QUANTITATIVE INHERITANCE STUDIES IN THE GARDEN PEA (*Pisum sativum* L.)

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ABSTRACT

A quantitative inheritence study of leaf form in the garden pea, *Pisum sativum* L., was carried out using an eight parent F_1 half diallel cross. The inheritance of yield and its components were also studied.

The parental lines used for the diallel contained combinations of the following genes which act in the homozygous recessive condition = *af* converts normal pea leaflets to tendrils, *tl* converts normal pea tendrils to leaflets and *st* reduces the size of the stipule. A combination of *af* and *tl* together results in a mass of small leaflets.

The characters measured included length, width, areas and weights of leaflets, stipules and tendrils and the components of yield. The data from the twenty-eight F_1 crosses and their eight parents were analysed with Hayman-Jinks diallel method. The adequacy of the additive-dominance model was determined by the relationships of Wr and Vr: the analysis of variance of (Wr - Vr), the Wr on Vr regression analysis and the WrVr graphical analysis.

The results indicated the predominance of additive genetic variance for the vegetative characters although dominance variance and non-allelic interactions were important. The inheritance of yield and its components were mainly attributable to additive genetic variance while the type of dominance varied from partial to complete for both types of characters. Heritabiity was high for the vegetative characters and medium to low for the components of yield.

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TABLE OF CONTENTS

TABLE OF CONTENTS (CONTINUED)

TABLE OF CONTENTS (CONTINUED)

LIST OF TABLES

PAGE

PAGE

LIST OF FIGURES

LIST OF PLATES

INTRODUCTION

Peas, together with green beans, broadbeans, chickpeas and lentils are some of the more important types of edible temperate legumes. Peas provide a source of human dietary protein which complements the carbohydrate component of the cereals (Duckworth 1966).

Although the early history and the early progenitors of peas are not known, the cultivation of the pea is considered to be as ancient as that of wheat and barley (Zohary and Hopf 1973). Probable centres of origin have been suggested by Vavilov (1949) and these include: Ethiopia, the Mediterranean and Central Asia, with a secondary centre of diversity in the New East.

Traditionally the pea has been used as a fresh vegetable or in the form of the dry seed, either as split peas for soup or canned. In recent years the use of the crop has changed. A portion of the world pea crop, mainly in the developed countries is now harvested at an immature stage and frozen. This product has become one of the more important modern convenience foods (Pate 1977).

In New Zealand, the "garden pea", *Pisum sativum* L. is the most widely grown of all horticultural crops with 8000 hectares under production annually (Anon 1981). The bulk of the crop is processed by quick freezing and small proportions are canned or utilised as a fresh vegetable. As an export crop, frozen peas are valuable. They earned $6.2 million in foreign exchange in 1979-80 (Bolland 1981). The "field" or "dried" pea, *Pisum arvense* L. makes up the largest proportion of the New Zealand pea crop, producing $14 million in export returns in 1980 while seed peas were worth slightly less (Anon 1981).

The main requirement for the production of peas suited to the freezing industry is the necessity for harvesting

all peas at a given stage of maturity. As the optimum time of harvest is confined to a period of hours rather than days, the efficiency of the harvesting operation is important. Part of this efficiency is determined by the through-put of peas through a mobile pea viner. Through-put is decreased by excessive vegetative growth (Snoad 1974). Excessive vegetative growth however, is not a serious problem with the use of the "pod picker" harvesting machinery.

Another problem which may arise is that the pea crop is prone to lodging or the collapsing of the canopy (Davies 1977a). Prior to harvest the increase in weight of the pea pod will almost invariably cause the plants to collapse. This is due to the weakness of the basal region of the stem in relation to the weight of the upper part of the plant. This can result in an increase in humidity within the crop, leading to pathogen attack and to a reduction in quality of the peas through the pods contact with the soil. Also a yield reduction may occur because of a restriction in assimilate transport through the stem.

Recent research has attempted to solve these problems by altering the morphology of the pea plant, particularly the leaves and stipules. This work has been reviewed by Davies (1977b) and Snoad (1980). The objective of this study was to estimate the quantitative inheritance of the vegetative structures, the leaves, stipules and tendrils, using different foliage types. Quantitative inheritance of the yield components of these altered phenotypes was also investigated.

REVIEW OF LITERATURE

1.1 The pea crop

The pea crop has two important defects: its proneness to lodging or collapsing of the canopy and the excessive amounts of vegetative growth produced (Snoad *et al* 1971, Snoad 1973, 1975, Davies 1977a). This can effect pea yield and quality, and the efficiency of the harvesting operation.

In recent years pea breeders have overcome some of these problems. This has been achieved with the incorporation of genes which can modify the morphology of the plant, particularly leaves and stipules (Snoad *et al* 1971, Snoad 1973, Snoad *et al* 1974, Ali 1980).

1.2 Pea genetics

1.2.1 The Normal Pea leaf

The normal pea leaf is compound, usually pinnate with one or more pairs of leaflets. The petiole has two large stipules at its base and ends in several tendrils (Blixt 1974, Sutcliffe and Pate 1977). During ontogenesis the leaf goes through a series of metamorphoses (Blixt 1974). The scale leaves are followed by approximately three simpler leaves with one pair of leaflets and one terminal tendril. Full complexity is reached at about the time of appearance of the seventh leaf; the number and combination of leaflets and tendrils being characteristic for a particular genotype. Blixt (1972) notes at the end of ontogenesis there is a slight tendency to return to greater simplicity.

1.2.2 Foliage Mutants

The morphology of the normal pea leaf is subject to modification by a number of genes (Blixt 1972, 1974). Genes which have an effect on the foliage of the plant include: "latum", *lat*[1], (Lamm 1957) increasing foliage area; "elongata", *elo* (Kellenbarger 1952); "folia oblonga", *fo* (Harstedt 1950); *y* (Brotherton 1923) reduces foliage width; "maximo-reductus", *mare* (Blixt 1972) foliage is thread like and reduced; "narrow rouge", *nr* (Blixt 1972) foliage narrow with pointed apex; "reductus", *red* (Lamprecht 1948) and "tenuifolius", *ten* (Lamprecht 1949) result in narrow leaflets; "unipetiole", *up* (Rosen 1944, Lamprecht 1963, Snoad and Davies 1972) has only one pair of leaflets; "Rogue" *X* (Mathews 1970, Brotherton 1923) foliage and pods narrow with pointed apices; sinuate leaf, *Sil* (Marx 1977); notched leaf, *nol*, (Sharma 1972b); and "insectus", *ins* (Lamprecht 1959) causes a deeply incised leaflet apex.

The "clavicula" gene, *tl*, produces the "acacia" phentotype where tendrils are replaced by leaflets (Vilmorin 1910, Vilmorin and Bateson 1912, White 1917, Lamm 1957). Wellensiek (1959) has produced this phenotype by neutron radiation. In the heterozygous form the tendrils are slightly strap-shaped (Sverdrup 1927, Nilsson 1933). Another allele at the *tl* locus was reported by Lamm (1957). This type of acacia phenotype, tl^{pet}, has extended petioles and is recessive to the short petioled form, tl^{w} (= *tl* earlier) (Solovjeva 1958, Khangildin 1966). The acacia type has been shown to be linked with wrinkled seed (Pellew 1913, Vilmorin 1910, Vilmorin and Bateson 1912). A recombination fraction of 0.0159 was reported by Vilmorin and Bateson (1912).

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1 NOTE: Throughout the text capitalized gene symbols indicate that the mutant in question is dominant and the lower-case symbols refer to genes that are recessive to the normal.

1.2.3 Stipules

A number of separate genes can influence stipules. Blixt (1972) reports cases where stipules may become longer, increased in size or narrower than normal. The gene, *st*, results in a reduction in stipule size (Pellew and Sverdrup 1923). Other genes affecting stipules include the "Cochleata" gene, *coch*, which results in spoon-shaped stipules on a long petiole (Wellensiek 1959, 1962, Marx and Mishanec 1970); "stipula imminata", *stim*, (Lamprecht 1960) causes stipula to be narrow and diamond shaped; and *cist* (Kumar and Sharma 1975) results in a circular stipule.

Several genes affect both the size of leaflets and stipules. The gene "tenuifolius", *ten*, produces narrower leaflets and stipules than the normal type (Lamprecht 1949, Yarnell 1962); "Lathyroides", *lath*, results in leaflets and stipules which are pointed and narrow (Lamprecht 1959b). Genes which increase length and breadth ratios of leaflets have similar effects on stipules. Four independent genes are involved, these are *fo*, *fob*, *fol* and *Fom* (Yarnell 1962).

The reduced stipule form, *st*, is recessive to the normal (Pellew and Sverdrup 1923, Sverdrup 1927), however Brotherton (1923) found dominance for a similar smaller form. This was the result of using the "rogue" pea (Bateson and Pellew 1915, 1920) which always behaves as a dominant, giving a very peculiar form of segregation.

1.2.4 Tendrils

The action of the "afila" gene, *af*, results in the leaflets of a pea plant being transformed into tendrils (Kujala 1953, Solovjeva 1958). The recessive condition of afila in the presence of the acacia, *tl*, background (*afaftltl* genotype) results in a mass of small leaflets (Goldenberg

1965) and can cause in an increase in total leaf area (Harvey 1972). Another gene, the tendrilled acacia, *tac*, produces a leaf with tendrils and an apical leaflet (Sharma 1972a, Sharma and Arabindan 1972, Sharma *et al* 1972).

Marx (1977) reports a pea phenotype where adventitous tendrils arise from clefts in the tips of stipules. This occurs when the sinuate leaf mutant, *sil*, is in combination with the afila background.

1.3 Modified plant types

1.3.1 Agronomic aspects

Of all the genes which can modify the pea plant, three have received considerable attention during the last decade. These are the *af*, *st* and *tl* types. They form the genetic basis of the "leafless", *afst* , and "semi-leafless", *af* forms.

Yield evaluations[2] have shown that pea cultivars containing these genes have yields equivalent to those of the conventional types (Snoad 1974, Snoad and Gent 1975, 1976, Goldberg 1973). Solovjeva (1958) has reported increased yields with semi-leafless cultivars. Snoad *et al* (1977) in describing the fruiting characteristics of one normal and three recessive foliar mutants showed the recessive genes individually had little effect upon yield. However in combination they caused a significant reduction in the yield of a single plant. Similar results were obtained by Harvey (1978) and Harvey and Goodwin (1978). Gritton (1972) recorded lower yields with leafless and semileafless types compared with the normal, however he was dealing with heterozygous plants within heterogeneous populations. Snoad (1981) also obtained lower yields, although the leafless type had a higher harvest index.

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[2] NOTE: Yield results discussed in this section include both green pea and dry pea yields.

The reasons given for differences in yield between conventional and modified leaf types include the variation in the adaptation of the genotype to environment and the genetic background of the cultivar. Lafond *et al* (1981) using near-isogenic lines from two different genetic backgrounds have shown the importance of the genetic background.

The single plant yield reductions observed can be overcome by increasing plant density through the use of higher seeding rates. Hedley and Ambrose (1979) studied the effect of shading on the yield components of different leaf genotypes. They showed there was no source limitation to the yield of these types at normal light intensities. Further work with a range of plant densities (Hedley and Ambrose 1980) showed conventional peas only outyielded the other types at lower densities but not at higher densities. These observations could suggest that the contrasting yield trial results have arisen from competition effects.

1.3.2 Physiological Studies

Physiological studies carried out on leafless and semileafless peas (Harvey 1972, 1974) have shown that these types have a similar photosynthetic efficiency to the conventional pea in relation to carbon dioxide uptake per unit area of leaf or tendril. The pattern of translocation is also similar (Harvey 1974).

In terms of seed production per plant the normal stipules of the semileafless phenotype can virtually compensate for the reduced photosynthetic area. Similarly the leaves appear to be able to compensate for the genetic reduction in stipule area (Snoad *et al* 1977, Harvey 1978). The components of yield have also been examined (Harvey 1978, Harvey and Goodwin 1978). In considering the water requirements in relation to seed production, Harvey (1980) showed that leafless phenotypes utilized less water and correspond-

ingly produced a lower total seed dry-weight than the conventional pea. Wilson *et al* (1981) found that semi-leafless peas made more efficient use of water under dry conditions than the normal pea type. The results from all these physiological studies indicated that the altered plant types are not radically different physiologically to the normal types.

1.4 Components of Yield

A knowledge of the factors which determine yield and the environmental effects influencing it are necessary for an understanding of the inheritance of the components of yield.

Handwick and Milbourn (1967) have partitioned the final yield of a green pea plant into the following components:

$$\text{Yield} = \begin{matrix}\text{Number of}\\\text{Podding Nodes}\end{matrix} \times \begin{matrix}\text{Pods per}\\\text{Node}\end{matrix} \times \begin{matrix}\text{Peas per}\\\text{Pod}\end{matrix} \times \begin{matrix}\text{Weight}\\\text{per pea}\end{matrix}$$

Another component, the lateral branch is considered relatively unimportant as it contributes to only a small fraction of the total yield under commercial conditions (Snoad 1981b). Pods formed on the lateral branches are usually less mature than those on the main stem. Higher plant densities will decrease the number of branches (Kruger 1977).

1.4.1 Number of podding nodes

Flowering of peas commences after the shoot apex switches to the production of flower primordia in the leaf axil and the development of primordia into mature open flowers (Murfet 1977). The flower initials develop in the axils

of successive leaves until the senescence of the apical meristem (Hole and Hardwick 1976). This senescence is a result of developing fruits (Lockhart and Gottschalk 1961) and also to flower inhibitors produced by the *Sn* gene (Reid 1980). A longer vine length can provide more fruiting nodes and this may contribute to an increased yield. However a lengthy vine is an undesirable characteristic for processing peas. It results in a wider range of maturity, decreases the harvesting efficiency due to the greater through-put required through the viner, increases lodging and reduces light transmission through the canopy (Snoad 1974).

1.4.2 Number of pods per node

The inflorescence of the pea plant is a raceme. The number of flowers on each inflorescence varies from one to several (Blixt 1972). However the eventual number of pods per node at harvest depends on a series of developmental processes. The maxiumum number of flowers is characteristic of a particular genotype (Yarnell 1962) and the actual number depends on the environmental condition at flower initiation (Hole and Hardwick 1976). A reduction in the number of flowers or pods formed can occur with either flower abortion or pod abscission (Meadley and Milbourn 1970).

1.4.3 Number of peas per pod

Terasvouri (1915) reported the number of ovules per ovary in the pea ranges from four to twelve. Most cultivars have between seven and nine ovules per ovary.

Environmental conditions influence ovule number although it is less sensitive than seed number (Manner 1958, Linck 1961). Linck (1961) studying embryo failure in the cultivar *Alaska* found a third of the embryos failed to

develop. Failure was most frequent with the ovules in the end positions of the pod. Similar results were reported by Manner (1958). Lack of fertilization was not considered to be the cause of embryo mortality. Pate and Flinn (1977) observed high frequencies of abortion of ovules in peas grown under adverse environmental conditions.

1.4.4 Weight per pea

The weight of green peas per pod is controlled by the maturity of the pea and to a lesser extent by its size. This may be influenced by management practices such as irrigation.

Anderson and White (1974b) and also Maurer *et al* (1968) studied the effect of plant density and irrigation on pea size. Irrigation of plants grown at lower densities resulted in more podding nodes which were less mature and smaller in size than those grown at higher densities.

With the onset of maturity there is an accumulation of starch in the pea seed. Pate and Flinn (1977) found up to 45 percent of the total dryweight in round seeded types and 35 percent total dryweight in wrinkled pea types was starch. The increase in yield over the stage at which peas are harvested as a function of time is a non-linear relationship (Anderson and White 1974a). Lynch and Mitchell (1953) have shown that quality changes over this period, it reaches an optimum level then declines. Sykes (1953) considered the quality factors of tenderness and flavour to be strongly dependant upon the stage of maturity of the pea.

1.4.4.1 Pea Maturity

A number of methods have been used to estimate the level of maturity of the pea. Many of these are discussed by Lynch and Mitchell (1953) and by Torfason *et al* (1956).

The more common methods used are;

(i) the tenderometer (Martin 1937),
(ii) the maturometer (Lynch and Mitchell 1953) and
(iii) the alcohol insoluble-solids content (Kertesz 1934, 1935).

The tenderometer measures the resistance of a constant volume of peas to the shearing forces of two grids; the tougher the peas, the greater the resistance and hence the higher the maturity. The maturometer measures the mass resistance of peas to puncturing by steel pins, the more resistant, the more mature. The alcohol insoluble-solids test is a chemical analysis which measures starches, hemicelluloses, fibre and proteins, the sugars are dissolved. The proportion of the insoluble compounds increases with the advancement of maturity. Comparisons between the different methods have been discussed by Sayre (1954), Adam (1957) and Ottoson (1968). A good correlation exists between the alcohol soluble solids chemical method and that of the widely used tenderometer.

1.5 Quantitative Genetics

1.5.1 Introduction

Quantitative genetics has been defined by Falconer (1981) as the study of the inheritance of continuous characters. Quantitative genetics is based on the assumption that continuous characters are determined by genes which behave in the same way as the genes of major effect which control discrete characters. However the distinct classes of the classical mendelian methods do not occur.

1.5.2 Partitioning genetic variance

The basis of quantitative genetics is the partitioning of the phenotypic value of a character for an individual

into components attributable to the influence of the genes and of the environment (Johannsen 1903, 1909).

$$P = G + E$$

where P is the phenotypic value, G is the genotypic value and E is the environmental deviation.

The genotypic value can be further divided into three components (Kempthorne 1954, 1955, Cockerham 1954):

$$G = A + D + I$$

where A is the sum of the additive effects of genes at all loci or the average gene effect; D is the sum of dominance deviations (or intra-locus interaction effects) and I is the sum of the inter-loci interactions or epistatic effects of genes at two or more loci.

The additive genetic component arises from the differences of a pair of corresponding homozygotes (Mather and Jinks 1971, 1977). It is the departure of one of the homozygotes from the midparent or origin. It is positive for the homozygote with the increasing allele and negative for that with the decreasing allele.

The dominance component results from the departure of the heterozygote from the mean of the corresponding pair of homozygotes (Mather and Jinks 1971, 1977). It is positive when the heterozygote is similar to the higher homozygote and negative when it is more like the lower homozygote.

Non-allelic interaction arises from the modification of the additive and dominance effects at one locus resulting from allelic substitution at other loci.

The variances of these values are the parameters estimated from quantitative genetic experiments (Fisher *et al* 1932, Mater 1949).

$$\sigma^2_P = \sigma^2_G + \sigma^2_E$$

and

$$\sigma^2_G = \sigma^2_A + \sigma^2_D + \sigma^2_I$$

The epistatic effects can be further partitioned (Cockerham 1954).

$$\sigma^2 I = \sigma^2 AA + \sigma^2 AD + \sigma^2 DD$$

Where $\sigma^2 AA$ is the additive x additive variance, $\sigma^2 AD$ the additive x dominance interaction and $\sigma^2 DD$ the dominance x dominance variance. The environmental variance, $\sigma^2 E$, can be partitioned in other ways also, depending upon experimental design (Le Clerg *et al* 1962, Comstock and Moll 1963).

1.5.3 Experimental designs

The simplest of the experimental mating designs used to obtain estimates of genetical components are the basic generations and random biparental matings.

The basic generation consist of F2, first backcrosses B1 and B2 and an F1 for a cross between a pair of pure-breeding lines P1 and P2 (Mather and Vines 1952, Opsahl 1956, Hayman 1958b, 1960b, 1960c). The means and variances of the six families permit the estimation of the additive and genetic components D, H and F, and the environmental component, E. Their determination is known as the generation means analysis. This also detects: non-allelic interaction, genotype x environment interaction and reciprocal differences.

The random biparental mating (RBIP) design involves crossing parents in pairs to produce full sib families (Kearsey 1965, Mather and Jinks 1971). Mather (1949) discusses using F3's produced from intercrossing pairs of F2's.

Total variation can be subdivided into the variation between full sib family means (full sib covariance) and the mean variation within full sib families.

The random biparental design is limited to only two degrees of relationship among progeny, either full sibs or unrelated. Other degrees of relationship require families with only one parent in common. For example, half sibs among offspring of a randomly mating population includes the North Carolina 1 and 2 designs and diallels.

The North Carolina 1, or hierarchical, design is where a random sample of males is mated to a number of different females (Comstock and Robinson 1948, 1952a, Kempthorne 1957). The males being common parents to a number of progeny families. Morley (1960) has extended this design by the inclusion of genotype x environment interaction.

The North Carolina 1 design has made no allowance for either common family environmental effects or maternal effects (Mather and Jinks 1971). This bias has been removed with the North Carolina 2 design in which half sib families have a common mother as well as a common father (Comstock and Robinson 1948, 1952a, Kempthorne 1957). This has been achieved by a systematic crossing programme in which n_1 males are crossed with n_2 females in turn to produce $n_1 n_2$ progeny, i.e. a factorial mating design where the males and females are different.

Other methods have been proposed for investigating randomly mating populations. These include:

1. Inbreeding a random sample of the population (Mather and Jinks 1971, Kearsey 1970, Hillel *et al* 1972).

2. Making test crosses to purebreeding lines or their F1's (Comstock and Robinson 1952b, Kearsey and Jinks 1968).

3. The triple test cross (Kearsey and Jinks 1968, Jinks and Perkins 1970, Pooni and Jinks 1976, 1978), where a random sample of individuals from a population are crossed to three testers (two inbred lines and their F1).

4. Combining the generation means analysis with the triple test cross (Jinks and Perkins 1969, Perkins and Jinks 1970).

Although these multiple mating designs were developed for the analysis of random mating populations, they are also applicable to other kinds of populations including inbred and F2 populations.

1.6 Diallels

The diallel cross is a mating system in which a set of inbred lines is crossed in all possible combinations. It was first introduced by Schmidt (1919) to denote all possible crosses among a collection of male and female animals. The diallel can be regarded as a special case of the North Carolina 2 or factorial design where the N_1 males and N_2 females are identical (Cockerham 1963).

1.6.1 Diallel cross designs

Diallel cross designs may be classified into a number of types:

1. designs involving P monoecious individuals or inbred lines (after Griffing 1956a, 1956b). These include designs with and without parents and with and without reciprocal crosses.

2. Partial diallels. These designs overcome the constraint of the large number of crosses required when the number of parents increases (Gilbert 1958, Kempthorne and Curnow 1961, Curnow 1963, Fyfe and

Gilbert 1963, England 1974, Mathur and Narain 1976).

3. Two level designs which contain a diallel cross of individuals within a diallel cross of a population (Hinkelmann 1974).

4. Triallels. Rowlings and Cockerham (1962a) have extended the diallel to analyse three-way hybrids, a cross between an inbred line and an unrelated F1 hybrid. They have presented a model for the estimation of additive and dominance variance components.

5. Partial triallel cross designs have been developed as an extension of the triallel (Hinkelmann 1965).

6. Four way mating designs or the tetra-allel cross design for analysing double cross hybrid populations have been discussed by Rawlings and Cockerham (1962b). Hinkelmann (1968) has presented a partial diallel cross design for this model. It considers a sample of all possible four-way crosses to determine combining abilities. However prediction formulae are available for determining the outcome of double crosses from the performance of single crosses (Jenkins 1934, Eberhart *et al* 1964).

1.6.2 Analysis of diallel cross data

Early methods for the analysis of diallel crosses involved the use of regression techniques (Hull 1946), and factorial analyses (Yates 1947). These were later followed by the Hayman-Jinks analysis (Jinks and Hayman 1953, Jinks 1954, Hayman 1954a). This method was based on an idea introduced by Fisher (1918) and later developed by Fisher *et al* (1932) and Mather (1949). It was basically an extension of Mather's (1949) method for crosses between two inbred lines.

Alternative methods of diallel analyses were developed by Kempthorne, Gardner, Griffin and Wearden. Kempthorne (1956) analysed the diallel in terms of variances of inbred parents, crossbred progeny and the covariance between parents and progeny. Gardner (Gardner and Eberhart 1966, Eberhart and Gardner 1966) gave a model to provide the genetic expectations of means of a fixed set of random-mating parents in a diallel cross while Wearden (1964) discussed the diallel cross replicated in a randomised block design. Griffin (1956a, 1956b) (See Section 1.6.4) estimated combining ability effects from a diallel cross.

The Hayman-Jinks analysis involves the partitioning of the second degree statistics, Variance (Vr) and Covariance (Wr) of parental arrays. It can be separated into:

1. The analysis of variance of the diallel table (Hayman 1954b, Walters and Gale 1977). This later being extended to the half-diallel (Jones 1965, Walters and Morton 1978) and F2 and backcrosses (Hayman 1958a, Jinks 1956).

2. The analysis of variance of (Wr-Vr), the difference of the array covariance and variance.

3. The WrVr graphical analysis. This shows:

   (a) a test of the adequacy of the additive-dominance model

   (b) a measure of the average level of dominance

   (c) the distribution of dominant to recessive genes among the parents

   (d) the presence of non-allelic gene interaction (Hayman and Mather 1955, Hayman 1957, Mather 1967, Coughtrey and Mather 1970).

4. The estimation of the genetical components D, H1, H2 and F and their derived statistics. D measures additive gene effects, H1 and H2 measure dominance

effects and F measures the relative frequencies of dominant and recessive alleles. From Falconer (1960), when parents are inbred lines (f = 1), D = $2\sigma^2A$, where σ^2A is the additive genetic variance of a random mating population and H1 = $4\sigma^2D$ where σ^2D is the dominance variance of a random mating population. The derived statistics will give direct estimates of the degree of dominance, the ratio of dominant to recessive alleles, the symmetry of gene distribution, number of effective factors and estimates of heritability.

1.6.3 Genetical assumptions

The interpretation of the genetical components depends on the validity of a number of assumptions (Hayman 1954a). These are:

1. diploid segregation
2. no differences between reciprocal crosses
3. independent action of non-allelic genes and in the diallel cross
4. absence of multiple allelism
5. homozygous parents
6. independent distribution of genes between parents.

The validity of the assmptions are tested by the homogeneity of the (Wr-Vr) variance, a significant Wr on Vr regression and a non-significant deviation of the regression line from unity (Jinks and Hayman 1953, Hayman 1954a).

If the assumptions fail, Hayman and Jinks have recommended removing arrays from the diallel table until the assumptions can be satisfied. This procedure has been severely criticised (Gilbert 1958, Kempthorne 1956, Baker 1978, Sokol and Baker 1977). Kempthorne (1956) considered that with the removal of arrays, the parents were no longer a random sample from the population of inference. He insisted parents must be a random sample of inbred lines which are the result of unselected inbreeding from a random mating population rather than just a set or even sample of inbred

lines. Kempthorne's comments are not justified in this context as his remarks have only beenmade in terms of cross-pollinated crops.

1. Diploid Segregation

The assumption of diploid segregation is usually made (Cockerham 1963) because knowledge concerning gene action is with reference to diploid species. However certain polyploids do behave as diploids during meiosis thus fulfilling this assumption (Strickberger 1968). An example is common wheat, a hexaploid with a diploiding gene (McFadden and Sears 1947).

2. Reciprocal differences

Differences between reciprocal crosses can occur and are usually assumed to be the result of maternal effects. Cockerham (1963) reported for many species of plants reciprocal effects have not been found to be significant. Many results for peas have shown an absence of reciprocal differences (Krarup and Davis 1970a, 1970b; Ibarbia and Bienz 1970a; Kumar 1973; Pandey and Gritton 1975, Gritton 1975) however Davies (1975) found a reciprocal difference for seed size.

3. Non-allelic interaction

The assumption of non-allelic interaction or lack of epistasis is considered by Sokol and Baker (1977) to be biologically unrealistic as the absence of epistasis cannot be assumed when dealing with quantitative characters (Mather 1943, Horner *et al* 1955, Gilbert 1958, Cockerham 1959). It is usual to assume lack of epistasis. However if epistasis is present, a fraction of the additive comonent of the epistatic variance will be confounded with both the additive genetic variance and the dominance variance.

4. Multiple alleslism

The assumption of no multiple allelism has been included by Hayman (1954a) in an effort to remove the complicat-

ing effects which could occur. Most practical situations consist of a comparison between two alleles per locus, so this is not an unreasonable assumption.

5. Homozygous parents

The use of homozygous parents is assumed when dealing with self pollinated crops. Heterozygous parents can be used as demonstrated by Oakes (1967). He investigated the effect of non-homozygosity and multiple allelism in parental lives and showed that most of the information obtained using homozygous parents could still be extracted if the parents were heterozygous. Dickinson and Jinks (1956) have presented an analysis for the use of heterozygous parents.

6. Independent distribution

The failure of the assumption of independent distribution of genes between parents can effect the WrVr graphical anlaysis in the estimation of dominance (Hayman 1954a). Sokol and Baker (1977) consider independent distribution will be assumed only if the parents of the diallel are chosen as a random sample.

1.6.4 Combining ability diallel analysis

A second approach to the analysis of the diallel cross is the combining ability analysis (Griffing 1956a, 1956b). The concepts of general and specific combining ability have been defined by Sprague and Tatum (1942). General combining ability, GCA, is the average performance of a line in hybrid combination. Specific combining ability, SCA, is defined as the deviation of a hybrid from its expectation based on the average performane of its parents.

Griffing (1956b) has outlined procedures for analysing four types of diallels. These include combinations of the presence and absence of parents and reciprocal crosses.

The inclusion of parents in the analysis was considered by Griffing to bias the results. With the combining ability diallel the interest is usually in the performance of the F1 crosses.

The GCA and SCA variances, σ^2GCA and σ^2SCA, can be related to covariance among relatives (Griffing 1956a).

$$\sigma^2 GCA = COV\ (HS)$$
$$\sigma^2 SCA = COV\ (FS) - 2\ COV(HS)$$

Where COV(HS) and COV(FS) are the half sib and full sib covariances respectively.

Kempthorne (1957) has defined these covariances:

$$COV(FS) = \frac{1 + F}{2}\sigma^2_A + \left(\frac{1 + F}{2}\right)^2 \sigma^2_D + \left(\frac{1 + F}{2}\right)^2 \sigma^2_{AA} + \left(\frac{1 + F}{2}\right)^3 \sigma^2_{AD} + \left(\frac{1 + F}{2}\right)^4 \sigma^2_{DD} + \cdots$$

$$COV(HS) = \frac{1 + F}{4}\sigma^2_A + \left(\frac{1 + F}{4}\right)^2 \sigma^2_{AA} + \cdots$$

Where F is the inbreeding coefficient. With self-fertilization F = 1, then

$$\sigma^2_{GCA} = \tfrac{1}{2}\sigma^2_A + \tfrac{1}{4}\sigma^2_{AA}$$

and $$\sigma^2_{SCA} = \sigma^2_D + \tfrac{1}{2}\sigma^2_{AA} + \sigma^2_{AD} + \sigma^2_{DD}$$

These genetic variances can be used to calculate heritability ratios.

Griffing's combining ability model has been extended to permit analysis over a number of environments (Singh 1973a, 1973b, Dhillon and Singh 1977).

1.7 Quantitative Genetics in Peas

A number of quantitative genetic studies have been reported for peas. These include the use of the generation means analysis for the inheritance of yield components (Johnson 1957, Marx and Mishanc 1962, Ibarbia and Bienz 1970a, 1970b, Singh and Singh 1979, Chandel and Joshi 1979). Diallels have also been widely used for yield components (Krarup and Davis 1970a, 1970b, Snoad and Arthur 1973a, 1973b, 1974, Singh and Singh 1970, Koranne and Singh 1974, Pandey and Gritton 1975, Davies 1975, Gritton 1975, Singh *et al* 1980, Srivastava and Sachar 1975, Kumar and Das 1974, 1975a, 1975b, Brahmappa and Singh 1977, Dahiya *et al* 1977, Sharma *et al* 1977, Weber 1976, Singh *et al* 1975, Bhullar *et al* 1976). Flowering has been considered by Rowlands (1964) and Watts *et al* (1970) while leafroll virus resistance has been examined by Crampton and Watts (1968). Most of these quantitative genetic studies have shown that the components of yield are controlled by an additive genetic system.

Very few studies in quantitative inheritance have been carried out for the vegetative characters. However Guzhov (1976) examined the connection between type of leaf and yield while Lichter (1959) considered the length-width ratio of leaflets and found this character to be under the control of additive gene action although non-allelic genes had only a small effect.