Favourable floral morphology, convenience of control pollination and large number of kernels resulting from a single pollination has more frequently led to the choice of maize plant for several basic investigations which provided better understanding and have yielded valuable results of economic importance. Through these studies in maize a number of basic genetic principles have been formulated or further substantiated. During the past three decades, voluminous literature has been accumulated by maize workers on various facets of crop improvement. The breeding methodologies developed by the maize breeders have also been used by several other crop breeders. The present review will, however, relate to the problems of direct interest to the present study. Published literature on the following aspects will be reviewed:

1. Nature and components of genetic variances
2. Methods used in the estimation of genetic parameters
3. Recurrent selection schemes
4. Genetic architecture of selected and unselected population of maize
5. Genetic architecture of yield and other agronomic traits
6. Genotype-environmental interaction
1. **Nature and components of genetic variances:**

The phenotype, of most of the characters of economic importance, with which the breeder, has frequently to reckon with is fairly complex. Not only large number of genes each with small individual effects, are involved in its inheritance, but these genes interact among themselves in a complex manner and are highly influenced by the environmental effects. In the selection of an appropriate breeding methodology with a view of maximising gains per unit of time, it is vital to have information on the proportion of heritable genetic variation as well as a measure of genotype environment interaction. Several eminent statisticians like Galton, Haldane, Fisher and Wright have greatly contributed to our present knowledge of variation.

Fisher (1918) divided total genotypic variation into three of its logical components: (i) due to average effects of the genes (additive genetic variance) (ii) due to allelic interactions of segregating genes (dominance variance) and (iii) due to non-allelic interaction of segregating genes (epistatic variances). Wright (1935) defined and gave a detailed treatment to components of genotypic variances: (i) additive genetic variance (ii) variance due to dominant deviations from the additive scheme and (iii) variance due to epistatic deviations from the additive scheme. More recently Cockerham (1961), Kempthorne (1955), Rawlings and Cockerham(1962)
have further partitioned epistasis into additive x additive, additive x dominance, dominance x dominance, additive x additive etc. type of non-allelic interactions.

Gardner (1963) outlined the following genetic parameters, of special interest to plant breeders, information on which should be gathered so as to formulate the most efficient improvement programme:

(a) Additive genetic variance ($\sigma^2_A$) which results from additive effects at all segregating loci.

(b) Dominance variance ($\sigma^2_D$) which results from intra-allelic interactions of genes at segregating loci.

(c) Epistatic interaction which results from inter-allelic interaction of genes at two or more segregating loci and it is divisible into additive x additive ($\sigma^2_{AA}$), additive x dominance ($\sigma^2_{AD}$) and dominance x dominance ($\sigma^2_{DD}$) for the two loci and additive x additive x additive ($\sigma^2_{AAA}$) etc. for the three or more loci.

(d) Average degree of dominance or the ratio of dominance variance to additive genetic variance.

(e) Genotype x environment interaction which may be divided into additive gene effects x environment and non-additive gene effects x environment.

(f) Genotypic correlations among various characters.
Reply to the comments of the examiner(s)

Item 1. As desired $C^2$ has been corrected throughout the thesis.

2. The term ear girth (originally meant to describe ear diameter) now has been replaced throughout with ear diameter.

Following replies are in response to the comments communicated to me and refer to the page and line number of the thesis submitted earlier.

Page 1, line 13

Richey (1922) in 'table 2' of his paper has pointed out that 136 of the 244 hybrids tested, gave better yield than the better parent. He further observed that 60 out of 244 hybrids (24.6 per cent) recorded 6 to 15 per cent more yield than the better-parent. In view of the comments of examiner, I have suitably revised the work of Richey (1922) on page 1 para 1.

Page 3, line 11

Necessary correction has been made.

Page 4, line 5

Necessary correction has been carried out. Details of the work reported by various authors have also been presented in review of literature.

Page 3, line 19-21

Necessary correction has been made.
Necessary correction has been made. In the present context, the term 'simple recurrent selection' refers to the scheme which was proposed by Jenkins (1940) and generally referred to as recurrent selection. Still in a broader sense, the term recurrent selection could be used to cover all schemes including mass selection; wherein repeated cycles of selections are followed. Due to paucity of space, I have used the term recurrent selection in the restricted sense (as of Jenkins 1940).

Necessary correction has been made.

Seven per cent gains per cycle have been reported in reciprocal recurrent selection programme. Each cycle of reciprocal recurrent selection requires three crop seasons. Necessary correction has been made.

Under purely overdominance model, the hybrids showed substantial improvement while the parents showed a decline after five cycles of reciprocal recurrent selection. Necessary correction has been made.

Necessary correction has been made.
Page 16, line 6

This is a citation from the paper of Cress (1967) page 566.

Page 16, line 20

Necessary correction has been made.

Page 17, line 12 and 13

Necessary correction has been made.

Page 28

Work of Comstock and Moll (1963) on genotype-environment interaction has been included.

Page 32 and 33

Details of the procedure used in the development of $G_1$ versions of $J_1$ and Cuba 11J have been recorded.

Page 34 and 35, line 1

Necessary correction has been made.

Page 35, line 25

Necessary correction has been made.

Page 35, line 27

Conventionally in the Indian Maize Improvement Program, data on days to silk are recorded when 75 per cent plants in a plot have silked. However, 50 per cent, days to silk have also been reported in literature by several authors.
For grain yield the estimates from combined analysis were in all cases lower than those of individual years except for Cuba 11J (C0) where the combined estimates closely approached the estimates obtained in 1971 – the lower of the two estimates (Table 4) recorded in individual years.

Needful has been done. The components of variance on theoretical consideration are expected to be positive (Lindsey, et al. 1962). The estimates at times may be negative particularly when the corresponding effects are too small or zero. Thus one of the possible explanation for negative values would be non-existence of the corresponding effects. In the present case both estimates of $G^2Ay$ and $G^2Dy$ for $J_1$ (C0) and $G^2Dy$ in $J_1$ (C1) were negative (Table 11). The estimates of $G^2my$ and $G^2fy$ for $J_1$ (C0 and C1) were observed to be non-significant. In fact $G^2my$ ($J_1$ C0) and $G^2fy$ ($J_1$ C1) were negative (Table 9). Table 7 also supported the fact that the component, male x block x year and female in male in block in year were not significant both for C0 and C1 versions. Thus the low estimates as recorded in Table 7 resulted in negative interaction estimates of $G^2Ay$ and $G^2Dy$.

One of the main objectives of the present study was to compare the C0 and C1 versions of the two populations. Besides studying the relative magnitude of additive and non-additive genetic
variance, present data provided an opportunity to predict the likely genetic advance through mass selection and full-sib family selection in $C_0$ and $C_1$ versions. Predictions for the likely gains have been made for mass selection and full-sib family selection for the $C_0$ and $C_1$ versions. The hybrid performance has not been studied in the present treatise. Comparisons have been made for $C_0$ and $C_1$ versions within each populations. The comparison of $J_1$ vs. Cuba 11J, however, has limited meaning.

Page 108

Necessary correction has been made.

Page 109

Estimates based on pooled analysis are more reliable. This point has been given due consideration in discussion.

Page 106

Needful has been done.

Page 113

The gains through mass selection and full-sib family selection have been predicted for $C_0$ and $C_1$ versions. Procedure for such prediction has been given on page 55.

Page 113, last paragraph

The first sentence applies to Cuba 11J ($C_0$) population. Necessary addition has been made.
Overall gains for two years were predicted since data from individual years showed contradictory trend for C₀ and C₁ versions. This was done since pooled data are more reliable than the individual environment information.

I agree, such results are expected.

Needful has been done.

Necessary addition has been made.

Standard errors have been calculated and included in Table 50 and 51. The test of significance, through 't' test, has also been made.

I agree with the examiner that the reciprocal recurrent selection was primarily designed to improve the performance of F₁ hybrids. The present study, however, was undertaken with a view to study the genetic architecture of selected and unselected populations following one cycle of reciprocal recurrent selection.

I agree with the examiner. Part of the difference could also
be due to differential number of replications. In present study only two replications were used while previous study involved 4 replications.

Page 127 (Table 52)

Necessary correction has been made.

Page 130, line 12-14

Needful has been done.

Page 134

Present investigation was designed to study the genetic architecture of original and selected populations following one cycle of reciprocal recurrent selection. The information primarily was sought for genetic make-up of populations and changes which may have occurred during selection. It is in this context, the information at the intra-population level has been presented.

Page 134, line 2 and 3

Work of Lonnquist et al. (1966) has been included.

Page 134, line 7 and 8

Needful has been done.

Page 134, line 8 and 9

Necessary correction has been made.

Page 134, line 10

Necessary correction has been made.
The method of estimation of heritability of D.S. Falconer is based on full-sib correlation or offspring parent regression. For these types of estimates the standard errors are readily available, being the standard errors of correlations or regression co-efficient used, but in the present study heritability has been estimated as the ratio of additive genetic variance and total variance by the formula $\frac{4\sigma^2_m}{\sigma^2_m + \sigma^2_e}$. Although the S.E. of individual components used is available, the S.E. of the combined expression is not possible because the components are not independently estimated. As such no formula has been given by any author. Hence it has not been possible to attach standard errors to heritability.

I agree with the examiner that the pooled estimates are more reliable and they deserve more emphasis than the individual year data.
2. **Methods used in the estimation of genetic parameters:**

Fisher, Immer and Tedin (1932) were among the first ones to propose an experimental approach for separating and measuring additive and dominance effects, using second and third degree statistics. During the last three decades a number of biometrical and statistical approaches have been developed for the estimation of genetic parameters. Various models are based on specific assumptions and require data from parents and their progenies in various segregating generations. Theoretical expectations have been worked up for various models. The contribution of Mather (1949), Hayman (1954a), Gamble (1962), Rawlings and Cockerham (1962), Powers (1950), Comstock and Robinson (1952) and others are outstanding. The important methods for the partitioning of genotypic variances are as follows:

(a) **Estimates based on segregating generations from crosses of two pure lines:** Under the simplest scheme developed by Mather (1949), data from two homozygous parents, their $P_1$ and $P_2$ and backcrosses are used in the estimation of additive and dominance variance. Epistasis is assumed to be absent under this model. Components of variation in $P_2$, backcrosses and their advanced generations have been reported by Mather and Jinks (1971).
(b) **Diallel and partial diallel analysis:** Jinks and Hayman (1953), Hayman (1954, 1958 and 1960) and Jinks (1956) developed the diallel approach for the estimation of various genetic parameters viz., $D$, $H_1$, $H_2$, $h^2$ and $F$ for homozygous inbred lines. Both analytical and graphical analyses have been developed which provided information on the magnitude of additive and dominance variance. The presence of epistasis can also be detected by the distribution of array points in $W_r$, $V_r$ analyses. Valuable information relating to degree of dominance, frequency of dominant and recessive alleles, symmetry of positive and negative alleles showing dominance and number of gene or gene groups involved in the inheritance of a particular character and exhibiting dominance is also provided from this analysis. The diallel approach, involving homozygous lines was extended by Dickinson and Jinks (1956) for heterozygous parents.

The combining ability analysis developed by Sprague and Tatum (1942) was further developed by Griffing (1956a). This scheme provided for the estimation of relative degree of dominance from experiments of varied composition, such as the presence or absence of parents as well as of reciprocal crosses. Combining ability estimates can be made both under fixed as well as random effect models.

Various sampling schemes for partial diallel analysis have been suggested and can be used with varied degree of...
precision (Kempthorne, 1956, Kempthorne and Curnow, 1961 and Fyfe and Gilbert, 1963). Partial diallels also provide an estimate of additive and non-additive variances.

(c) **Tri-allel and quadri-allel analyses:** The diallel analysis was further extended by Rawlings and Cockerham (1962a,b) to provide genetic information on three-way and double cross hybrid populations. From these schemes it is possible to estimate the magnitude of various components of inter-allelic interactions and to measure the order effect of lines and crosses.

(d) **Powers partitioning method:** The scheme was developed by Powers (1950, 1951, 1955 and 1963). Under this procedure data on means, variances and frequency distribution are partitioned into their components on the basis of the genotypes of segregating generations. Tests for validity of genetic models postulated are made by comparing observed and expected frequency distribution and variances.

Phenotypic dominance was determined by comparing the means of two parents with their $F_1$. Genetic dominance was determined from the study of means, variances and phenotypes of different genotypes. The scheme also provides for an estimation of number of factors involved in the inheritance of a particular trait.

(e) **Covariance of half-sib and full sib:** This technique developed by Comstock and Robinson (1948) and
Anderson and Kempthorne (1954) have alone contributed mere in understanding the nature of gene action in heterozygous maize populations and advanced generations of single crosses among homozygous inbred lines than any other technique. These schemes in contrast to others provide the possibility of determining nature of gene action in a specific population for a set of characters. In these schemes various types of relatives are developed and their covariances are expressed as components of genetic variance. Covariances of half-sib, contain additive and additive x additive type of gene action while covariances of full-sib contain additive, dominance and epistatic interactions for relatives developed from heterozygous populations. The covariances can be expressed as linear functions of components of genetic variances without specifying anything about the gene frequency.

Comstock and Robinson (1948) outlined three experiments commonly known as North Carolina Designs I, II and III. Design I involved the evaluation of a number of sets of full-sib and half-sib progenies developed by mating plants at random. A randomly selected male plant is crossed to three or four female plants. Four or five such male groups are tested in each set. Number of sets may vary in an individual study where ten or more sets may be evaluated for estimating degree of dominance. The genetic variances were partitioned into $C^2_m$ and $C^2_f$ from which additive and non-additive fractions were estimated and relative dominance was determined. Design II is more akin to diallel
cross and is better suited to prolific or multiflowered species. It involved all possible crosses between two sets of inbred lines (designated as male and female). Usually a set of 10 inbred lines is divided into two groups of five each and twenty-five crosses among them are developed for each set. The variance in the progenies are divided into three components \( G^2_m \), \( G^2_f \) and \( G^2_{mf} \). Design III involved mating randomly chosen \( F_2 \) or advanced generation plants back to parental lines producing pairs of backcross progenies. The variances were separated into \( G^2_m \) and \( G^2_{ml} \).

The assumptions involved in deriving the expected mean square and the genetic interpretations for the three designs as noted by Comstock and Robinson (1948) were as follows:

(a) Random choice of individuals mated for production of experimental progenies

(b) Random distribution of genotype relatives to variations in environment

(c) No non-genetic maternal effects. Design II and Design III are useful in the presence of maternal effects, since maternal effects do not contribute to the pertinent mean square in the variance analysis of these two designs.

(d) Regular diploid behaviour at meiosis

(e) No multiple allelism

(f) No correlation of genes at separate loci. This implies no linkage among genes effecting the character studied or that, if linkage exist, the distribution of genotypes is at equilibrium with respect to coupling and repulsion phases

(g) No epistasis, i.e., the effect on variation in genotype at any single locus is not modified by genes at other loci.
(h) For estimating degree of dominance, gene frequencies should be one half at all loci where there is segregation (not necessary for Design III)

The expected variances for each of the three designs have also been reported by Comstock and Robinson (1948) and have been summarised by Gardner (1963). In Design I and III, $O_m^2$ accounts for one fourth of additive genetic variance while $O_f^2$ in Design I has been associated with one fourth of additive genetic variance and one fourth of dominance variance, while in Design II $O_m^2$ and in Design III $O_ml^2$ have been equated to $(1 + f)O_A^2$ where 'f' is coefficient of inbreeding. $O_{mf}^2$ in Design II on the other hand represents $(1 + f)O_D^2$. In heterozygous populations 'f' may be considered as '0'. Under such condition the expected variation would reduce to one fourth $O_A^2$ for $O_m^2$ (Design I) and $O_A^2$ (Design III), and one fourth $O_D^2$ for $O_{mf}^2$ (Design II) respectively. The relative dominance can be determined from any of the three designs. Estimates of one have generally been considered to represent complete dominance and value above and below this are over and partial dominance respectively. In the absence of multiple alleles Robinson et al. (1955) suggested that the values of dominance ratio $O_A^2/O_A^2$ for a single locus could be calculated for different degree of dominance and different gene frequencies. Authors presented values for gene frequencies ranging from 0.5 to 0.99.
3. **Recurrent selection schemes:**

Recurrent selection schemes have been proposed by various authors to overcome the problems arising out of continuous inbreeding for characters which are quantitatively inherited. It is well appreciated that the lines established their individuality and had limited genetic variability in early generations of inbreeding (Jenkins, 1940). Selection among the lines has long been recommended. Such a selection imposes serious limitations in selecting the most desired genetic recombinant. The ultimate aim in any of the improvement programmes is to increase the frequency of favourable genes. This can more effectively be done through recycling of selected lines. The various recurrent selection schemes are:

(i) Simple recurrent selection
(ii) Recurrent selection for general combining ability
(iii) Recurrent selection for specific combining ability
(iv) Reciprocal recurrent selection

From operational point of view the four schemes are alike and differ only in the manner of evaluation of the lines involved. The recurrent selection schemes basically involve: (a) inbreeding in the base population, (b) evaluation of lines and (c) recombining the selected lines. The simple recurrent selection scheme does not require the generation of test crosses. In recurrent selection for general combining ability,
a heterozygous source, like the parental variety, a synthetic or advanced generation of a hybrid may be used as a tester. Under recurrent selection for specific combining ability an elite inbred line or a single cross hybrid is generally used as a tester. In reciprocal recurrent selection, however, both populations under improvement are used reciprocally as tester parents.

Simple recurrent selection (Jenkins, 1940; Sprague and Brimhall, 1950; Sprague, Miller and Brimhall, 1952; Jenkins et al., 1954) and recurrent selection for general combining ability (Sprague and Brimhall, 1950; Lonnquist, 1950) capitalises on additive genetic variance, while recurrent selection for specific combining ability as recommended by Hull (1945) is specifically designed to make maximum use of over-dominance.

Reciprocal recurrent selection exploits both additive and non-additive genetic variances. It was first proposed by Comstock, Robinson and Harvey (1949). This scheme involves two heterozygous populations. The inbred lines developed in one population are top-crossed to other parent as a tester. The two sets of top crosses are evaluated in a number of environments. The selected lines are used to reconstitute the two populations. Penny et al. (1963) have summarised the data available from earlier studies on various recurrent selection schemes including the limited work done on reciprocal recurrent selection. In one of the studies involving Stiff Stalk Synthetic and Corn Borer Synthetic gains of 6.3 per cent and
3.7 per cent respectively were realized in two cycles of selection. The low level of gains were attributed to low genetic variance estimated in the base population.

Reciprocal recurrent selection has been used in various maize improvement programme and data on its efficiency have been accumulated in recent years. The contribution of Collier et al. (1959), Douglas et al. (1961), Penny et al. (1963), Moll and Robinson (1966), Eberhart (1967), Allison (1968), Anonymous (1968), Tobgy et al. (1970), Hallauer (1970), Hallauer (1971), Moll and Stuber (1971), Penny and Eberhart (1971) and Hallauer (1972) are of special interest.

Reciprocal recurrent selection programme has been most effectively used at Kitale, Kenya, wherein reciprocal recurrent selection programme between Kitale II and Ecuador 573 has been used over a period of years and the hybrids between the two improved versions has been commercially exploited. Gains of approximately 7 per cent in first cycle were realised (Eberhart, 1967). Each cycle of reciprocal recurrent selection takes a minimum of 3 crop seasons. Additional data on two cycles of reciprocal recurrent selection in these two populations have been reported by Darrah et al. (1972) who obtained a gain of 13.1 per cent against the predicted value of 11.9 per cent in the $F_1$ hybrid. In both studies a close agreement between observed and predicted gains was recorded.
Reciprocal recurrent selection programme has also been used at North Carolina in Jarvis and Indian Chief. Data relating to the efficiency of this scheme has been reported by Moll and Robinson (1966) and Moll and Stuber (1971). Moll and Robinson (1966) compared reciprocal recurrent selection and full-sib family selection in their effectiveness for improving both crossbred and purebred performance. After 3 cycles of selection it appeared that full-sib family selection was at least as effective as reciprocal recurrent selection in improving crossbred performance. Moll and Stuber (1971) observed that the hybrid among the reconstituted population recorded 9.67 per cent improvement per cycle. It was also observed that the full-sib family selection was 2.1 times more efficient than reciprocal recurrent selection in improving the two parental populations, while the reciprocal recurrent selection scheme was 1.3 times more efficient than that of full-sib family selection for $F_1$ hybrid.

Collier (1959) presented data on three cycles of reciprocal recurrent selection in yellow Sure Cropper and Ferguson Yellow Dent. The combining ability of the reselected population was considerably improved and considerable variations for various characters was recorded. Tobgy et al. (1970) used reciprocal recurrent selection in American Early and Giza Baladi. Even though marked difference in both parents was recorded but difference between the respective original and reconstituted population was significant only for American Early.
Marked improvement in heterosis was also recorded.

Illg (1969) while comparing the half-sib progenies of maize and their respective crosses concluded that the reciprocal recurrent selection scheme based on half-sib family selection was most effective.

Allison (1968) in contrast to earlier reports recorded little improvement in general and specific combining ability of populations reconstituted after four cycles of reciprocal recurrent selection. Brown and Allard (1971) recorded no change in gene frequencies after two cycles of reciprocal recurrent selection.

Cress (1967) reported extensive data on computer simulation programmes, assuming two alleles at each of the 40 independently segregating loci. Information on reciprocal recurrent selection assuming complete dominance and purely overdominance models at varied levels of initial gene frequency was envisaged. Under the completely dominant model, marked improvement in both the parental populations as well as the hybrid was recorded for the 20 generations for which the estimates were made. The improvement was very much marked when the initial gene frequency in the two parents was 0.1.

Under the purely overdominant model, the hybrids also showed substantial improvement while the parents showed a decline after 5 cycles of reciprocal recurrent selection. From his computer simulation studies, author observed that the
following two points are necessary in order to ensure maximum genetic potential and rapid rate of progress.

(1) "All genetic material entered into a long term programme of selection with progeny testing should be combined into one synthetic population. Any subsequent population required would be obtained by sampling the synthetic. This procedure reduces the problem of multiple alleles and can only increase, and not decrease, the genetic potential".

(2) "One generation of selfing (or inbreeding) should precede the test cross, where the real time lapse measured against rate of progress showed this to be more efficient".

In India reciprocal recurrent scheme has also been used successfully in four sets of composite populations, namely, \( J_1 \), Cuba 11J; \( B_1 \), Puerto Rico Group I; \( A_2 \), Cuba 11J, and \( B_1 \), \( B_{11} \). Gains of 10 per cent in first cycle of selection with hybrid were recorded in \( J_1 \) and Cuba 11J (Anonymous, 1968).

Reciprocal recurrent selection schemes have been under evaluation at Iowa since 1949. These studies were undertaken between Iowa Corn Borer Synthetic and Iowa Stiff Stalk Synthetic. Data on the efficiency of these selection schemes have been reported by Eberhart et al. (1973), Penny and Eberhart (1971) and Penny et al. (1963). Significant improvement in the performance of the hybrids following recurrent selection was reported. Moreover, considerable improvement was recorded in Stiff Stalk Synthetic over the
first three cycles of reciprocal recurrent selection, while in Corn Borer Synthetic there was little or no improvement. The gains realised from the selection schemes were 1.7 per cent per cycle against 7.2 per cent gains calculated from the pooled heritability and selection differential. After five cycles of selection 4.6 per cent linear increase per cycle was recorded in the hybrid with little or no change in the performance of parental varieties (Eberhart et al., 1973). Penny et al. (1963) while summarizing the earlier studies observed that regardless of the type of the recurrent selection schemes the observed gains from the $F_2$ single cross populations were consistently lowest, those from the open-pollinated variety, highest while those from synthetic varieties were intermediate. It was pointed out that difference in the extent of genetic variability and genetic linkage might provide part of the explanation.

4. Genetic architecture of selected and original populations of maize:

One of the primary criterion in the selection of any population improvement programme is to ensure possibility of improvement of a specific trait over a period of time. Availability of substantial proportion of genetic and more particularly additive component is vital for the success of any intra-population improvement programme. Accordingly it is necessary to have an estimate of variance in consecutive cycles of selection wherein favourable shifts in mean performance of
the population were obtained. Such information from reciprocal recurrent selection programme even though vital is available only from few studies.

Hallauer (1970) using North Carolina Design II estimated the additive and non-additive components in the parental variety and their F₁ cross in the original and reconstituted populations after four cycles of reciprocal recurrent selection. The additive component of the Corn Borer Synthetic for Co (original) and C₄ (reconstituted) were comparable while some reduction was observed in Stiff Stalk Synthetic as well as their hybrid. None of the changes in the estimation of dominance component was significant between the populations. The dominance ratio \( \frac{\sigma_D^2}{\sigma_A^2} \) was, however, observed to be less than one in case of original and reselected populations of hybrids as well as Corn Borer Synthetic. For Stiff Stalk Synthetic the dominance ratio decreased from more than one \( (C_0) \) to less than one \( (C_4) \). A slight positive shift in the dominance ratio \( \frac{\sigma_D^2}{\sigma_A^2} \) for Corn Borer Synthetic and the hybrid was also recorded. The estimates of heritability registered a marginal improvement in two parental varieties with a slight decrease in the hybrid population.

Chioco et al. (1970) estimated genetic variances of 12 maize composites derived from six cycles of reciprocal recurrent selection in Ferguson Yellow Dent and Yellow Sure Cropper. In Ferguson Yellow Dent a decrease in genetic variability was recorded for days to silk, ear height, ear
length and ear diameter while in Yellow Sure Cropper a decrease in genetic variability was registered for ear length. Increase in genetic variances for prolificacy was recorded in both populations.

Hallauer (1971) studied the genetic variances in original and reconstituted populations after four cycles of reciprocal recurrent selection for yield and other characters. The additive genetic variance decreased and dominance variance increased for kernel depth following selection for yield. The heritability estimates were relatively high for silking date, plant height and ear height, were intermediate for ear length and ear diameter, and were relatively low for kernel depth and yield.

Penny and Eberhart (1971) recorded that the genetic variances within Corn Borer Synthetic and Stiff Stalk Synthetic in sixth cycle of reciprocal recurrent selection were higher than those from previous 3 generations. This was in contrast to observations of Hallauer (1970). Darrah et al. (1972) observed that estimates made in the original and improved populations after 7 years of selection showed no change in genetic variance for yield.

5. Genetic architecture of yield and other agronomic traits:

With the growing realization of the importance of genetic architecture in the choice of most appropriate selection scheme and the availability of experimental methodology, in
mid-forties, to measure the relative magnitude of components of variance created considerable interest among maize breeders. In a number of studies involving, open-pollinated varieties, advanced generations of single crosses among inbred lines, data on genetic architecture have been reported. In most of these studies information on the relative magnitude of additive and non-additive components and their ratio have been estimated. In most of these studies, Design I and II (Comstock and Robinson, 1948, 1952) and diallel analysis (Sprague and Tatum, 1942 and Hayman, 1954, 1958 and 1960) have been widely used.

The genetic architecture to a great deal depends upon the nature of material (gene frequency) under study and its past selection history. Accordingly the available information on the genetic architecture for yield and other agronomic traits will be presented separately for homozygous and heterozygous base populations.

**Homozygous base populations:**

1. **Grain yield:** In several studies greater importance of non-additive genetic variance was registered and the relative dominance was observed to be in the over-dominance range. This was more particularly true of materials which had previously been subjected to intensive selection (Robinson *et al.*, 1949; Rojas and Sprague, 1951; Lonnquist, 1953; Gardner *et al.*, 1957; Gardner and Lonnquist, 1959;
Lindsey et al., 1960; Gamble, 1962; Sprague and Russell, 1962; Wessels, 1967 and Darrah and Hallauer, 1972). On the other hand studies of Lonnquist (1953); Rumbaugh and Lonnquist (1959); Rinke and Hayes (1964); Wessels (1969); Rutger et al. (1971) and Singh (1974) suggested that the additive component was more important than non-additive fraction.

The importance of linkage in the estimates of genetic variances have been suggested by Robinson et al. (1949), Gardner et al. (1953) and Comstock and Robinson (1952). Comstock and Robinson (1952) pointed out that theoretically it was possible to obtain estimates in the over-dominance range due to tight linkage of certain genes in repulsion phase, even though individual genes were in no more than in partial dominance range. Experimental data on the importance of linkage have been provided by studies made in $F_2$ and advanced generations by Comstock et al. (1957), Gardner and Lindsey (1960); Moll et al. (1957, 1960 and 1964); Lonnquist (1959); Robinson et al. (1960) and Gardner (1963). Most of these populations showed over-dominance in $F_2$ and partial to complete dominance in advanced generations.

It has been fairly well established that the estimates of additive genetic variance may be variedly modified by the extent of coupling and repulsion phase linkage. Robinson et al. (1960) observed that the additive genetic variance decreased from $F_2$ to later generations, thereby suggesting the
preponderance of coupling phase linkages. On the other hand Gardner and Lonnquist (1959) and Moll et al. (1964) noted an increase in the additive genetic variance in the later generations. These observations clearly suggest the pseudo-dominance could result from repulsion phase linkage of genes that are in partial to complete dominance range. This, however, does not exclude the possibility of the existence of over-dominance at some loci, but it does not appear to be as important as suggested by Hull (1952).

Relatively few studies have been reported in literature on the role of epistasis in inheritance of yield. The studies of Anderson and Kempthorne (1954); Sentz et al. (1954); Jinks (1955); Hayman (1957); Bauman (1959); Gamble (1962); Gorsline (1962); Sprague et al. (1962); Russel and Eberhart (1970) and Hallauer (1972) have suggested the presence of epistasis. On the other hand Stuber et al. (1966), Sprague and Thomas (1967), Moll and Robinson (1967) and Singh (1974) concluded that epistasis was not of much importance in the inheritance of yield.

Stuber and Moll (1971) from their studies on the type of gene action in selected and unselected lines of maize reported that three cycles of reciprocal recurrent selection did not materially alter the variance due to epistasis. The frequency of sets showing significant epistasis was apparently reduced in selected populations. Darrah and Hallauer (1972) on the other hand observed that the second cycle inbred lines
demonstrated significantly more epistasis than the first cycle lines.

2. Days to silk:

   Genetic analysis for days to silk has been reported by several workers. Predominance of additive effects was recorded in the studies of Yang (1949), Gauman and Lonnquist (1959), Giesbrecht (1960), Hallauer (1965), Manda and Chase (1967) and Singh (1974). On the other hand non-additive genetic variance was found to be more important than the additive genetic variance by Jones (1954) and Hallauer and Russell (1962). The studies of Gardner et al. (1953), Mohamed (1959) suggested that both additive and non-additive variance were equally important in the inheritance of days to silk. Presence of epistasis has also been reported by Stringfield (1950), Anderson and Kempthorne (1954); Bagshaw (1954) and Darrah and Hallauer (1972).

3. Plant height:

   In several studies predominant role of additive genetic effects has been reported by various workers (Robinson et al., 1949; Gardner et al., 1953; Gardner and Lonnquist, 1959; Rumbaugh and Lonnquist, 1959; Moll et al., 1964; Stuber et al., 1966 and Singh (1974). Presence of epistasis has also been reported by Sentz et al. (1954) and Gorsline (1961).
The published reports are at variance in regard to the relative importance of additive and non-additive variances in the inheritance of ear height. Robinson et al. (1949); Gardner et al. (1953); Gardner and Lonnquist (1959); Rumbaugh and Lonnquist (1959) and Singh (1974) recorded the predominance of additive genetic effects, while Ahmed (1968), Thompson et al. (1971) and Darrah and Hallauer (1972) observed the preponderance of non-additive genetic component. Importance of epistasis in the inheritance of this character has also been reported by several workers (Stringfield, 1950; Anderson and Kempthorne, 1954; Sentz et al., 1954; Bauman, 1959 and Darrah and Hallauer, 1972).

5. Ear length:

The studies of Robinson et al. (1949) and Gardner and Lonnquist (1959) suggested greater importance of additive genetic variance, while those of Gardner et al. (1953), Gamble (1962), Darrah and Hallauer (1972) and Singh (1974) recorded the major role of non-additive genetic variance. Presence of epistasis was reported by Sentz et al. (1954); Gorsline (1961) and Darrah and Hallauer (1972).

6. Ear diameter:

Robinson et al. (1949); Gardner and Lonnquist (1949) and Singh (1974) found that the additive genetic variance was larger than the dominance variance. This was in contrast to
the studies by Gamble (1962) and Darrah and Hallauer (1972).

The important role of epistasis in inheritance of ear diameter has been reported by Sentz (1954), Gorsline (1961) and Darrah and Hallauer (1972).

7. Ear number per plant:

The importance of additive genetic variance in the inheritance of this character has been shown by Comstock et al. (1949), Gardner et al. (1953), Gardner and Lonnquist (1959), Gardner (1963), Thomas (1962) and Compton et al. (1965).

Heterozygous base populations:

1. Grain yield:

In a number of studies involving heterozygous base populations predominance of additive genetic effects was recorded and degree of dominance was observed to be in the partial to complete dominance range (Robinson and Comstock, 1955; Robinson et al., 1955; Sprague and Russell, 1957; Robinson et al., 1958; Sprague et al., 1959; Sentz et al., 1960; Lonnquist and Gardner, 1961; Lindsey et al., 1962; Penny et al., 1962; Timothy, 1962; Chaudhry, 1964; Chopra, 1955; Compton et al., 1965; Williams et al., 1965; Eberhart et al., 1966; Stuber, 1966; Hallauer and Wright, 1967; Moll and Robinson, 1967; Cerrate, 1968; Hallauer, 1968; Robinson, 1968; Sentz et al., 1971; Singh et al., 1971 and Wright et al., 1971). These results were explained in terms of partial to complete
dominance at all loci or a mixture of partial and over dominance loci. On the other hand non-additive component was observed to be more important than additive component by Matzinger et al. (1959), Stringfield (1964), Hallauer and Eberhart (1966), Castro et al. (1968), Hallauer and Sears (1968), Tripathi (1968), Chi et al. (1969), Kalsy and Sharma (1970), Mukherjee and Thawan (1973) and Dhillon (1973).

Gardner (1963) found that the dominance/additive genetic variance ratio was three times larger for the homozygous populations as compared to those obtained from open pollinated varieties.

From further analysis of the above studies it was interesting to note that in greater number of studies reporting greater importance of non-additive genetic variance were based on diallel analysis, in contrast to the reports wherein partial to complete dominance was recorded, were mostly based on Design I or II of Comstock and Robinson (1948). In studies of Troyer and Hallauer (1968), Bolton (1971), Eberhart (1971), Mukherjee et al. (1971), Kumar (1972) both additive and non-additive variances were observed to be important.

Compton et al. (1965) observed that the additive genetic variance was higher in inter-varietal crosses than the intra-varietal populations. Similar results have also been reported by Hallauer (1970). Cress (1967) also came to similar conclusions from computer simulation studies and recommended the constitution of one population from which appropriate sampling
could be made. On the other hand Robinson et al. (1958), Sprague (1956) obtained contrasting results.

Even though the variance by definition are expected to be positive but in certain studies negative estimates for additive and dominance component have been reported. Such negative estimates have been recorded by Robinson et al. (1955), who explained these on the basis of sampling error. Negative estimates have also been reported by Lindsey et al. (1962), Compton et al. (1965), Williams et al. (1965), Goodman (1965), Eberhart (1966) and Singh (1968). Lindsey et al. (1962) suggested that the negative estimates of dominance variance may result from sampling error and/or lack of random mating while making full-sib family groups. Such assortative mating may result in over-estimation of variance due to males (\(O_m\)) and under-estimation of variance due to females (\(O_I\)).

Several investigations have suggested that the role of epistasis is negligible in the inheritance of this grain yield (Pollak, 1957; Robinson and Cockerham, 1961; Eberhart et al., 1966; Stuber et al., 1966 and Moll and Robinson, 1967). On the other hand, studies of Sprague and Thomas (1967); Stuber and Moll (1969) and 1971) and Wright et al. (1971) have shown that even though epistasis was present but was not of major importance.

2. Days to silk:

Published literature suggests that the additive genetic
variance was more important than the non-additive variance. The degree of dominance was in partial to complete dominance range (Robinson et al., 1955; Lindsey et al., 1962; Compton et al., 1965; Stuber et al., 1966; Hallauer and Wright, 1967; Castro et al., 1968; Robinson, 1968; Mukherjee et al., 1971; Singh et al., 1971; Wright et al., 1971 and Dhillon, 1973). On the other hand Hallauer (1968), Kalsy and Sharma (1970), Mukherjee and Dhawan (1970) and Eberhart (1971) observed that the dominance and additive genetic variance were equally important. Mukherjee et al. (1973) however recorded that non-additive genetic variance was more important.

3. Plant height:

Additive genetic variance has been reported to be more important from the non-additive genetic variances in several studies (Robinson et al., 1955; Lindsey et al., 1962; Stuber et al., 1966; Hallauer and Wright, 1967; Castro et al., 1968; Cerrate, 1968; Robison, 1968; Sentz et al., 1971; Singh et al., 1971; Wright et al., 1971 and Dhillon, 1973). Hallauer (1968), Kalsy and Sharma (1970) and Mukherjee and Dhawan (1970) on the other hand observed that both additive and non-additive variance were equally important in the inheritance of plant height. Non-additive genetic variance was, however, found to be more important by Eberhart et al. (1966) and Chi et al. (1969).
4. Ear height:

In a number of studies involving heterozygous maize populations the degree of dominance was observed to be in the partial to over-dominance range (Robinson et al., 1955; Lindsey et al., 1962; Moll et al., 1964; Compton et al., 1965; Eberhart et al., 1966; Stuber et al., 1968; Hallauer and Wright, 1967; Robinson, 1968; Chi et al., 1969; Eberhart, 1971; Sentz et al., 1971; Singh et al., 1971 and Wright et al., 1971). In studies of Hallauer (1968), Kalsy and Sharma (1970), Mukherjee and Dhawan (1970), the additive and non-additive components were found to be equally important. Epistasis was also found to be present in the studies of Eberhart et al. (1966), Chi et al. (1969) and Stuber and Moll (1967).

5. Ear length:

Most of the published reports support that the additive genetic variance was of greater importance than the non-additive component (Robinson et al., 1955; Lindsey et al., 1962; Williams et al., 1965; Eberhart et al., 1966; Hallauer and Wright, 1967; Hallauer, 1968; Chi et al., 1969; Sentz, 1971 and Wright et al., 1971). On the other hand results of Kalsy and Sharma (1970), Mukherjee et al. (1973), Singh et al. (1971) reported that additive and non-additive components were of equal importance. Dhillon (1973), however, observed that the non-additive genetic variance was of higher magnitude than the additive component.
6. **Ear diameter:**

Predominant role of additive genetic variance has also been reported in the inheritance of ear diameter by Robinson *et al.* (1955), Lindsey *et al.* (1962), Williams *et al.* (1965), Eberhart (1966), Hallauer and Wright (1967), Hallauer (1968), Sentz *et al.* (1971), Singh *et al.* (1971), Wright *et al.* (1971), Mukherjee *et al.* (1973) and Dhillon (1973). Dominance variance was found to be important in few studies (Chi *et al*., 1969; Kalsy and Sharma, 1970 and Mukherjee *et al*., 1970).

7. **Ear number per plant:**

Several workers have shown that the additive genetic variance is of prime importance in the inheritance of this character (Stuber *et al*., 1966; Eberhart *et al*., 1966; Robinson *et al*., 1955; Chopra, 1964 and Lindsey *et al*., 1962). On the other hand non-additive genetic variance were found to be more important in studies by Chaudhry (1964) and Lindsey *et al.* (1962).

From the above review it would appear that a marked variation in the magnitude of additive and non-additive genetic variance for various characters has been recorded. This disparity could be due to genetic composition of the populations (particularly the status of coupling and repulsion phase linkage), previous breeding history of the material under study and the experimental approach followed in the estimation
of genetic parameters. From the available information following general conclusions with certain limitations may be drawn.

1. Sufficient additive genetic variance is present in heterozygous maize population with the degree of dominance in partial to complete dominance range thereby suggesting the feasibility of intra-population improvement for yield and other agronomic traits. The magnitude of dominance variance indicated that probably it was operative in majority of the loci involved.

2. Linkage disequilibrium can be mistaken for overdominance.

3. Epistasis seems to be of importance in highly selected materials and its contribution in relatively unselected material was negligible.

6. **Genotype-environmental interaction:**

One of the primary objectives of any basic plant breeding investigation is to estimate the relative magnitude of additive and non-additive genetic variances so as to devise the most efficient breeding methodology for realising optimum gains over a desired period of time. Such genetic estimates based on a single environment have limited practical utility since they are confounded with genotypic environmental component. It is, therefore, necessary to have an estimate of genotype-environmental interaction involving additive and non-additive
fractions. The importance of genotypic-environmental interaction was fully realised by Sprague and Fedrer (1951), Rojas and Sprague (1952), Sents et al. (1954), Comstock et al. (1955), Hayman (1958), Robinson and Moll (1959), Gamble (1962), Singh et al. (1971) and several others who have greatly contributed to our present understanding. Khotyleva and Tarutina (1971) indicated that both the additive and non-additive components of genetic variance were variable and their magnitude depended on the genetic structure of the crosses analysed and the environmental conditions in which they were grown.

Sprague (1966) pointed out that the information on genotype-environmental interaction was useful for several purposes since (i) it provided a basis for the appreciation of the extent of bias in estimate of various genetic components, (ii) the rate of progress to be expected from a given breeding and testing system, (iii) a more realistic characterisation of spatial environments and (iv) for better allocation of resources for testing by providing more realistic weightage to replications, years and locations. The magnitude of genotype-environmental interaction in maize has been studied through the use of North Carolina Designs as well as diallel analysis. Comstock and Moll (1963) have emphasized that genotype-environment interaction is sufficient in the plant world so that all of its possible implications deserve attention.

Rojas and Sprague (1952) estimated the magnitude of
genotype-environment interaction from diallel analysis of selected lines grown over years and locations. Author observed that the genotype-environment interactions involving specific combining ability for grain yield (SCA x yield and SCA x location) were larger than their corresponding estimates associated with general combining ability. These observations suggested greater instability of non-additive genetic variance. Similar results have also been further substantiated by Vasal (1966), Gamble (1962) and Singh (1974). In heterozygous populations similar results have also been reported by Gardner (1961), Kalsy and Sharma (1970), Mukherjee et al. (1971) and Dhillon (1973). On the other hand Matzinger et al. (1959) working with unselected inbred lines, observed that the genotype-environment interaction involving general combining ability was significantly larger than specific combining ability x environment. Gamble (1962), however, recorded that the genotype-environment interaction involving GCA and SCA were of equal importance.

Eberhart et al. (1966) reported that there was little evidence of epistasis in eight characters studied in two open-pollinated varieties of corn. Authors, however, noted a rather substantial amount of epistatic x environmental interaction which suggested that testing should be done over a series of environments.

In a number of studies involving North Carolina Design I
and II estimates of genotype-environment interaction have been reported. Female x environment interaction measured genotype x environmental interaction while male x environment interaction provided an estimate of additive x environment interaction.

Chopra (1964) observed that male x location interaction was significant and was smaller than female in male x location. On the other hand Williams et al. (1965) observed that male x environment interaction was not significant. Allard and Bradshaw (1964) have critically reviewed genotype x environmental interaction and have suggested multilocal testing of materials so as to minimise the environmental bias. Singh et al. (1971) observed that the estimates of $\sigma^2_{ml}$ (male x location) and $\sigma^2_{fl}$ (female x location) were of equal magnitude.