REVIEW OF LITERATURE

The literature, mostly recent, pertaining to the different aspects of the present study, namely, nature and magnitude of genetic variances, combining ability and heterosis in pearl millet, and also studies on partial diallel analysis have been reviewed in this chapter.

Components of Genetic Variance and Their Estimation

Fisher (1918) was the first to recognize the importance of components of genetic variance. He partitioned the total genetic variance into three components — additive variance, the portion resulting from the average effects of genes; dominance component, resulting from the interaction of alleles; and epistatic part, associated with interaction of non-allelic genes. The epistatic variance has further been partitioned into additive X additive, additive X dominance, dominance X dominance and other higher order interactions (Cockerham, 1954; Anderson and Kempthorne, 1954; Hayman and Mather, 1955).

Different statistical models have been put forward for analyzing gene actions, such as, partitioning of variance into components (Fisher, Immer and Tedin, 1932; Povers, 1942; Mather, 1949), variance and covariance of parents and progenies (Comstock and Robinson, 1952), analysis of generation means (Jinks and Jones, 1958; Hayman, 1958) and analysis of diallel cross (Jinks and Hayman, 1953; Jinks, 1954; Hayman, 1954,1958, 1960).
Kempthorne (1956) and Gilbert (1958), disagreeing with Hayman's (1954a) assumption of independent distribution of genes and absence of epistasis, suggested that the analysis of variance used in the past for the diallel cross is of little use unless epistasis can be removed.

Griffing (1956b) gave the method of estimating general and specific combining ability in a diallel cross with or without parents and reciprocals. Eight different analyses were presented. These were the results from a consideration of four different diallel crossing systems together with two alternative assumptions with regard to sampling nature of the experimental material.

Hill (1964) and Nasser (1965) described the effect of correlated gene distribution in the analysis of diallel crosses. They suggested that the associated distribution produces a significant upward curvature of \( Wr/Vr \) graph. Similarly the non-random gene distribution alters the apparent level of dominance, association resulting in an underestimation and dispersion in an overestimation.

Durrant (1965) extended the reciprocal analysis of Jinks and Hayman (1953) for recognising the mechanism and determination of reciprocal differences. He suggested two more forms of inheritance which could be subdivided into multi-factor inheritance and associated group inheritance as \( \alpha \) and \( \beta \) inheritance.

Gardner and Eberhart (1966) presented a model for the estimation of genetic effects from the diallel cross and related
population of a fixed set of random mating varieties with 
arbitrary gene frequencies at all loci, assuming diploid inher-
ance, two alleles per locus and no epistasis. They criticised 
Griffing’s (1956b) method II and model I, and pointed out that 
the Griffing’s method failed to give a clear-cut picture of 
heterosis and gene effects. They claimed that their method 
is believed to be the best for such a set of material.

Mather (1967) described the effect of duplicate and 
complementary gene interaction on variance of the segregating 
populations and types of selection which favour these inter-
actions. He suggested that with diallel crosses the Wr/Vr graph 
becomes characteristically concave upward with complementary and 
concave downward with duplicate interactions.

Tandon, Joshi and Jain (1970) compared the graphical and 
combining ability analyses of diallel crosses in wheat using F₁ 
and later generations data. They reported that combining ability 
analysis was better than the graphic analysis in predicting the 
the prepotency of cultures. It was specially so in later genera-
tions when the expression of dominance effect is reduced.

Perkins (1970), Perkins and Jinks (1970) and Jinks and 
Perkins (1970) used the diallel cross analysis in Nicotiana 
rustica and estimated environmental and genotype environmental 
components of variability. They also detected linkage, environ-
mental and epistatic components of variation for metric traits. 
A general method for detecting additive, dominance and epistatic 
components of variation was also given by them.
Hone (1971) published the theoretical models for diallel crosses within and between populations of diploid cross-pollinated species. His first model is considered with single diallelic locus and specifies additive and dominance effects. He reported that if the difference between two populations of the same species depends only on the allelic frequencies at a locus, a heterozygous cross between these two populations will give the same information as a diallel cross within each population. But if there are different alleles in the two populations, a diallel cross between them cannot be used to estimate genetic effects within each population. The second model is considered with two diallelic loci. In addition to specified additive and dominance effects at each locus, there are defined parameters for interaction between the loci and for the recombination frequency between them. A diallel cross between the two populations will give the same information as a diallel cross within each of them provided that the only difference between them is the frequency of the alleles.

**Partial Diallel**

The partial diallel cross (PDC) analysis offers a wider scope for selection among crosses and the general combining ability of a large number of parents could be assessed, although with a moderate loss in the precision which is compensated for by the greater genetic gain obtained from more intense selection that could be applied to the parents.
Gilbert (1958) gave the method of analysis of partial sets of crosses. Bringing out the analogy between PDC and incomplete block design, he termed the technique as 'Fractional Diallel Analysis'. Hinkelmann and Stern (1960) brought out methods, viz., Type I and Type II, which showed in detail how to construct and analyse partial diallel sets of test crosses.

Kempthorne and Curnow (1961) discussed the subject further and suggested the method of sampling the crosses. They also discussed the usefulness of analysis of PDC. They assumed that a breeder can handle a total of NS/2 crosses. Where N was the number of inbred lines and S was a whole number greater or equal to two. Each line occurs in S crosses and the total number of crosses sampled is NS/2. They termed this method as 'Circulant Partial Diallel'. Fyfe and Gilbert (1963) pointed out that the partial diallel design of Kempthorne and Curnow is not a well balanced, and suggested adoption of 'Triangular' and 'Factorial' designs. They claimed that their designs are better balanced, thus giving more information per mating about the parental General combining ability. These designs are, however, more restricted as to the number of crosses to be grown and the number of parents must not be a prime number. They also demonstrated that same information with about the same precision could be obtained from the triangular and the factorial designs with a much less number of replications as compared to that obtained by the Kempthorne and Curnow's design.

Anand and Murty (1969) compared the diallel and the partial diallel analysis for yield contributing characters in linseed
following the circulant sampling design outlined by Kempthorne and Curnow (1961). They found that the magnitude of the GCA and SCA variances were significant for all the characters they studied and for all the values of s. The predominant role of non-additive gene action was reflected in full as well as in all partial diallel sets for all the characters. However, the GCA effect tended to be overestimated with decrease in the S, particularly when S was less than N/2 for all the characters, although the order of the parents remained essentially the same in their GCA effect for different values of the S. They suggested that even with limited samples, a partial diallel with \( S = \frac{N}{2} \) may be adequate for screening parents for their GCA effects.

Anand and Rana (1970) compared the relative efficiencies of the triangular and the factorial designs of Fyfe and Gilbert with the full diallel and circulant design of Kempthorne and Curnow in a diallel cross of 10 inbreds in linseed. They found that considerable GCA estimates were obtained for designs II and IV with underestimation for design I, indicating superiority of the former designs over the latter. Designs II and IV were better balanced and can be equally compared with the circulant design when \( S = \frac{n}{2} \). The underestimation of SCA estimate was observed for all the three designs used.

**Nature of Gene Action and Genetic Variances for Different Characters in Pearl Millet**

Burton (1959), in 38 forage yield trials, found considerable variation between inbred populations. On an average 55.9%
of the total genetic variance for forage yield was non-additive. Jain, Ahluwalia, Shankar and Joshi (1961) in a 6 x 6 diallel cross study reported that length and girth of spikes were governed mostly by additive genes with partial dominance and epistasis. Tillering, plant height and yield per tiller involved full dominance, overdominance and partial dominance respectively, with conspicuous epistatic effects.

Ahluwalia and Patnaik (1963) suggested that a large portion of the genetic variance was contributed by non-additive variation for seed size and length of spike. Dominance for earliness over lateness was also reported.

Harinarayana (1965) reported that non-additive gene action was predominant for early vigour, tiller number, ear length, ear girth and number of seeds per sq.cm. of ear, while substantial additive component was found for days to flower, ear length and leaf size. The results indicated that heterozygosity was maintained in pearl millet in the form of balanced genetic load for qualitative as well as for yield contributing characters. Mor (1965) reported complementary type of interaction between genes for plant height, number of internodes per stem, weight of 1000 grains and grain yield. In case of grain yield and head weight, the interactions were of very high order and complex in nature. For head length, gene frequencies were almost equal, but for other characters the distribution of gene frequencies were asymmetrical.
Mahadewappa and Ponnaiya (1966) made the following observations regarding gene action for different characters. Days to heading were controlled by additive, together with a few partially dominant genes. Complementary epistasis affected plant height at ear emergence and 1000 grain weight was influenced by unknown type of non-allelic interactions.

Murty, Arunachalam and Anand (1967) reported that non-additive gene action was present for tiller number, ear length and ear girth, while substantial additive gene action was also present for ear length. They also found partial dominance for tiller number and ear girth and overdominance for ear length in the crosses with Tift. 23A. But the hybrids with Tift. 18A exhibited partial dominance for tiller number and ear length and slight overdominance for ear girth.

Gupta and Nanda (1968) in a diallel cross study reported that overdominance and epistasis were operative in the inheritance of grain yield and grain hardness while for grain density and grain size partial dominance and epistasis were operative. They further reported that additive gene effects played an important role in the inheritance of all the characters studied.

Gill, Gupta and Nagi (1968) studied mode of the inheritance for days to earing, plant height, tiller number, ear length and girth, and stem girth. They observed overdominance for tallness and high tillering, while increased ear length showed partial dominance and there was almost no dominance for days to earing, ear length, ear girth and stem girth. Epistasis was found to be absent for all the characters. They also
reported high heritability (in narrow sense) for all the characters except for plant height and tiller number.

Lal and Singh (1968) reported that thick peduncle, long spike and bold grains showed complete dominance to their contrasting characters. Partial dominance of the better parent was showed for stem thickness. Only additive effects were observed to control the expression of number of tillers, number of spike bearing tillers, peduncle length and spike thickness.

Mahadewappa (1968) analysing diallel crosses in pearl millet reported that length of peduncle, density of grain, diameter of peduncle and surface of the primary ear were under influence of both intra-allelic and inter-allelic interactions. The interactions with regard to the first two characters were of complementary type. Yield of primary ear was conditioned by complementary genes besides some additive factors.

Phul (1969) analysed phenotypic variability to determine the mode of inheritance of four characters. He found that additive variance appeared to be more important than non-additive variance in days to flowering and plant height. For stem girth and ear length the importance of the two variance components ranged from 31 to 89 percent for days to flowering, 11 to 89 percent for stem girth, 35 to 50 percent for plant height and 27 to 84 percent for ear length.

Phul and Athwal (1969) reported superdominance over the higher parental value of grain size and grain hardiness. Each
of these characters exhibited additive as well as non-additive variations. In the case of grain size, inter-allelic interaction of dominance X additive type accounted for most of the non-additive variation, while in the case of grain hardiness, dominance effects were relatively more important.

Lal and Singh (1970) studied heritability and genetic advance for six populations of pearl millet for 15 characters related to grain and fodder yield. They reported high heritability for number of spike bearing branches, leaf length and grain weight, whereas moderate to low heritability for other characters under study.

Phul, Singh and Gupta (1970) in a diallel cross involving 9 inbred lines of pearl millet found that F₁ generation exhibited nearly complete dominance of earliness. The Wr, Vr regression analysis as well as the components analysis revealed the importance of additive type of gene action for this character. Frequency of the dominant genes was higher than the recessive genes and earliness was dominant over lateness. The number of group of genes exhibiting dominance was nearly five.

Srivastava (1970) found predominance of non-additive type of gene action for developmental traits, although additive effects were also considerable for these traits. Further, he reported that the gene action was non-additive for ergot and additive for resistance to blast.
Gupta and Singh (1971) reported dominance of the better parents in all the four characters studied when the overall \( F_1 \) and parental means were compared. Overdominance observed for grain yield appeared to be due to complementary epistasis. Additive gene action appeared to control ear length and was also important for ear girth. In addition, complementary epistasis was also operative for these two ear characters. Rao, Srinivasulu and Jayaramaiah (1971) reported high heritability for ear length and grain yield.

Bains (1971) studied gene action for plant and ear characters and reported the prevalence of epistatic variation with a nonsignificant contribution of additive and dominance components of genetic variance for tiller number. For days taken to flower, the importance of additive genetic variance was greater than that of dominance components with directional dominance towards the recessive alleles. However, for ear thickness additive genetic variance and additive \( X \) additive type of genetic interaction were suggested to be important. An appreciable magnitude of effect of epistasis, besides \( D \) and \( H \) components, was observed for tiller number, whereas this effect was not so marked for other characters.

Upadhyay and Murty (1971) from a Line \( X \) Tester analysis reported predominantly additive type of gene action for early vigour, tiller number, plant height, ear length, number of seeds per sq.cm. of ear and non-additive gene action for flowering and ear girth. They also studied a diallel cross and
observed that the non-additive gene action was predominant for all the characters they studied. Although, the additive component of variation was substantial for flowering, tiller number, ear length and yield. They also suggested that the differences in nature of gene actions obtained from two systems may be due to the bias in the estimations obtained from Line X Tester analysis because only two cytoplasmic male sterile testers were used.

Satija (1972) reported that the nature of gene action was predominantly non-additive for early growth vigour, days to 50 percent heading, plant height, effective tillers per plant, ear length, ear girth, 200 grain weight and for grain yield/sq. meter. He found low to medium heritability for all the characters. The maximum heritability was recorded for days to 50 percent heading (42-43%).

Singh (1972) studied a diallel cross involving 10 parents in pearl millet. He reported overdominance for total tillers, ear bearing tillers, ear length, ear girth and for grain yield by graphic analysis of diallel. On the other hand, except for grain yield, all the characters showed partial dominance by analytical approach. For all the characters, additive and dominance types of gene actions were significant, but, the amount of additive component was less than that of dominance.

Hirachand, Ahmad and Singh (1973) reported significant additive gene effects for grain density and dom. X dom. effect for 1000 grain weight.
Studies on Combining Ability in Pearl Millet

The concept of combining ability, which has been very useful in crop improvement programmes, has received considerable attention of the pearl millet breeders in the last one decade.

Jain, Ahluwalia, Shankar and Joshi (1961) reported that overall GCA variances were highly significant for both length and girth of spike. The same workers also found that the diversity of the origin of materials plays an important role in manifestation of the GCA effects of the parents and also for the expression of heterotic effect. Bains, Athwal and Gupta (1967) and Nanda and Gupta (1967) pointed out that the GCA was found to be more important for various yield components while for a complex entity, like yield, the SCA was more important. High SCA was observed in crosses involving at least one high general combining parent. Genetic diversity among the parents appeared to have an important role in expression of combining ability.

Gupta and Singh (1967) observed that the performance of the crosses was related to the GCA of the parents. High SCA was associated with high combining ability of either parent and high X high combinations were the best. In their study, Indian X American combinations were superior to American X American combinations. They suggested that high combining ability was associated with diversity of the origin of the parents. It was further suggested that the reason for getting
crosses with highest specific combining ability from the combination of high general combiners may be due to the contribution of favourable genes by both the parents. Pokhriyal, Mangath and Gangal (1967) found that the estimates of GCA variances were larger than the SCA variances for most of the characters. Mahadewappa (1968) reported the reverse trend, the SCA variances were larger than the GCA variances.

Gill, Phul and Rana (1969) studied a diallel cross for combining ability and reported that the GCA variances appeared to be predominant in case of plant height, leaf number, stem diameter, ear length, ear diameter and protein content, whereas the SCA variances were more important for grain yield, grain size and grain hardness.

Ahmad (1970) and Gupta and Sidhu (1970) reported that the magnitude of the SCA variances were higher than the GCA variances for developmental traits.

Gupta and Gupta (1971) found different magnitudes of variances for specific and general combining ability for different characters and different parents. All the superior combinations involved high X high, or high X average combining parents. None of the high X low or low X low combinations showed high SCA.

Upadhyay and Murty (1971) reported that the East African material was good general combiner for vegetative traits and the West African stocks for reproductive traits. The Nigerian
material was promising for ear characters but possessed undesirable vegetative features.

Satija (1972) found that the ratio of $\frac{2GCA}{\sigma}$ to $\sigma_{SCA}$ in the $F_2$ is more than in the $F_1$ for early vigour, plant height, and yield per meter. Thus additive components had increased for these characters in the $F_2$.

Singh (1972) reported that for days to flowering, plant height, effective tillers per plant, grain yield, ear length, ear girth and grain weight in the $F_1$ and the $F_2$ generations, both the GCA and SCA variances were highly significant, but the proportion of GCA variance was higher than that of SCA.

Thakare and Murty (1972) reported that dwarfing genes do not affect the GCA of the parents for yield or developmental characters. Ahmad and Zuberi (1973) studied the components of genetic variation for the developmental traits and reported substantial reduction in $\frac{^2g}{\sigma}$ in the $F_2$ and the $F_3$ generations than the $F_1$ and an increase in $\frac{^2e}{\sigma}$ in the $F_2$ and $F_3$ of diallels for estimating combining abilities provided a large number of parents are involved and no selection is practised at any stage.

Phul, Nanda and Gupta (1973) in a diallel cross involving nine inbreds of pearl millet reported significant general and specific combining ability variances for days to flowering, plant height, number of ears, ear girth, ear length, protein content and grain yield.
Tiwari (1973) studied combining ability of seven inbreds from different eco-geographical regions. He found that, both, the GCA and SCA variances were highly significant. He further observed that the higher magnitude of GCA variance was predominantly governed by the additive X additive components of genetic variance.

Singh, Singh and Singh (1974) in a Line X Tester analysis for combining ability reported that additive X additive and additive X dominance types of gene interactions were predominant. They also observed a high degree of association between general combining ability effects and the mean performance of the lines but no association was recorded between per se performance of the crosses and their specific combining ability effects.

**Studies on Heterosis and Inbreeding Depression in Pearl Millet**

Burton (1958), for the first time, succeeded in developing a cytoplasmic male sterile line and its counterpart. In 1962 two male sterile lines were made available to the Indian pearl millet improvement programme. The first hybrid bajra HB-1 (Tift. 23A x Bil. 3B) was released for general cultivation during 1965 (Athwal and Rachie, 1965) and yield levels were increased significantly. Some of the important studies on heterosis and inbreeding depression in pearl millet are reviewed in the following paragraphs.
Kadam, Patil and Kulkarni (1940) studied the effect of inbreeding and reported a sudden decrease in the first generation of selfing. Burton (1948) reported that selfing in pearl millet resulted in decreased vigour and hybridisation restored it.

Rao (1949) reported 16 to 163 percent increase in yield for certain crosses over the parental means and produced two hybrids, \( X_1 \) and \( X_2 \), in which the increase in yield was 20 to 30 percent over the yield of inbreds.

Burton (1951, 1952) reported heterosis of yield, plant height, stem diameter, ear length and diameter, and internode length. He showed that seed size, a heritable character, decreases with inbreeding. Studying the immediate effect of genetic relationship on seed size, he found that 30 \( S_1 \) lines when top crossed produced 9.5 percent heavier seeds than when selfed. The immediate gametic effect on seed size ranged from zero in some hybrids to more than 40 percent in the others.

Ahuwalia (1962) reported lack of positive heterosis in most of the combinations involving indigenous inbreds whereas Ahluwalia and Patnaik (1963) reported heterosis in cross combinations of indigenous and exotic parents for yield and other quantitative characters. They obtained a significant increase in yield ranging from 32 to 70 percent as compared to the superior parents. The expression of heterosis was more or less similar in respect of other characters, like seed size, length
of spike, plant height, etc., except the girth of spike. Heterosis for earliness and negative heterosis for some of the characters was also observed.

Sundarapandian, Menon and Ponnaiya (1964) reported heterosis for grain yield, weight and size of individual grain, length and breadth of main ear, height and thickness of stem and peduncle.

Pokhriyal, Rao, Mangath and Rajput (1966) obtained highly significant inbreeding depression in yield and other characters. The different plant characters showed varying degrees of depression in the different lines. They found that except in case of days to flower, peduncle thickness and number of leaves, plant height, grain weight and straw yield showed high degree of inbreeding depression (20%). The length and thickness of stem were moderately affected (12%). In other characters the depression was below 10 percent.

Bains, Athwal and Gupta (1967) reported that heterosis was higher in crosses involving high X high or high X medium combinations. Burton (1967, 1968) reported that the average heterosis for forage yield was closely parallel to the heterozygosity of the material tested.

Bhalla and Athwal (1968) reported that the most suitable cross combinations are those which exhibit maximum hybrid vigour in F₁ and least depression in F₂ generation. One of the crosses that they studied gave an increase of 110 percent
over the standard variety. Only in one case overdominance was observed in $F_2$. They found that $F_2$ generation did not appear to be of much value in commercial application of heterosis. Heterosis and superdominance were also observed in a number of crosses for plant height and tiller number, but in no case these showed significant heterosis in $F_2$ generation.

Lal and Singh (1968) and Singh and Lal (1969) studied heterosis and inbreeding depression for 15 grain and yield contributing characters and reported highly significant heterosis for plant height, number of internodes, number of branches, number of spike bearing tillers and days to flower. Except for days to flower, highly significant inbreeding depression was found in all the characters under observation. They also suggested that except for days to flower all the characters were associated with dominant gene effects.

Mahadewappa (1968) studied heterosis for 10 grain and yield characters and reported that heterosis in grain density and peduncle length was due to overdominance and complementary epistasis. The primary ear yield was conditioned by both complementary and additive genes. Complementary and overdominant genes were found to be responsible for heterosis in plant height, whereas epistasis was responsible for heterosis in tillering capacity and grain yield. He also found marked reciprocal differences for three vegetative characters and suggested that the spike characters were less influenced by maternal parent than the vegetative traits. Phul and Singh (1970) reported pronounced heterosis for plant height and ear length.
Singh (1970) reported that maximum heterosis over the superior parent was observed in case of the number of nodal heads (190%) followed by plant height (132%), yield per plant (37%) and earliness in flowering (9%). The number of basal and tillers showed a negative heterosis. Tiwari (1970)/ Tiwari, Singh and Lal (1971) reported positive heterosis over the better parent for increased number of tillers. The range of heterosis in the crosses varied from 2.2 to 45.0 percent. The positive heterosis for spike bearing tillers over the superior parent was restricted to six of the 11 crosses studied. The range of increase in these crosses varied from 0.1 to 47 percent. The F$_1$ hybrids took less time for panicle emergence than their parents. Further, Tiwari (1972) reported positive heterosis for number of internodes, plant height and main tiller.

Singh (1972) studied a set of 10 X 10 diallel cross of pearl millet in F$_1$ and F$_2$ generations. He reported low estimates of heterosis for days to flower, plant height, earbearing tillers and test weight, while for total tillers, ear length and ear girth, the heterotic effect was high. For yield characters still higher heterotic effects were recorded.

Hirachand, Ahmad and Singh (1973) collected data on expression of heterosis and inbreeding depression for nine characters related to quality and productivity. They reported that the magnitude of heterosis was very low in all the crosses for most of the characters because of mutual cancellation of
different types of gene effects. Inbreeding depression was obtained for 1000 grain weight only in two crosses out of four studied.

Phil, Nanda and Gupta (1973) studied a diallel cross involving 9 inbreds for days to flowering, plant height, number of ears, ear girth, ear length, protein content and grain yield. They reported negative estimates of heterosis for days to flowering and protein content, while positive heterosis for all the other characters was reported.