cent and number of grains per panicle in the F_1 generation and protein per cent, number of grains per panicle, and 1000-grain weight in the F_2 generation were significant. Oil per cent was negatively correlated with hull per cent in both generations, indicating that selection for low hull per cent would increase oil content, while it was positively correlated with plant height, heading date, grain yield, number of panicles per plant and 1000-grain weight in the F_1 generation, and with plant height, heading date, grain yield, and number of panicles per plant in the F_2. The highly significant and positive genetic and phenotypic correlation coefficients between oil per cent and each of grain yield and its component, number of panicles per plant, in both generations, must be considered in oat improvement programs and suggests that selection for high yield combined with higher energy could be achieved without difficulty in oats. These results are in agreement with those reported by Baker and McKenzie (1972), Brown and Craddock (1972), Frey et al. (1975), and Klinck (1967). The positive and significant correlations between oil per cent and each of plant height and heading date in both generations may result in some difficulties for oat breeders in selecting for short and early maturing cultivars with high levels of oil. These associations may be due to pleiotropy or linkage. Lush (1948) and Lermer (1950) have suggested that if the genotypic correlation is due to pleiotropic genes, selection for two traits in the same direction will cause a negative change; simultaneous selection for two traits in opposite directions will cause a positive change in the genotypic correlations. If such a relationship between oil per cent and each of plant height and heading date is due to pleiotropy, it is unlikely a new combination of traits can be attained. On the other hand, if the genotypic correlations are due to linkage, it may be possible to break the linkage by breeding techniques such as mutagenesis or intercrossing segregating populations. Environmental correlation coefficients between oil per cent and each of plant height and heading date were lower than either phenotypic or genetic correlations. The positive and significant values of these environmental correlation coefficients indicate that these characters were affected by the environmental conditions in the same way.

Negative and significant phenotypic and genetic correlation coefficients were found between hull per cent and all other characters except protein per cent, heading date, and number of grains per panicle, in the F_1 generation and heading date and number of grains per panicle in the F_2 generation. The significant negative correlations between hull per cent and plant height in both generations indicate that short plants would produce grains with high hull content. Such an association is undesirable in oat breeding programs, but due to the fact that these negative associations were low in magnitude, one would expect that plant breeders could select for desirable levels of both characters without difficulty. The fact that O.T.184, which is the shortest cultivar, has a relatively low hull per cent (Table 4) may support such a conclusion. On the other hand, the significant negative correlations between hull per cent and each of grain yield and its components, number of panicles per plant and 1000-grain weight, indicates that breeding for high yielding cultivars could result in grains with low hull per cent and high feeding value. Significant negative environmental correlations occurred between hull per cent and each of plant height, grain yield and its three components in the F_1 generation, and between hull per cent and 1000-grain weight in the F_2 generation, indicating that these characters were influenced by environmental factors in the opposite direction.

In the present study, positive phenotypic and genetic correlations occurred between plant height and each of number of panicles per plant and 1000-grain weight in the F_1 generation, and between plant height and each of grain yield, number of panicles per plant and 1000-grain weight in the F_2 generation. Significant positive environmental correlation coefficients occurred between plant height and each of heading date, grain yield, and number of grains per panicle in the F_1 generation, while in the F_2 generation, both grain yield and number of grains per panicle were environmentally correlated with plant height. Although positive and significant phenotypic and genetic relationships occurred between plant height and each of grain yield and its two components, number of panicles per plant and 1000-grain weight, their low values suggest that it would be possible for oat breeders to select for short plants with high yielding ability. This conclusion was in contrast to that reported by many authors (Petr and Frey, 1966; Wallace et al., 1954), but is supported by the results of Kiesselbach et al. (1940).

Heading date was positively correlated with grain yield, number of panicles per plant, and number of grains per panicle in the F_1 generation, and with grain yield and number of panicles per plant in the F_2 generation. The genetic correlations were higher than the corresponding phenotypic correlations, indicating that it would be difficult for the plant breeder to combine the extremes of the characters, earliness and high yielding ability, in a single cultivar.

These results agreed with those reported by Johnson and Aksel (1964), but were in contrast to those reported by Lyrene and Shands (1975). The phenotypic and genetic correlations between heading date and 1000-grain weight were non-significant and very low in magnitude. The lack of association between the two characters could be attributed to the fact that the formation of the grain took place after the initiation of the panicle which was taken as an expression of heading date, while grain plumpness seemed to be dependent on conditions affecting translocation of synthesized materials into the grain. A negative environmental correlation occurred between heading date and number of panicles per plant in the F_1 generation, indicating that both characters were affected by the same environmental conditions in the opposite way. In the F_2 generation, the environment correlations between heading date and any of grain yield and its three components were non-significant.

Highly significant and positive associations were obtained between grain yield and each of number of panicles per plant and number of grains per panicle in the F_1 generation, while the three yield components showed highly significant and positive correlations with grain yield in the F_2 generation. The present association suggests that selection for the two yield components; number of panicles per plant and number of grains per panicle, which are genetically controlled by additive gene effects and are highly heritable (Tables 10 and 11), would result in yield improvement.

Several authors have agreed with these results, for example in oats (Petr and Frey, 1966; Sampson and Tarumoto, 1976), in wheat (Fonseca and Patterson, 1968), and in barley (Rasmusson and Cannell, 1970; Hsu and Walton, 1970). Petr and Frey (1966) found that head number per plant in oats was the most important component determining yield per plant. Likewise, Rasmusson and Cannell (1970) reported that selection for number of heads in barley reflected changes in grain yield that were similar to those observed when selection was for yield itself. Environmental correlation coefficients were positive and highly significant between grain yield and its three components in the F_1 generation, while it was not significant between grain yield and 1000-grain weight in the F_2 generation. This indicates that grain yield and its components, particularly number of panicles per plant and number of grains per panicle, were influenced by the same environmental factors in the same way.

Genetic and phenotypic correlations among the three yield components, number of panicles per plant, number of grains per panicle and 1000-grain weight, varied in magnitude and sign from one generation to another. Associations among the three yield components were non-significant in the F_1 generation, indicating that it should be possible to elevate grain yield through selection for its two components, number of panicles per plant and number of grains per panicle, which were highly correlated with grain yield, without affecting grain weight. In the F_2 generation, number of panicles per plant showed negative and significant genetic correlation with number of grains per panicle, while positive and significant phenotypic and genetic correlations were found between number of panicles per plant and 1000-grain weight. No association was found between number of grains per panicle and 1000-grain weight in either generation. Since the negative and significant genetic correlation coefficient between number of panicles per plant and number of grains per panicle was low in magnitude (less than 0.50) it should not be difficult to select for high levels of the three yield components in one plant. To obtain such high levels of yield components, selection must be practised under adequate environmental conditions.

It should be emphasized that the correlations observed apply only to the specific genotypes analyzed. The interrelationships might be quite different in other material in which different gene associations may exist, or in which the mean values of the characters under study are at levels different from those observed in the present study.

4. Prediction of promising genotypes and crosses for future generations

Breeding self-pollinated crops, such as oats, efficiently depends first on accurate identification of the hybrid combinations that have the potential of producing maximum improvement, and secondly on identifying, in the early generations, superior lines among the progeny of the most promising hybrids (Crumpacker and Allard, 1962). Thus, the important task for the breeder is to choose parents which will combine to give superior progeny. Several guidelines for parental choice have been used with some success in developing cultivars superior for highly heritable characters. However, if the character to be improved is not highly heritable, such as yield and protein per cent in the present study, the method of choosing superior parents is, at best, only moderately successful. The lack of precise methods for selecting parents is one of the reasons why few crosses ever result in the release of a new cultivar. If prediction of superior crosses could be based on some parental information, development of promising oat cultivars could be much more efficient than is now possible.

One of the main purposes of the present study in the F_1 and F_2 generations is to predict which crosses will give the best chance of finding, for each character, high manifestations which could subsequently be fixed in pure lines. On the basis of the genetic information provided by the various analyses discussed earlier in this investigation, predictions of potential crosses for producing superior progenies can be made. Array[1] means (Table 14), together with GCA effects (Table 15) and other information, have been used for this purpose. In Table 14, the eight parents have been assigned the

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[1] Array is defined as one genotype (parent) and all the crosses from it.

TABLE 14. Array means (parents are included), parental order of means, and parental order of dominance for nine characters in the F_1 and F_2 generations of a diallel cross in oats*

Character Parent	Protein %	Oil %	Hull %	Plant height	Heading date	Grain yield per plant	No. of panicles per plant	No. of grains per panicle	1000-grain weight
1. Q.0.64.31	13.25	6.63	24.83	95.25	58.47	9.02	5.95	55.76	29.50
	13.85	6.23	25.23	96.65	57.81	8.70	5.91	53.77	28.44
2. Q.0.58.22	13.85	6.72	25.31	95.80	55.31	8.33	6.75	45.35	29.77
	13.64	6.26	24.93	95.86	54.34	8.26	6.94	44.16	28.01
3. Ajax	14.45	6.54	26.27	98.10	57.94	7.19	6.04	43.07	28.25
	14.42	6.08	26.51	96.08	56.84	7.15	6.24	44.07	27.23
4. Clintland 64	15.11	5.79	25.94	87.60	54.69	5.95	5.94	39.39	27.33
	15.35	5.42	26.33	89.86	55.22	6.35	5.92	42.42	26.20
5. O.T.184	12.17	6.56	26.49	64.70	61.25	8.48	6.23	54.68	26.31
	13.06	6.05	26.10	68.83	61.63	7.79	6.02	51.96	26.32
6. P.I.269182	13.99	8.01	24.99	100.96	61.78	8.04	7.01	43.87	29.33
	14.41	7.67	25.24	103.12	61.06	9.50	8.09	44.92	28.59
7. C.I.3387	13.50	8.39	23.75	99.47	60.16	8.96	7.69	41.03	30.47
	14.15	7.45	24.47	96.53	60.16	9.26	8.43	41.64	28.79
8. Hinoat	15.93	6.42	26.82	86.60	55.88	5.83	6.31	32.24	29.69
	16.19	6.09	26.52	89.47	55.47	6.67	6.73	37.39	28.82
Grand mean	14.02	6.88	25.55	90.62	57.80	7.59	6.41	43.88	29.07
	14.42	6.34	25.68	91.76	57.13	7.86	6.75	44.58	27.89
Parental order of means	84362715	76215384	71624358	58412376	42831756	17526348	76285314	15263748	78216345
	84367125	67218354	72165438	58423716	24831765	67125384	76283541	15623478	87612354
Parental order of dominance	54183726	43285176	75213648	57628143	28431576	56872431	65214387	85462731	75364128
	24185673	24538167	45762318	56184237	28413567	25638417	35124687	54263178	25368417

*F_1 estimates are in the first row and F_2 estimates are in the second row for each character, respectively.

TABLE 15. Estimates of GCA effects of 8 parents of oats for 9 characters measured from the F_1 and F_2 generations (ranks in parentheses) and their L.S.D. among them†

Character / Parent	Protein %	Oil %	Hull %	Plant height	Heading date	Grain yield/ plant	No. of panicles/ plant	No. of grains/ panicle	1000-grain weight
1. Q.O.64.31	−0.91 (7)	−0.26 (4)	−0.62 (3)	4.46 (4)	0.56 (5)	1.42 (1)	−0.48 (8)	10.43 (2)	0.82 (4)
	−0.58 (6)	−0.15 (4)	−0.24 (4)	5.02 (7)	0.47 (5)	0.67 (3)	−0.84 (8)	6.95 (2)	0.78 (4)
2. Q.O.58.22	−0.12 (5)	−0.17 (3)	0.01 (4)	4.92 (5)	−2.85 (2)	0.35 (4)	0.06 (4)	0.87 (3)	1.16 (2)
	−0.87 (7)	−0.14 (3)	−0.66 (3)	3.69 (5)	−3.36 (2)	−0.06 (4)	−0.01 (4)	−1.55 (4)	0.20 (5)
3. Ajax	0.41 (3)	−0.30 (5)	0.82 (6)	6.99 (6)	0.02 (4)	−0.71 (6)	−0.27 (6)	−2.32 (5)	−0.65 (6)
	−0.10 (4)	−0.28 (6)	0.98 (8)	2.98 (4)	−0.66 (4)	−1.07 (7)	−0.65 (5)	−1.80 (5)	−0.64 (6)
4. Clintland 64	1.12 (2)	−1.10 (8)	0.46 (5)	−2.85 (3)	−3.64 (1)	−1.64 (7)	−0.47 (7)	−5.35 (7)	−1.51 (7)
	0.97 (2)	−0.95 (8)	0.84 (7)	−1.17 (2)	−3.41 (1)	−1.42 (8)	−0.80 (6)	−2.15 (6)	−1.65 (7)
5. O.T.184	−2.05 (8)	−0.31 (6)	1.18 (8)	−29.75 (1)	3.85 (8)	1.07 (3)	−0.26 (5)	12.56 (1)	−3.19 (8)
	−1.33 (8)	−0.36 (7)	0.50 (5)	−25.58 (1)	3.43 (8)	−0.17 (5)	−0.86 (7)	8.12 (1)	−1.81 (8)
6. P.I.269182	0.19 (4)	1.05 (2)	−0.95 (2)	10.37 (8)	2.85 (7)	0.10 (5)	0.37 (2)	−1.08 (4)	0.65 (5)
	0.28 (3)	1.23 (1)	−0.77 (2)	11.92 (8)	3.30 (7)	1.75 (1)	1.50 (2)	−0.50 (3)	1.03 (2)
7. C.I.3387	−0.54 (6)	1.48 (1)	−1.99 (1)	9.10 (7)	1.31 (6)	1.19 (2)	0.88 (1)	−2.64 (6)	1.66 (1)
	−0.15 (5)	0.86 (2)	−1.19 (1)	3.86 (6)	2.09 (6)	1.27 (2)	1.56 (1)	−2.65 (7)	0.80 (3)
8. Hinoat	1.90 (1)	−0.40 (7)	1.10 (7)	−3.24 (2)	−2.10 (3)	−1.78 (8)	0.18 (3)	−12.46 (8)	1.07 (3)
	1.78 (1)	−0.21 (5)	0.53 (6)	−0.73 (3)	−1.86 (3)	−0.96 (6)	0.10 (3)	−6.42 (8)	1.28 (1)
L.S.D. (0.05)	0.54	0.26	0.65	2.45	0.79	1.07	0.66	3.76	0.82
	0.49	0.23	0.71	3.15	1.22	1.17	0.68	4.10	0.88

† F_1 estimates are in the first row and F_2 estimates are in the second row for each character, respectively.

numbers 1 to 8 and arranged in descending order, starting with the parent having the most desirable level for each character and carrying the most dominant alleles. This is called parental order of means and parental order of dominance, respectively. In Table 15, GCA effects in the F_1 and F_2 generations represent deviations from the grand mean of the 28 progenies in each generation, so that below-average results may be noticed at a glance by their minus sign. The GCA effects of each parent also provide here a measure of the breeding usefulness of that parent for individual characters. SCA effects for the nine characters under investigation in both the F_1 and F_2 generations are also presented in Tables 16 to 24.

For protein per cent, the order of parental means is almost the same in both generations, with parents 8, 4 and 3 having the highest levels of protein and parents 5 and 1 having the lowest levels (Table 14). Clearly, the "Hinoat" array (array 8), which is the parent showing the highest levels of protein in both generations and ranked as the first general combiner (Table 15) in the F_1 and F_2 generations, has the most promise. Moreover, because the genetic system controlling this character was mainly additive with minor, but significant, dominance effects (Tables 5 and 7), there is no reason to suspect that this array will not hold its supremacy in later generations. Although the high protein levels of "Hinoat" and its superiority as a general combiner, its specific combining ability effects with most of the other parents were relatively low (Table 16). The dominant

TABLE 16. Estimates of specific combining ability (SCA) effects for protein per cent in the F_1 and F_2 generations from an 8-parent diallel cross in oats†

Parents	Q.O.58.22 (2)	Ajax (3)	Clintland 64 (4)	O.T.184 (5)	P.I.269182 (6)	C.I.3387 (7)	Hinoat (8)
1. Q.O.64.31	0.306 -0.766	-0.637 0.120	0.371 0.327	0.864 0.320	-0.090 0.302	-0.945 -0.124	0.131 -0.179
2. Q.O.58.22		-0.017 -0.249	0.471 -0.253	-0.305 0.550	-0.980 1.122	0.614 0.885	-0.089 -0.289
3. Ajax			-0.372 1.284	0.031 -0.613	1.686 0.129	-0.849 -0.418	0.158 0.747
4. Clintland 64				-0.130 0.344	-0.065 -0.784	0.349 -0.311	-0.623 -0.606
5. O.T.184					-0.592 -0.041	0.563 -0.368	-0.430 -0.193
6. P.I.269182						-0.272 -0.456	0.314 -0.271
7. C.I.3387							0.539 0.792

† F_1 data are in the first row, F_2 in the second row, respectively.

S.E. of the difference between effects of two crosses having one parent line in common is 0.61 for F_1's and 0.55 for F_2's.

S.E. of the difference between effects of two crosses having no parent lines in common is 0.55 for F_1's and 0.49 for F_2's.

and recessive genes were more or less equal in this parent. The "Clintland 64" array has the next highest mean and is the second best general combiner in both generations, followed by the array "Ajax." The cross "Ajax" x "Clintland 64," the parents of which have the highest GCA effects after "Hinoat," showed the highest SCA effects in the F_2 generation. Also, their SCA effects with other arrays were among the highest. Other promising crosses are those of "Ajax" x "P.I.269182," which showed the highest SCA effects in the F_1 generation, "Q.O.64.31" x "O.T.184," "Q.O.58.22" x "C.I.3387," and "C.I.3387" x "Hinoat." Thus, Hinoat, which showed the maximum GCA effects and the highest levels of protein in both generations, could be used in building up breeding stock well responsive to selection, while crosses such as Ajax x Clintland 64, Ajax x P.I.269182, Q.O.64.31 x O.T.184, Q.O.58.22 x C.I.3387 and C.I.3387 x Hinoat, could provide great potential in a hybridization program where a high level of protein is the main objective.

The order of dominance of the arrays determined by $W_r + V_r$ is 43285176 in the F_1 and 24538167 in the F_2 generation for oil per cent, while the order of parental means for this character is 76215384 and 67218354 in the F_1 and F_2 generations, respectively (Table 14). Parents P.I.269182 and C.I.3387 had the highest levels of oil in the F_1 and F_2 generations and carry the most recessive alleles for this character. At the same time these two parents were the highest general combiners (Table 15), and they showed relatively high SCA

TABLE 17. Estimates of specific combining ability (SCA) effects for oil per cent in the F_1 and F_2 generations from an 8-parent diallel cross in oats†

Parents	Q.0.58.22 (2)	Ajax (3)	Clintland 64 (4)	O.T.184 (5)	P.I.269182 (6)	C.I.3387 (7)	Hinoat (8)
1. Q.0.64.31	-0.064 0.525	0.024 -0.030	0.227 -0.015	-0.426 -0.235	0.251 -0.160	0.171 0.367	-0.183 -0.452
2. Q.0.58.22		-0.113 0.062	0.211 0.607	-0.283 -0.143	0.434 -0.998	-0.246 -0.232	0.061 0.180
3. Ajax			0.249 -0.148	-0.074 0.362	-0.158 -0.433	0.122 0.313	-0.051 -0.125
4. Clintland 64				0.229 -0.103	-0.394 0.352	-0.534 -0.812	0.012 0.120
5. O.T.184					0.042 0.742	0.252 -0.702	0.259 0.080
6. P.I.269182						0.079 0.683	-0.254 -0.185
7. C.I.3387							0.156 0.382

† F_1 data are in the first row, F_2 in the second row, respectively.

S.E. of the difference between effects of two crosses having one parent line in common is 0.29 for F_1's and 0.26 for F_2's.

S.E. of the difference between effects of two crosses having no parent lines in common is 0.26 for F_1's and 0.23 for F_2's.

effects with other parents (Table 17). The SCA effects were comparatively high for the crosses of P.I.269182 with Q.0.58.22 and 0.T.184. Other interesting crosses are those of P.I.269182 x C.I.3387 x Hinoat. These crosses appeared to be the best ones in terms of their future potentialities, and as the gene system governing this character is simple and mainly additive in its effect (Tables 5, 7, 10 and 11), one would expect these crosses to show their superiority in early generations without many complications.

Parent 7 (C.I.3387) has the lowest array for hull per cent in both F_1 and F_2 generations and possesses the most dominant alleles for this character (Table 14). The superiority of this parent is indicated also from its high GCA effects in both generations (Table 15). The next promising arrays are those of Q.0.64.31, Q.0.58.22 and P.I.269182. Therefore, the crosses among these four parents could result in segregants with low hull per cent. Although arrays Clintland 64, 0.T.184 and Hinoat ranked the lowest as general combiners for this character (Table 15) and their mean performance was relatively low (Table 14), the crosses Clintland 64 x 0.T.184 and C.I.3387 x Hinoat showed the highest SCA effects in the F_1 and F_2 generations, respectively (Table 18), thus providing great potential in selecting oat cultivars with low hull per cent which may lead to a significant increase in the energy value of oats. These results are in agreement with those reported by Aksel and Johnson (1961) in barley and Chaudhary and Jana (1976) in pearl millet. They reported that parental performance only is not enough to be used in the prediction of superior

TABLE 18. Estimates of specific combining ability (SCA) effects for hull per cent in the F_1 and F_2 generations from an 8-parent diallel cross in oats†

Parents	Q.O.58.22 (2)	Ajax (3)	Clintland 64 (4)	O.T.184 (5)	P.I.269182 (6)	C.I.3387 (7)	Hinoat (8)
1. Q.O.64.31	0.396	-0.087	-0.839	0.421	0.068	-0.007	0.048
	0.348	-0.850	0.772	-0.368	0.012	-0.595	0.682
2. Q.O.58.22		-0.440	-0.262	0.458	-0.255	0.709	-0.605
		0.518	-0.350	-0.120	-0.080	-0.477	0.160
3. Ajax			-0.145	-0.265	-0.199	0.366	0.771
			-0.868	0.062	-0.218	0.015	1.342
4. Clintland 64				-1.127	0.169	0.104	2.099
				-0.107	-0.227	0.927	-0.147
5. O.T.184					1.139	0.144	-0.770
					-0.537	1.287	-0.217
6. P.I.269182						-0.349	-0.574
						0.857	0.193
7. C.I.3387							-0.969
							-2.013

† F_1 data are in the first row, F_2 in the second row, respectively.

S.E. of the difference between effects of two crosses having one parent line in common is 0.74 for F_1's and 0.80 for F_2's.

S.E. of the difference between effects of two crosses having no parent lines in common is 0.66 for F_1's and 0.72 for F_2's.

crosses in future generations. Other promising crosses are O.T.184 x Hinoat and Ajax x Clintland 64. Because the genetic system controlling this character appears to be relatively simple, selection of promising plants or progenies from these crosses should be expected.

For plant height, array O.T.184 (Table 14) is the most important one and its superiority was retained in both generations. It appears to carry the most dominant alleles for dwarf plants (Table 15). The crosses between this parent and the other parents showed the highest SCA effects. Therefore, the superiority of this parent reveals the possibility of using it in building up breeding materials responsive to selection for dwarf plants. The next array in the present breeding material is of Hinoat, and seems to carry dominant and recessive alleles in more or less equal proportions. Therefore, the cross of O.T.184 and Hinoat should be the most important one in selecting segregants for breeding short-strawed oats. However, in the present study, this was not true and the cross between these two parents had the most undesirable SCA effect (Table 19). Such effects as these could be due, in part, to the existence of non-allelic interaction. The crosses O.T.184 x Clintland 64 and O.T.184 x Ajax had the highest SCA effects in the F_1 and F_2 generations, respectively, indicating great potential in selecting among these crosses for dwarf oats.

Results of the F_1 and F_2 generations for heading date were very similar (Tables 14 and 15). Arrays Clintland 64 and Q.O.58.22 are the

TABLE 19. Estimates of specific combining ability (SCA) effects for plant height in the F_1 and F_2 generations from an 8-parent diallel cross in oats[†]

Parents	Q.O.58.22 (2)	Ajax (3)	Clintland 64 (4)	O.T.184 (5)	P.I.269182 (6)	C.I.3387 (7)	Hinoat (8)
1. Q.O.64.31	1.096	3.223	0.753	-3.107	-3.052	4.118	-3.030
	-2.732	4.442	-5.157	2.982	-5.300	2.263	3.502
2. Q.O.58.22		-0.240	1.389	-1.110	-2.615	-1.045	2.526
		-0.097	5.005	-3.487	-3.968	4.395	0.883
3. Ajax			-0.864	-3.034	2.411	0.481	-1.977
			-0.542	-9.073	0.635	4.098	0.537
4. Clintland 64				-1.224	6.361	-0.919	-5.497
				1.638	-0.213	0.850	-1.582
5. O.T.184					-0.039	2.711	5.803
					8.545	-7.442	6.837
6. P.I.269182						-5.294	2.228
						3.157	-2.855
7. C.I.3387							-0.052
							-7.322

[†] F_1 data are in the first row, F_2 in the second row, respectively.

S.E. of the difference between effects of two crosses having one parent line in common is 2.77 for F_1's and 3.55 for F_2's.

S.E. of the difference between effects of two crosses having no parent lines in common is 2.48 for F_1's and 3.18 for F_2's.

earliest arrays, carry the most dominant alleles for this character, and occupied the first and second positions as general combiners in both generations. These two parents resulted in good F_1 and F_2 families with other parents but not with each other (Table 20). The cross with the highest SCA effects in both generations was that of C.I.3387 x Hinoat. However, since C.I.3387 was one of the epistatic parents, particularly in the F_2 generation, as shown by the graphical analysis (Figure 10) and also was among the latest maturing parents, the superiority of its cross with Hinoat should be treated with caution. The other crosses with potential are Clintland 64 x Q.O.64.31, Q.O.58.22 x P.I.269182 and Q.O.58.22 x C.I.3387. Other crosses would be of less importance if the purpose is to select for early maturing plants.

Grain yield, for the purpose of the present study, has been analyzed for its three main components: number of panicles per plant, number of grains per panicle and 1000-grain weight. It was shown earlier (Table 3) that gene interaction played an important role in the genetic control of the two yield components, number of panicles per plant and 1000-grain weight in both the F_1 and F_2 generations. Exclusion of the parents contributing to such gene interaction validated the assumptions underlying the genetic analysis.

For grain yield, at first sight the F_1 and F_2 graphs (Figure 11A, B) might suggest from their low slope values the existence of gene interaction. However, these slopes did not differ significantly

TABLE 20. Estimates of specific combining ability (SCA) effects for heading date in the F_1 and F_2 generations from an 8-parent diallel cross in oats†

Parents	Q.0.58.22 (2)	Ajax (3)	Clintland 64 (4)	O.T.184 (5)	P.I.269182 (6)	C.I.3387 (7)	Hinoat (8)
1. Q.0.64.31	0.488	0.113	-1.470	0.030	-0.220	0.821	0.238
	2.262	0.054	-2.696	0.720	-0.405	-0.446	0.512
2. Q.0.58.22		0.280	1.446	-1.054	-2.054	-1.262	2.155
		1.137	2.137	-1.196	-2.321	-3.113	1.095
3. Ajax			0.321	0.321	-0.929	-0.387	0.280
			-0.321	2.845	-2.780	-0.821	-0.113
4. Clintland 64				-1.012	1.238	-2.220	1.696
				-1.155	-1.780	1.179	2.637
5. O.T.184					0.238	2.030	-0.554
					-0.613	0.095	-0.696
6. P.I.269182						3.280	-1.554
						7.220	0.679
7. C.I.3387							-2.262
							-4.113

† F_1 data are in the first row, F_2 in the second row, respectively.

S.E. of the difference between effects of two crosses having one parent line in common is 0.89 for F_1's and 1.37 for F_2's.

S.E. of the difference between effects of two crosses having no parent lines in common is 0.80 for F_1's and 1.23 for F_2's.

from b = 1. Thus, for this character, as with hull per cent, it does not seem justified to postulate gene interaction, although such a possibility could exist. No regular array patterns were found for this character but, in general, arrays Q.0.64.31 and C.I.3387 showed the highest means for grain yield in the F_1 and F_2 generations (Table 14) and appeared to carry more recessive than dominant alleles. At the same time, array Q.0.64.31 ranked as the first general combiner in the F_1 generation and was among the highest general combiners in the F_2, while array P.I.269182 was the highest general combiner in the F_2 but not in the F_1 generation. Array C.I.3387 occupied the second position as a general combiner in both generations (Table 15) and its cross with array Ajax showed the highest SCA effects in the F_1 generation (Table 21), indicating great potential by using this parent in an oat breeding program. Other potential crosses are Q.0.58.22 x Clintland 64, Q.0.64.31 x C.I.3387 and Clintland 64 x P.I.269182.

For the two yield components, number of panicles per plant and 1000-grain weight, the regression lines b W_r/V_r (Table 3) of the F_1 and F_2 generations were far from a slope b = 1, and it can be said with confidence that gene interaction played a significant part in determining the control of these characters. The nature of this interaction may be one of two types. It may be localized and specific to particular arrays or it may be of a more generalized type (Whitehouse et al., 1958). The localized type of interaction can be

TABLE 21. Estimates of specific combining ability (SCA) effects for grain yield per plant in the F_1 and F_2 generations from an 8-parent diallel cross in oats†

Parents	Q.O.58.22 (2)	Ajax (3)	Clintland 64 (4)	O.T.184 (5)	P.I.269182 (6)	C.I.3387 (7)	Hinoat (8)
1. Q.O.64.31	0.646 -0.350	0.268 1.546	-0.456 -1.803	-0.976 -1.103	1.249 0.293	1.585 1.742	-2.317 0.674
2. Q.O.58.22		-0.383 -0.715	0.051 2.283	0.733 0.721	0.348 -1.673	-2.136 -0.514	0.742 1.248
3. Ajax			-0.898 -1.453	-0.017 0.454	-1.258 -0.068	2.342 -0.198	-0.054 0.434
4. Clintland 64				-0.154 0.370	1.939 1.013	0.092 -0.373	-0.575 -0.038
5. O.T.184					-1.439 -0.026	0.168 -0.622	1.685 0.207
6. P.I.269182						-1.705 1.476	0.865 -1.015
7. C.I.3387							-0.346 -1.510

† F_1 data are in the first row, F_2 in the second row, respectively.

S.E. of the difference between effects of two crosses having one parent line in common is 1.20 for F_1's and 1.32 for F_2's.

S.E. of the difference between effects of two crosses having no parent lines in common is 1.08 for F_1's and 1.18 for F_2's.

compared with the model where allele "A" normally contributes "a" units to the character, allele "B" contributes "b" units, allele "C" contributes "c" units and so on. If genotypes "AB" contribute something other than "a + b" units then there is interaction between alleles "A" and "B." The more generalized type of gene interaction involves many genes all interacting with one another so that the effect of putting one desirable allele into a given genotype depends on the number of other desirable alleles in the genotype. For example, put allele "A" with a few other desirable alleles and the increment due to "A" will be small; put "A" with a large number of other desirable alleles and the increment due to "A" will be large. Thus, the net effect of allele "A" will be some form of product depending on its own contribution and the contributions of all the other factors with which it interacts.

If the interactions are of the first type (localized), then it should be possible to attribute them to particular genotypes (arrays), and to do this arrays must be found which, on omission from the data, leave a diallel for a certain character which is free from interaction, i.e., where b = 1. If such smaller diallels can be found among the data, then the gene interaction can be attributed to the omitted parent or parents. If the interaction is of a more generalized type, then it should be handled by the scaling methods described by Mather (1949). In the present study, it appears that the gene interaction was of the localized type for number of panicles per plant as well as for heading date, while it was of the generalized type for 1000-grain weight. For a breeding program, the value of knowing the nature of the gene interaction is that if the interaction is of the generalized type there is nothing special about any particular part of the genotype, and the breeding policy should be directed towards accumulating as many desirable genes as possible. This means that, in effect, the gene system should be treated as if it were additive. However, if gene interaction is of the specific localized type, then it must be decided whether or not the interaction is affecting the character in the desired direction, and the breeding policy should be to fix or get rid of the interacting genes according to their desirability (Whitehouse et al., 1958).

In the present investigation it can be seen that array C.I.3387 has the highest number of panicles per plant (Table 14) and this parent was possibly also the main contributer to the interaction (Table 3). Thus, if this interaction is a localized one, it would seem ~~to be in~~ favour of a high number of panicles per plant and the oat breeder should try to fix such desirable gene interaction. It is clear, also, that this array was the first general combiner in both generations (Table 15) and its crosses with each of arrays P.I.269182 and Hinoat showed the highest SCA effects in the F_1 and F_2 generations, respectively (Table 22). Although array P.I.269182 also contributed to the gene interaction occurring for this character, it had the second highest mean for the character and occupied the

TABLE 22. Estimates of specific combining ability (SCA) effects for number of panicles per plant in the F_1 and F_2 generations from an 8-parent diallel cross in oats†

Parents	Q.O.58.22 (2)	Ajax (3)	Clintland 64 (4)	O.T.184 (5)	P.I.269182 (6)	C.I.3387 (7)	Hinoat (8)
1. Q.O.64.31	0.147 -0.049	-0.146 0.721	-0.173 -0.223	-0.245 0.386	0.438 -0.580	0.347 -0.057	-0.368 -0.199
2. Q.O.58.22		-0.390 -0.521	-0.043 0.936	0.729 0.869	0.204 -1.121	-0.385 0.176	-0.262 -0.290
3. Ajax			0.301 -0.120	-0.067 0.141	-0.747 -0.202	1.182 -0.447	-0.133 -0.429
4. Clintland 64				-0.034 0.220	0.833 0.916	0.102 -1.565	-0.985 -0.164
5. O.T.184					-0.871 0.288	-0.098 -1.164	0.586 -0.741
6. P.I.269182						-1.083 1.395	1.226 -0.696
7. C.I.3387							-0.064 1.661

† F_1 data are in the first row, F_2 in the second row, respectively.

S.E. of the difference between effects of two crosses having one parent line in common is 0.75 for F_1's and 0.77 for F_2's.

S.E. of the difference between effects of two crosses having no parent lines in common is 0.67 for F_1's and 0.68 for F_2's.

second position as a general combiner. Also, its crosses with other parents showed relatively high SCA effects, thus indicating it could be an important parent in oat improvement. On the other hand, Q.O.64.31, which contributed to gene interaction, had almost the lowest number of panicles per plant (Table 14) and occupied the lower position as a general combiner (Table 15). It may be inferred that the interaction of Q.O.64.31 is the one that leads to a low number of panicles per plant and is, therefore, undesirable for purposes of oat improvement related to this character. It would thus seem best in terms of breeding for high number of panicles per plant, to concentrate on crosses involving C.I.3387 and P.I.269182 as parents and to try to find inbred selections which contain those genes which may interact to give high manifestation for this character.

Arrays Q.O.64.31 and O.T.184 are the most important ones for their high number of grains per panicle (Table 14), with the first carrying most of the recessive alleles and the second carrying most of the dominant alleles for this character in both generations. These two arrays showed the highest GCA effects in both generations, indicating that the crosses involving these two parents should be promising in future generations, although the cross between these two parents in the present study did not show such superiority in either generation (Table 23). The crosses of Q.O.64.31 x Ajax, Q.O.64.31 x C.I.3387, and Clintland 64 x C.I.3387 are the most important ones. The cross P.I.269182 x Hinoat showed the highest SCA effects in the

TABLE 23. Estimates of specific combining ability (SCA) effects for number of grains per panicle in the F_1 and F_2 generations from an 8-parent diallel cross in oats†

Parents	Q.0.58.22 (2)	Ajax (3)	Clintland 64 (4)	O.T.184 (5)	P.I.269182 (6)	C.I.3387 (7)	Hinoat (8)
1. Q.0.64.31	2.058	5.103	-1.350	0.780	1.903	4.735	-13.230
	-5.829	5.606	-7.239	-7.655	6.350	3.966	4.800
2. Q.0.58.22		0.325	2.652	-2.108	0.565	-7.663	4.172
		3.980	5.315	-2.822	-2.037	-5.230	6.623
3. Ajax			-7.403	1.757	-5.340	5.512	0.047
			-10.630	-1.187	3.128	0.695	-1.592
4. Clintland 64				-0.327	3.177	2.938	0.313
				4.208	-1.137	8.580	0.903
5. O.T.184					-3.033	-1.052	3.983
					-2.814	5.313	4.956
6. P.I.269182						-3.228	5.957
						-0.562	-2.929
7. C.I.3387							-1.242
							-12.762

† F_1 data are in the first row, F_2 in the second row, respectively.

S.E. of the difference between effects of two crosses having one parent line in common is 4.25 for F_1's and 4.63 for F_2's.

S.E. of the difference between effects of two crosses having no parent lines in common is 3.80 for F_1's and 4.14 for F_2's.

F_1 generation but not in the F_2, and could also be important. Ajax x C.I.3387 showed reasonably high SCA effects in both generations and could be carried forward if the purpose is to select oat plants with a high number of grains per panicle.

The third yield component, 1000-grain weight, was highly affected by gene interaction in the present study. This was indicated from the very low b values (Table 3) in both generations. The elimination of parents contributing to this gene interaction removed, to some degree, such epistatic effects. Unfortunately, in removing the interacting arrays (arrays Q.O.64.31, Q.O.58.22 and P.I.269182) the number of families fell from 36 to 15 in each of the F_1 and F_2 generations. Hence, the analysis is not as comprehensive as in the complete data. Nevertheless, certain consistencies are obvious over the two generations. Examination of the tables of array means and GCA effects (Tables 14 and 15) indicates that parents C.I.3387 and Hinoat had the highest array means for grain weight with C.I.3387 having no consistency in dominant and recessive alleles (parental order of dominance) and Hinoat carrying more recessive than dominant alleles. Clearly, the epistatic parents (parents 1, 2 and 6) had a fairly high grain weight and the crosses involving these parents may result in segregants with high grain weight. The crosses of the epistatic parent Q.O.64.31 with each of P.I.269182 and C.I.3387, and the epistatic parent Q.O.58.22 with both O.T.184 and Hinoat, are of a high potential in oat breeding programs. Another interesting cross is

TABLE 24. Estimates of specific combining ability (SCA) effects for 1000-grain weight in the F_1 and F_2 generations from an 8-parent diallel cross in oats†.

Parents	Q.0.58.22 (2)	Ajax (3)	Clintland 64 (4)	O.T.184 (5)	P.I.269182 (6)	C.I.3387 (7)	Hinoat (8)
1. Q.0.64.31	-1.364	-0.286	-0.243	-1.659	2.119	1.104	0.330
	-0.890	-0.555	-0.323	-1.080	0.193	2.457	0.198
2. Q.0.58.22		-1.701	2.582	-1.354	-1.476	-0.941	4.255
		0.482	0.063	0.857	-0.770	0.993	-0.735
3. Ajax			0.090	0.674	0.312	0.667	0.244
			0.078	1.112	-1.585	-0.402	0.870
4. Clintland 64				0.987	0.295	-1.619	-2.092
				0.173	3.107	-1.360	-1.738
5. O.T.184					-0.421	2.164	-0.389
					0.220	-1.877	0.595
6. P.I.269182						0.072	-0.901
						-0.893	-0.272
7. C.I.3387							-1.446
							1.082

† F_1 data are in the first row, F_2 in the second row, respectively.

S.E. of the difference between effects of two crosses having one parent line in common is 0.93 for F_1's and 0.99 for F_2's.

S.E. of the difference between effects of two crosses having no parent lines in common is 0.83 for F_1's and 0.88 for F_2's.

that of Clintland 64 with P.I.269182 (Table 24). Since the gene interaction was of the generalized (or multiplicative) type as indicated earlier for this character, and was in the desirable direction, this interaction should be fixed in the breeding materials. It appears that C.I.3387 and Hinoat, as well as the three epistatic parents which showed the highest arrays, contain the most desirable genes for this character, and it is upon these parents and their crosses that attention should be focused when considering future oat breeding programs.

In general, this genetical analysis demonstrated the importance of some of these genotypes or their crosses as genetic materials for different breeding purposes. For example, Clintland 64 as a source of earliness, O.T.184 as a source of short-strawed oats, P.I.269182 and C.I.3387 as a source of high oil content, and Hinoat as genetic material for improving the protein level in oats. However, the relation between the mean performance of these selected parents and their crosses was not accurate for certain characters in most cases. These results were in agreement with those reported by Aksel and Johnson (1961), Jinks (1954), and Johnson and Aksel (1959), while they were in contrast to those reported by Aggarwal (1976) and Gilbert (1958). Gilbert reported that the performance of the parents themselves gives a valuable prediction of the relative behaviour of the crosses.

It should be emphasized here that these predictions were made after extracting from the analysis as much information as is theoretically possible. It may be that this extraction has gone too far and that the analysis is not sufficiently accurate to permit such a rigorous interpretation. If this is so, these predictions are too optimistic and should have been made in more generalized terms. Therefore, we may have to accept the statement made by Murphy (1974) that the selection of parents in self-pollinated species such as oats is largely a matter of guesswork.

CHAPTER V

SUMMARY AND CONCLUSIONS

Three different diallel analysis techniques were used in the present investigation to study the genetic mechanisms involved in the inheritance of nine important quality and agronomic characters in oats (Avena sativa L.) in the F_1 and F_2 generations. These characters were protein per cent, oil per cent, hull per cent, plant height, heading date, grain yield per plant, number of panicles per plant, number of grains per panicle and 1000-grain weight. The genetic information obtained from the various diallel analysis techniques involved in the present study was used first in the prediction of the most promising genotypes and/or crosses which would give the best chances of finding high manifestations of each character in later generations and, secondly, in the evaluation of the diallel techniques and the possibility of using them as a tool for plant improvement. Phenotypic, genetic and environmental correlations among all characters were also investigated. The genetic materials were planted in a randomized complete block design with four replications. The statistical and genetic analyses for the measured characters showed the following results.

1. Statistical analysis of the F_1 and F_2 generations, as well as their parents, showed a highly significant variation for each character. This would permit selection among these genotypes and their crosses for the desirable characters, such as high levels of protein and oil, low hull per cent, shortness, earliness and high yielding ability. These characters are of great importance in developing new oat cultivars. In addition, the significant variation among the genotypes and their crosses for all characters in the present study reveals that the genetic analysis by means of diallel techniques could be carried forward.

2. Tests of the assumptions required for the genetic analysis indicated that one or more of these assumptions, including that of no epistasis and gene correlation, were not strictly valid, particularly with characters such as heading date, number of panicles per plant and 1000-grain weight in both generations. This partial failure of some of the assumptions underlying the genetic analysis seemed unlikely to disturb the genetic analysis for some characters. Removal of the parent(s) contributing to the epistatic effects succeeded, to some extent, in removing such failure.

3. Results of the combining ability analysis indicated that although both GCA and SCA effects were significant for the characters under investigation, the role of GCA was greater than that of SCA for all characters. However, the importance of GCA relative to SCA was nearly equal for grain yield and its three components, and much higher for other characters (Table 5). The Jinks-Hayman analysis, as well as the graphical analysis, revealed, also, the predominant role of additive genetic variance in the control of most of the characters under investigation. At the same time, the dominant genetic effects were also significant but of low magnitude in relation to that of the additive genetic variance (Table 7). These results suggest the use of breeding methods utilizing non-additive as well as additive genetic variance. Such procedures would be effective in manipulating the characters under study. Accordingly, the following breeding methods are suggested for oat improvement:

(a) Composite or synthetic cultivars could be produced from parental lines showing high GCA effects (parents Hinoat and Clintland 64 for protein per cent, C.I.3387 and P.I.269182 for oil per cent, hull per cent, and number of panicles per plant, O.T.184, Clintland 64 and Hinoat for plant height, Clintland 64, Q.O.58.22 and Hinoat for early maturing types, Q.O.64.31 and C.I.3387 for grain yield, O.T.184 and Q.O.64.31 for number of grains per panicle and C.I.3387 and Hinoat for 1000-grain weight).

(b) Assuming a male sterility mechanism can be discovered in this species and the technical problems of cross pollination solved, hybrid oats could be produced from inbred lines derived from parents showing high SCA effects (Tables 16-24).

(c) Alternatively, hybrid oats could be developed using reciprocal recurrent selection (Comstock et al., 1949) to make efficient use of inbred lines showing both relatively high GCA and SCA effects.

4. The degree and direction of dominance varied with characters and generations. In the F_1 generation, partial dominance occurred for all characters, while overdominance and/or complete dominance occurred in the F_2 generation. Positive and negative alleles were almost equally distributed among the genotypes involved in the present study for protein and oil per cent, but were unequally distributed for most of the other characters, particularly hull per cent, grain yield, number of panicles per plant and 1000-grain weight. This unequal distribution of positive and negative alleles with the non-allelic interaction led to a partial failure of assumptions required for the genetic analysis. More dominant than recessive alleles were present in the genotypes for all characters except protein per cent and plant height. The number of effective genes or groups of linked genes controlling these characters varied from one to three.

5. Heritability estimates calculated from the general and specific combining ability method were, in general, higher than that calculated from the Jinks-Hayman analysis, but the two methods showed the same order for all characters in both generations. Broad sense heritability estimates were relatively high and higher in magnitude than the corresponding narrow sense estimates for all characters except for oil per cent, grain yield and number of panicles per plant in the F_1 generation, calculated from the Jinks-Hayman analysis only. Heritability estimates were relatively high for oil per cent and heading date, intermediate for protein per cent, hull per cent, plant height, number of panicles per plant and number of grains per panicle, and low for grain yield and 1000-grain weight. Genetic advances from selection as well as the relative genetic advances from selection were relatively higher when calculated by the Griffing's analysis than that calculated by the Jinks-Hayman analysis. Relative genetic advance from selection was high for oil per cent, plant height, grain yield, number of panicles per plant and number of grains per panicle in both generations, indicating that selection for these characters in the early generations would be effective. Protein per cent, heading date and 1000-grain weight showed an intermediate RG_s, while less progress from selection occurred with hull per cent in the two generations.

6. In general, the correlation coefficients among all characters under investigation were similar in the F_1 and F_2 generations. The genetic correlation coefficients were relatively higher

than the corresponding phenotypic coefficients in most cases, but they were similar in sign, indicating that the significant phenotypic associations were mainly due to genetic causes. Likewise, the environmental correlation coefficients, particularly the significant coefficients, were similar with both phenotypic and genetic coefficients in sign in most cases, indicating that the two correlated characters were influenced by the environmental conditions in the same direction. The present results also indicated that selection in the desirable direction for most characters would be possible without negative effects on other characters.

7. In the evaluation of the diallel cross techniques the plant breeder must keep in mind the basic elements of plant breeding. Most plant breeding programs consist of two basic functions: (i) choosing potential parents from all those genotypes that are presently available; (ii) selecting, in the population developed by mating the chosen parents, lines with characters approaching certain plant breeding goals. In order for a diallel analysis to be useful in plant breeding, it must supply information that helps plant breeders in the choice of parents for a particular breeding program or information that will lead them to a more effective selection program. The present study showed that the diallel cross analysis provided an overall genetic and performance evaluation. It has provided, among many other things, very useful information about the relative importance of general and specific combining ability, the relationship

between hybrid performance and general combining ability, and the relationship between hybrid performance and the performance of inbred parents. The comparison of parents and their hybrids also affords an estimate of overall heterosis. In addition, the diallel cross analysis provided information on the genetic identity of the characters under investigation, on dominance-recessive relationships, on genetic interaction and on probable linkage associations. This information is very important in most cereal breeding programs, greatly outweighing that obtainable from parental observation, and enables the plant breeder to eliminate low yielding arrays on a reasonably sound basis. Our results indicated that the performance of the parents per se is not necessarily a good indicator of their combining ability in later generations for most characters. These results contradict the statement raised by Gilbert (1958) that, for the plant breeder, the information gained from analysis of diallel crosses is little more than that obtained from the parents themselves.

Despite the valuable information provided by the diallel analysis in the present investigation and its use as an easy and systematic way of crossing parental lines, the assumptions required for the genetic analysis, the size of the diallel cross, the nature of the genetic materials and the required time and costs could be obstacles to the use of the diallel cross technique in plant improvement. Diallel crosses should be evaluated against other mating designs and, as stated by Matzinger (1963), "it would seem desirable to decide on the types and generations of material which would give maximum information for a given number of plots, rather than deciding on an easy crossing system and working out the analysis after the experiment is completed."

CHAPTER VI

CONTRIBUTIONS TO KNOWLEDGE

This is the first comprehensive study concerning the evaluation of diallel analysis techniques as a tool for oat improvement.

1. The use of diallel analysis in plant improvement has been reported by several investigators. To the best of the author's knowledge, however, there have been no reports in the literature on attempts to study and/or compare the results from different diallel analysis techniques applied to certain characters in certain populations and generations. In this dissertation, an attempt was made to study and compare results by three different diallel analysis techniques in two generations. The application of the results was discussed in relation to plant breeding methods. Such an attempt is believed to be unique and is considered to be a contribution to original knowledge.

2. The use of two methods to test the assumptions required for the genetic analysis is by itself a contribution to original knowledge. It is important to know that if only one test of the assumptions underlying the genetic analysis is used, faulty conclusions could result.

3. To assess the importance of general and specific combining ability in the genetic control of some characters, several research workers have compared the mean squares of these two types of combining ability with each other. Unfortunately, this procedure always results in an underestimation of the importance of specific combining ability (Baker, 1977). In the present investigation, the relative importance of general to specific combining ability was established for each character by two different procedures. To the knowledge of the author, this is the first report of this having been done in oats.

4. The estimation of variance components, heritability, genetic advance from selection and relative genetic advance from selection for all characters in the F_1 and F_2 generations is considered to be very important in oat improvement. The importance of these estimates is also due to the fact that different methods of estimation were followed and the results were compared.

5. Information about the phenotypic, genetic and environmental correlations among the quality and agronomic characters involved in the present investigation are of great importance to

cereal breeders and it is believed that this is the first attempt to obtain such information and to discuss their utilization in oat improvement.

In general, the author believes that the information resulting from this investigation will provide useful guidelines for practical oat breeding programs and will enable the oat breeder to evaluate his genetic material on a sound genetic basis.

CHAPTER VII

SUGGESTIONS FOR FURTHER RESEARCH

In planning for research work, researchers are faced with two main considerations. The first is setting up clear and well defined objectives, and the second is the question of when they can consider that their research work is completed. The second consideration is usually difficult to ascertain. In many cases a continuation of the research and establishing suggestions for future research are of considerable importance. The following suggestions for further research are aimed at increasing oat productivity and improving its quality.

1. Hayman (1963) recommended that an analysis of variance of the parents and F_1 populations separately, together with their analysis of covariance, supplies the full information. In another paper, the same author (1957) also recommended that to take advantage of the F_2 data, the two generations (F_1 and F_2) are better compared with each other than investigated separately by analogous procedures.

Although Hayman's recommendations were considered in the present investigation, the author believes that to obtain good estimates of different genetic and environmental parameters in oats, such investigation should be conducted for several years and generations (at least two years with F_1, F_2 and F_3 generations). Different environments are also required for valid genetic and environmental parameters. The different environments could be different locations (Macdonald College, Guelph and La Pocatière), or different levels of environmental variables such as fertilizer applications, planting dates, etc., at the same location. In fact, an extension of the present study was carried forward by the author for one more year and up to the F_3 generation at the Macdonald Research Station in 1977, but the data were not analyzed for this dissertation.

2. In order for the statistical or genetical variance components obtained from a diallel cross to be significant estimates that could lead to greater oat breeding efficiency, the size of the diallel cross should be adequate and the parents should be randomly selected. However, it should be remembered that any increase in the size of the diallel set increases the number of treatments (progenies) to a level which cannot conveniently be handled over a range of locations. The author believes that a diallel cross of ten parents would be adequate to provide the necessary information.

3. Although diallel crosses may be used as a systematic procedure of crossing parental lines, the genetic information and predictions resulting from such a procedure should be evaluated against that from other mating designs and breeding systems. Determination of efficiency should be focused on the accuracy of these estimates and the practical aspects of the work, with particular reference to the considerable labour, time and expense involved in the conducting of each system. Since these factors are important in resource allocation, a compromise has to be reached when comparing such systems.

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APPENDIX

APPENDIX TABLE 1. Array covariance (W_r), Variance (V_r) and their differences for protein per cent in the F_1 generation from an 8-parent diallel cross in oats

Parent	All parents included			Parent 3 eliminated		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Q.O.64.31	2.060	1.424	0.636	2.466	1.635	0.831
2. Q.O.58.22	2.601	1.820	0.781	2.961	2.087	0.874
3. Ajax	2.123	2.443	-0.320	-	-	-
4. Clintland 64	1.757	1.082	0.675	2.038	1.261	0.777
5. O.T.184	1.413	0.510	0.903	1.608	0.584	1.024
6. P.I.269182	3.403	3.206	0.198	3.576	2.715	0.861
7. C.I.3387	2.441	2.054	0.387	2.926	2.356	0.570
8. Hinoat	2.188	1.645	0.543	2.458	1.860	0.598
Y-Intercept	1.10	0.00		0.98	0.00	

$\hat{b} = 0.65 \pm 0.13$ $\hat{b} = 0.89 \pm 0.09$

APPENDIX TABLE 2. Array covariance (W$_r$), Variance (V$_r$) and their differences for protein per cent in the F$_2$ generation from an 8-parent diallel cross in oats

Parent	All parents included			Parent 2 eliminated		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Q.O.64.31	1.725	1.234	0.491	1.797	0.923	0.874
2. Q.O.58.22	0.876	1.350	-0.474	-	-	-
3. Ajax	3.032	2.977	0.055	3.247	2.535	0.712
4. Clintland 64	1.622	0.841	0.781	1.751	0.759	0.992
5. O.T.184	1.787	1.103	0.684	2.047	1.271	0.776
6. P.I.269182	1.913	1.190	0.722	2.302	1.332	0.970
7. C.I.3387	2.415	1.713	0.702	2.836	1.995	0.841
8. Hinoat	1.761	1.153	0.608	1.904	1.093	0.811
Y-Intercept	0.84	0.00		1.00	0.00	

$\hat{b} = 0.72 \pm 0.24$ $\hat{b} = 0.89 \pm 0.05$

APPENDIX TABLE 3. Array covariance (W_r), Variance (V_r) and their differences for oil per cent in the F_1 generation from an 8-parent diallel cross in oats

	Parent	All parents included		
		W_r	V_r	W_r-V_r
1.	Q.O.64.31	1.760	0.896	0.864
2.	Q.O.58.22	1.608	0.757	0.851
3.	Ajax	1.569	0.716	0.853
4.	Clintland 64	1.096	0.375	0.721
5.	O.T.184	1.652	0.852	0.800
6.	P.I.269182	1.989	1.151	0.838
7.	C.I.3387	1.787	1.000	0.787
8.	Hinoat	1.641	0.809	0.832
	Y-Intercept	0.73	0.00	

$\hat{b} = 1.11 \pm 0.07$

APPENDIX TABLE 4. Array covariance (W_r), Variance (V_r) and their differences for oil per cent in the F_2 generation from an 8-parent diallel cross in oats

Parent	All parents included			Parent 2 eliminated		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Q.O.64.31	1.458	0.666	0.792	1.719	0.755	0.964
2. Q.O.58.22	0.525	0.163	0.362	-	-	-
3. Ajax	1.272	0.486	0.786	1.479	0.565	0.914
4. Clintland 64	0.949	0.514	0.435	1.130	0.564	0.566
5. O.T.184	1.186	0.757	0.429	1.364	0.858	0.506
6. P.I.269182	1.846	1.263	0.583	2.087	1.183	0.904
7. C.I.3387	2.619	2.234	0.385	3.022	2.533	0.489
8. Hinoat	1.449	0.609	0.840	1.695	0.709	0.986
Y-Intercept	0.64	0.00		0.92	0.00	

$\hat{b} = 0.92 \pm 0.12$ $\hat{b} = 0.85 \pm 0.13$

APPENDIX TABLE 5. Array covariance (W_r), variance (V_r) and their differences for hull per cent in the F_1 and F_2 generations from an 8-parent diallel cross in oats

Parent	F_1			F_2		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Q.O.64.31	1.629	1.640	-0.011	1.863	1.633	0.230
2. Q.O.58.22	1.274	1.378	-0.104	1.392	1.232	0.160
3. Ajax	1.738	1.290	0.448	1.560	1.034	0.526
4. Clintland 64	2.735	2.434	0.301	0.253	0.409	-0.156
5. O.T.184	0.769	0.660	0.109	0.444	0.623	-0.179
6. P.I.269182	1.952	2.243	-0.291	1.194	0.672	0.522
7. C.I.3387	0.251	0.855	-0.604	0.623	1.918	-1.295
8. Hinoat	2.700	3.838	-1.138	2.852	3.535	-0.683
Y-Intercept	0.32	0.00		0.35	0.00	

$\hat{b} = 0.73 \pm 0.17$ $\hat{b} = 0.66 \pm 0.21$

APPENDIX TABLE 6. Array covariance (W_r), variance (V_r) and their differences for plant height in the F_1 generation from an 8-parent diallel cross in oats

Parent	All parents included		
	W_r	V_r	W_r-V_r
1. Q.O.64.31	245.000	217.973	27.027
2. Q.O.58,22	207.402	172.116	35.286
3. Ajax	252.857	224.098	28.759
4. Clintland 64	250.196	214.845	35.352
5. O.T.184	56.394	26.388	30.006
6. P.I.269182	189.571	159.125	30.446
7. C.I.3387	191.643	139.464	52.179
8. Hinoat	212.787	150.315	62.472
Y-Intercept	42.50	0.00	

$\hat{b} = 0.97 \pm 0.08$

APPENDIX TABLE 7. Array covariance (W_r), variance (V_r) and their differences for plant height in the F_2 generation from an 8-parent diallel cross in oats

Parent	All parents included			Parents 5 & 6 eliminated		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Q.O.64.31	154.830	101.661	53.169	40.466	23.946	16.520
2. Q.O.58.22	178.884	150.348	28.536	22.985	9.261	13.724
3. Ajax	249.536	242.938	6.598	65.755	35.333	30.422
4. Clintland 64	178.741	123.578	55.163	54.268	30.302	21.966
5. O.T.184	44.154	76.222	-32.068	-	-	-
6. P.I.269182	126.732	60.063	66.669	-	-	-
7. C.I.3387	259.857	238.589	21.268	86.162	50.598	35.564
8. Hinoat	157.911	101.828	56.083	70.467	59.483	10.984
Y-Intercept	50.07	0.00		16.93	0.00	

$\hat{b} = 0.87 \pm 0.19$ $\hat{b} = 1.13 \pm 0.26$

APPENDIX TABLE 8. Array covariance (W_r), variance (V_r) and their differences for heading date in the F_1 generation from an 8-parent diallel cross in oats

Parents	All parents included			Parent 5 eliminated		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Q.0.64.31	15.307	9.097	6.210	16.845	7.890	8.955
2. Q.0.58.22	3.529	1.924	1.605	3.464	1.113	2.351
3. Ajax	11.275	6.317	4.958	12.065	4.226	7.839
4. Clintland 64	7.400	3.835	3.565	8.013	3.455	4.558
5. O.T.184	18.384	9.179	9.205	-	-	-
6. P.I.269182	35.193	30.311	4.882	40.263	33.684	6.579
7. C.I.3387	34.358	32.695	1.663	38.787	33.676	5.111
8. Hinoat	4.407	2.679	1.728	4.304	1.265	3.039
Y-Intercept	4.34	0.00		5.020	0.00	
	$\hat{b} = 0.99 \pm 0.09$			$\hat{b} = 1.04 \pm 0.07$		

APPENDIX TABLE 9. Array covariance (W_r), variance (V_r) and their differences for heading date in the F_2 generation from an 8-parent diallel cross in oats

Parents	All parents included			Parents 3 & 7 eliminated		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Q.O.64.31	12.288	10.460	1.828	14.760	14.085	0.675
2. Q.O.58.22	1.311	2.249	-0.938	3.856	2.544	1.312
3. Ajax	13.740	9.767	3.973	-	-	-
4. Clintland 64	8.950	11.579	-2.629	8.492	14.342	-5.850
5. O.T.184	27.451	28.554	-1.103	37.737	39.300	-1.563
6. P.I.269182	29.056	33.299	-4.243	26.502	27.510	-1.008
7. C.I.3387	37.037	41.677	-4.640	-	-	-
8. Hinoat	8.405	4.919	3.486	14.000	5.375	8.625
Y-Intercept	2.43	0.00		3.06	0.00	

$\hat{b} = 0.83 \pm 0.06$ $\hat{b} = 0.84 \pm 0.15$

APPENDIX TABLE 10. Array covariance (W), variance (V) and their differences for grain yield per plant in the F_1 and F_2 generations from an 8-parent diallel cross in oats

Parents	F_1			F_2		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Q.O.64.31	6.214	4.870	1.344	3.973	4.469	-0.496
2. Q.O.58.22	3.267	3.496	-0.229	0.843	2.418	-1.575
3. Ajax	4.225	4.255	-0.030	3.273	2.915	0.358
4. Clintland 64	3.990	2.652	1.338	3.668	3.795	-0.127
5. O.T.184	1.927	1.227	0.700	1.983	0.907	1.076
6. P.I.269182	1.979	2.843	-0.864	2.452	2.523	-0.071
7. C.I.3387	2.972	4.654	-1.682	4.960	4.753	0.207
8. Hinoat	3.131	2.796	0.335	3.650	1.951	1.699
Y-Intercept	0.88	0.00		1.02	0.00	

$\hat{b} = 0.77 \pm 0.34$ $\hat{b} = 0.70 \pm 0.28$

APPENDIX TABLE 11. Array covariance (W_r), variance (V_r) and their differences for no. of panicles per plant in the F_1 generation from an 8-parent diallel cross in oats

Parents	All parents included			Parent 6 eliminated		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Q.O.64.31	1.447	0.555	0.892	1.448	0.508	0.940
2. Q.O.58.22	0.945	0.621	0.324	0.984	0.700	0.284
3. Ajax	1.519	1.260	0.259	1.554	0.820	0.734
4. Clintland 64	1.446	0.666	0.780	1.290	0.467	0.823
5. O.T.184	0.752	0.429	0.323	1.072	0.450	0.622
6. P.I.269182	0.218	1.013	-0.795	-	-	-
7. C.I.3387	1.810	1.866	-0.056	2.375	1.971	0.404
8. Hinoat	1.623	1.631	-0.008	1.213	0.555	0.658
Y-Intercept	0.70	0.00		0.81	0.00	

$\hat{b} = 0.51 \pm 0.35$ $\hat{b} = 0.78 \pm 0.16$

APPENDIX TABLE 12. Array covariance (W_r), variance (V_r) and their differences for no. of panicles per plant in the F_2 generation from an 8-parent diallel cross in oats

Parents	All parents included			Parents 1 & 7 eliminated		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Q.0.64.31	1.602	0.717	0.885	-	-	-
2. Q.0.58.22	1.615	1.069	0.546	0.648	0.789	-0.141
3. Ajax	1.084	0.703	0.381	0.636	0.767	-0.131
4. Clintland 64	1.411	1.405	0.006	1.626	1.715	-0.089
5. O.T.184	1.145	0.746	0.399	1.201	0.963	0.238
6. P.I.269182	2.044	1.896	0.148	-0.107	0.293	-0.400
7. C.I.3387	3.089	4.230	-1.141	-	-	-
8. Hinoat	2.803	2.325	0.478	0.881	0.672	0.208
Y-Intercept	0.93	0.00		-0.18	0.00	
	$\hat{b} = 0.56 \pm 0.10$			$\hat{b} = 1.15 \pm 0.24$		

APPENDIX TABLE 13. Array covariance (W_r), variance (V_r) and their differences for no. of grains per panicle in the F_1 and F_2 generations from an 8-parent diallel cross in oats

Parents	F_1			F_2		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Q.O.64.31	191.088	196.143	-5.055	114.900	110.104	4.796
2. Q.O.58.22	107.489	68.802	38.687	20.575	22.594	-2.019
3. Ajax	129.160	127.360	1.800	106.202	72.790	33.412
4. Clintland 64	82.569	69.685	12.884	16.842	56.323	-39.481
5. O.T.184	81.702	34.254	47.448	-6.304	7.657	-13.961
6. P.I.269182	90.930	61.731	29.199	98.977	51.619	47.358
7. C.I.3387	123.921	92.756	31.165	116.388	111.625	4.763
8. Hinoat	37.593	57.873	-20.280	125.877	107.291	18.586
Y-Intercept	36.61	0.00		-4.89	0.00	

$\hat{b} = 0.78 \pm 0.16$ $\hat{b} = 1.17 \pm 0.27$

APPENDIX TABLE 14. Array covariance (W_r), variance (V_r) and their differences for 1000-grain weight in the F_1 generation from an 8-parent diallel cross in oats

Parents	All parents included			Parents 1,2 & 6 eliminated		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Q.O.64.31	2.763	6.957	-4.194	-	-	-
2. Q.O.58.22	0.914	8.838	-7.924	-	-	-
3. Ajax	2.327	2.963	-0.636	3.936	4.606	-0.670
4. Clintland 64	2.078	4.615	-2.537	2.679	1.853	0.826
5. O.T.184	1.882	2.105	-0.223	3.639	2.937	0.702
6. P.I.269182	1.992	4.449	-2.457	-	-	-
7. C.I.3387	1.419	2.126	-0.707	1.957	1.580	0.377
8. Hinoat	2.483	8.746	-6.263	2.989	3.185	-0.196
Y-Intercept	1.94	0.0		1.41	0.0	

$\hat{b} = 0.01 \pm 0.09$ $\hat{b} = 0.58 \pm 0.18$

APPENDIX TABLE 15. Array covariance (W_r), variance (V_r) and their differences for 1000-grain weight in the F_2 generation from an 8-parent diallel cross in oats

Parents	All parents included			Parents 1,2 & 6 eliminated		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Q.O.64.31	2.825	4.161	-1.336	-	-	-
2. Q.O.58.22	1.620	1.021	0.599	-	-	-
3. Ajax	1.224	1.317	-0.093	2.016	2.088	-0.072
4. Clintland 64	0.915	3.528	-2.613	1.160	0.492	0.668
5. O.T.184	0.265	1.342	-1.077	0.330	1.771	-1.441
6. P.I.269182	-0.103	1.957	-2.060	-	-	-
7. C.I.3387	3.081	6.266	-3.185	4.688	7.305	-2.617
8. Hinoat	2.321	2.806	-0.485	3.801	3.901	-0.100
Y-Intercept	0.25	0.00		0.49	0.00	

$\hat{b} = 0.45 \pm 0.19$ $\hat{b} = 0.61 \pm 0.18$