2. REVIEW OF LITERATURE

Plant breeder is mainly concerned with quantitative characters showing continuous variation such as yield. As such the inheritance studies of these have attracted the attention of biometricians. To breed better crops with higher yield, the breeder should select on the sliding scale of ever changing environment.

The relevant literature reviewed on various aspects of the present investigation entitled “Genetic analysis for seed yield and other traits with molecular characterization for disease resistance in flax, *Linum usitatissimum* L.” has been given under the following heads:

2.1 Studies on gene action for seed yield, fibre and quality traits

2.2 Studies on gene action for oil content and fatty acid profile

2.3 Studies on heterosis and inbreeding depression

2.4 Studies on inheritance of diseases and other qualitative traits

2.5 Molecular studies

2.1 Studies on gene action for seed yield, fibre and quality traits

The characterization of genetic components using appropriate mating designs and field experimentation is imperative as it helps in estimation and partitioning of various components, which eventually determine the applicability and success of breeding procedures. Fisher (1918) and Wright (1922) provided the basic framework for characterizing and partitioning genetic variance into physically assignable components. Fisher (1918) was the first to divide the genetic variance into three components, *i.e.* additive, dominance and epistatic variance.
Dickerson (1963), Dudley and Moll (1969) and Mather and Jinks (1971) outlined the following components of genetic variance, which are of practical consideration in crop improvement programmes.

- Additive genetic variance associated with the average effects of individual genes. It measures the breeding value of genotypes and is fixable for effective selection.
- Dominance variance associated with intra-allelic interactions of genes at segregating loci and measures breeding behaviour of alleles in heterozygotes. It is of practical application to go for hybridization.
- Epistatic variances associated with inter-allelic (non-allelic) interaction of genes at two or more segregating loci. Epistasis involving additive effects is fixable and as such exploited in intra-population improvement. Other epistatic effects are exploited in hybridization programme.

Jeswani et al. (1962) found that the additive component accounted for a major part of the variability for maturity in one cross of linseed whereas in another, the dominant components were predominant for plant height. They also found complementary epistasis, which could be fixed to operate in a majority of the cases except for plant height where duplicate epistasis was prominent.

Singh and Singh (1979) found the major role of non-additive gene action in the expression of plant height, number of branches and number of capsules per plant, number of seeds per capsule and yield per plant in linseed. The additive gene action was observed for days to flowering, days to maturity and 1000-seed weight. They reported that additive and non-additive gene action were of equal magnitude for oil content in $F_1$.

Rao and Singh (1984) studied the inheritance of seed yield and its components, days to flowering, days to maturity, plant height, primary branches per plant, secondary branches per plant, seeds per capsule, 1000-seed weight in linseed and found that additive gene effects were predominant for all characters except plant height in No55 x NP (RR) 412; for days to maturity, plant height and
1000-seed weight in IP16 X Hira. The dominance x dominance type of interaction played a significant role in the expression of some quantitative characters in some crosses.

Rao and Singh (1985) using generation means \textit{viz.}, $P_1$, $P_2$, $F_1$, $F_2$ and $F_3$ of six crosses in linseed found that additive and dominance gene effects were adequate to account for expression of the majority of yield characters. Capsules per plant, primary branches per plant, secondary branches per plant and seed size were under the control of additive gene effects. They concluded that improvement could be achieved through indirect selection for seed yield.

Sharma (1986) in a study of $F_1$ and $F_2$ of a diallel cross of 10 plant varieties in linseed for yield and its components found significant non-additive effects for all the characters in $F_2$ and significant additive effects for all the traits except capsules per plant and seed yield in the $F_1$. It was further observed that additive gene action was predominant for height and 1000-seed weight but dominance components were more important for the other traits.

Thakur and Rana (1987) studied combining ability analysis for some quantitative characters in linseed and found that the gene action was predominantly non-additive for days to maturity, seeds per capsule, capsules per plant and seed yield per plant but it was additive for plant height.

Singh (1987) reported the preponderance of additive gene action along with partial dominance in the inheritance of plant height, branches per plant, and days to maturity and 1000-seed weight in linseed. Non-additive gene action and over dominance appeared to be pre-dominant in the inheritance of capsules per plant, seeds per capsule, seed yield per plant and oil content (\%).

Satapathi et al. (1989) studied genetic variability, correlation and path coefficient analysis in linseed and reported variation in seed yield per plant and seven related characters, and reported that the number of branches, capsules and seed yield per plant showed high heritability and high genetic advance, indicating additive gene effects.
Nie et al. (1991) studied combining ability of the principal agronomic characters in flax and found that non-additive effects were predominant for seed weight per plant and seed number per capsule.

Combining ability was studied by Mishra and Singh (1992) for eight characters in linseed. Seed yield per plant, capsules per plant and branches per plant had a high genotypic coefficient of variation. High heritability coupled with high genetic advance was observed for seeds per capsule, days to maturity and capsules per plant indicating the importance of additive gene action for these traits.

Khorgade (1992) reported that additive genetic variation was important for expression of capsules per plant, seed yield per plant and 1000-seed weight from the data on 21 F₁ hybrids derived from seven lines and three testers of linseed.

Tak (1996) evaluated 18 populations for gene effects controlling seed yield, fibre and oil content in linseed and revealed that seed yield was mainly controlled by duplicate type of gene effects while for fibre and oil content, complementary type of gene effects were more important and there was a predominance of non-additive gene action for the three traits.

Khotyljova and Polonetskaya (1997) studied diallel analysis of quantitatively inherited traits in fibre flax and reported the predominance of additive gene effects in the inheritance of fibre performance traits (plant height at different ontogenesis stages, total fibre per cent).

Popescu et al. (1996) studied 66 F₁ hybrids of linseed and showed that the gene or the group of dominant genes controlling the number of capsules per square meter operate in an overdominance type of genetic mechanism, dominance being unidirectional and dominance alleles having an increasing effect on this trait.

Yadav and Gupta (1998) estimated genetic variability and heritability for 1000-seed weight, seed yield per plant and oil contents in 45 F₁ populations of linseed, tested at three different locations. High heritability coupled with high
genetic advance suggested that selection may be effective because of predominance of additive gene action. High heritability coupled with low genetic advance for oil content indicated that selection in these traits will not be effective.

Patel et al. (1997) reported the importance of additive and non-additive type of gene action in the inheritance of all characters. They reported the preponderance of additive components for phenological traits (days to flowering and days to maturity) and equal importance of both additive and dominance components for other characters.

Foster et al. (1998) studied quantitative analysis for dual purpose traits in linseed and observed that dominance was predominant for plant height, number of branches and seed weight, while 1000-seed weight displayed no dominance.

Mahto and Rahman (1998) reported that additive gene effects predominantly governed plant height and 1000-seed weight, while non-additive gene effects were significant for primary branches, secondary branches, capsules per plant, seeds per capsule, seed yield per plant, harvest index. Days to 50 per cent flowering and days to maturity were under the control of both additive and non-additive gene action. They reported the importance of non-additive gene effects for oil content which has to be improved through hybridization.

Chandrashekhar and Rahman (1998) evaluated 17 diverse genotypes as parents and their hybrids developed in a line x tester mating design for 11 quantitative traits in flax and reported predominance of additive gene action in expression of number of capsules per plant, seed yield per plant, number of secondary branches per plant and 1000-seed weight.

The study conducted by Chandrashekhar et al. (1998) in linseed showed the predominance of additive gene effect in governing the expression of plant height and 1000-seed weight, while non-additive gene effect was predominant in primary branches per plant, secondary branches per plant, capsules per plant,
seeds per capsule, seed yield per plant, harvest index and oil content. Days to 50 per cent flowering and days to maturity were under the control of both additive and non-additive gene action.

Bhateria et al. (2001) studied combining ability for seed yield and its components in linseed in a line x tester analysis and found preponderance of non-additive gene action for seed yield per plant, 1000-seed weight, seeds per capsule, capsules per plant, plant height and harvest index.

Yadav and Srivastava (2002) studied 10 diverse flax lines over three environments and observed that both additive and non-additive gene actions were important for characters like days to 50 per cent flowering, days to maturity, 1000-seed weight and seed yield per plant.

Sood (2004) observed preponderance of non-additive gene action and over dominance for days to 50 per cent flowering, days to maturity, plant height, primary branches per plant, secondary branches per plant, capsules per plant, 1000-seed weight, seed yield per plant, harvest index and oil content over environments in a line x tester study.

Sood et al. (2007a) observed preponderance of additive gene action for plant height, technical height, capsules per plant, seed yield per plant, 1000-seed weight, straw yield per plant in a triple test cross analysis, whereas non-additive gene action was preponderant for seeds per capsule and biological yield per plant.

Sood et al. (2009) observed that out of 20 characters studied, the additive dominance model was found to be adequate only for four characters i.e. days to maturity, secondary branches per plant, seeds per capsule and line fibre indicating the presence of additive gene action.

Gauraha and Rao (2011) studied genetic analysis of seed yield and its components in six crosses of linseed through generation mean analysis and showed major contribution of dominance effects associated with dominance x
dominance type of interaction effects in the expression of all the characters in the crosses. Duplicate type of epistasis played a major role in the expression of most of the characters studied in the crosses.

### 2.2 Studies on gene action for oil content and fatty acid profile

In linseed, the quality of oilseed depends on the amount of oil and protein present in the seed, while the oil quality is measured by the proportion of saturated and unsaturated fatty acids. For evolving better and stable varieties for quality components, it is necessary to screen the available genotypes over a wide agroclimatic conditions for their direct commercial exploitation or effective utilization in breeding programme.

Green and Marshall (1981) studied genetic variation for oil quantity and quality in a diverse collection of linseed and found significant genetic variation in seed weight, oil content and fatty acid composition between and within varieties.

Green (1986) studied genetic variation for oil quantity and quality in linseed and observed that seeds of variety Glenelg when treated with EMS reduced linolenic acid content to 28-30 per cent.

Propescu et al. (1998) while evaluating 66 crosses of 12 linseed genotypes for oil content and yield observed predominance of additive gene action.

Kumar et al. (2000) studied line x tester analysis for seed yield and its components in linseed involving 17 lines and three testers and reported that line LCK-8526 was good general combiner for oil content.

Sood (2005) in a triple test cross analysis involving 12 lines and three testers reported the highest linolenic acid content in Janaki (57.41) and the lowest in KL-187 (40.73).

### 2.3 Studies on heterosis and inbreeding depression

Heterosis is the genetic expression of beneficial effects of hybridization. The term “Heterosis” was coined by Shull in 1914 to explain hybrid vigour. Heterosis represents percentage increase or decrease in the mean values of the
F₁ hybrids over their mid parental value. “Heterobeltiosis” which represents increase or decrease in the mean value of F₁ hybrid over the better parent and standard heterosis reveals increase or decrease of the mean value of F₁ hybrids over the checks. Some of the work done on heterosis, heterobeltiosis, standard heterosis and inbreeding depression is reviewed below.

Galkin (1973) studied 277 F₁ hybrids obtained in complete and incomplete diallel crosses. The extent to which heterosis occurred was greatly affected by the conditions of cultivation and the choice of parent forms. High heterosis was found in hybrids from crosses of ecologically and geographically distant forms. The yield component most affected by heterosis was the number of capsules per plant. Heterosis for this character was found in 55.9 per cent of the hybrids. High heterosis was also found for straw weight.

Kansal and Gupta (1981) found heterosis for yield and seven yield components in the F₁ and F₂ of four crosses. Capsules number per plant made the biggest contribution to seed yield and LC36 x Exotic1 showed the greatest heterosis for seed yield.

Singh et al. (1983) studied yield and seven yield components in 21 F₁ hybrids from a seven-parent diallel without reciprocals. Heterosis for yield over the better parent was observed in 18 crosses. Heterosis for yield was mostly due to secondary branches per plant, capsules per plant, test weight and capsule size.

Dakhore et al. (1987) studied line x tester crosses involving 10 lines and five testers and observed heterosis for all the traits studied except days to maturity and branches per plant in some of the crosses. AKL10 x LCK38 showed the highest heterosis over the standard variety for seed yield per plant (52.32 %) and 1000-seed weight (12.36 %) while JLS1 x C219-1-1 exhibited the highest heterosis over the standard variety for branches per plant (42.30 %) and useful heterosis being considered a better criterion for comparing heterosis effects than heterosis over the mid parental value or over the better parent.
Singh et al. (1987) studied yield components and oil content in 90 F$_1$ hybrids from line x tester crosses involving 30 maternal lines and three pollen parents. Considerable heterosis was found for all characters except seed number per capsule and oil content.

Tak and Gupta (1993) examined the nature and magnitude of heterosis in three crosses of linseed over mid parent. The oil content in general exhibited negative heterosis in the three crosses, while fibre content exhibited positive and significant heterosis. Days to 50 per cent flowering and maturity revealed negative and significant heterosis over the better parent in the three crosses indicating the trend towards earliness depicting the scope for its selection.

Verma and Mahto (1996) found significant differences for all characters in rainfed and irrigated environments. The highest heterobeltiosis was that of seed yield per plant (57.9 and 101.1%) for irrigated and rainfed treatments, respectively, followed by secondary branches per plant (52.8 and 62.2 %), capsules per plant (43.5 and 56.8 %), primary branches per plant (26.5 and 45.7 %), plant height (16.9 and 17.5 %), days to flowering (5.8 and 8.6 %), seeds per capsule (5.0 and 5.3 %) and days to maturity (3.4 and 3.5 %).

Chandrashekhar and Rahman (2001) studied heterosis in 30 linseed crosses for yield and its components. Considerable amount of heterosis over mid parent was observed for most of the characters. About half of the crosses showed significant heterosis for earliness over mid parent. The maximum heterotic effect was obtained for number of capsules per plant over mid parent as well as better parent. High heterosis was obtained for 1000-seed weight over mid parent and for number of capsules per plant over better parent. Seed yield per plant showed the maximum average heterosis.

Swarnkar et al. (2003) studied heterosis and inbreeding depression for 13 characters in 45 F$_1$’s and 45 F$_2$’s derived from 10 parents under salt affected soils. Out of 21, six crosses had high heterosis over superior parent to extent of
199.8, 96.4, 89.8, 64.7, 63.3 and 54.7 per cent respectively and exhibited comparatively low inbreeding depression of 22.2, 8.0, 8.8, 6.1, 13.8, and 19.1 per cent respectively for seed yield per plant.

Ratanaparkhi et al. (2004) found highest estimates of useful heterosis in the case of yield per plant followed by number of capsules per plant and harvest index.

Sharma et al. (2005) reported high significant and positive heterosis for seed yield per plant in the crosses LCK 9216 x Kiran, EC 1045 x Kiran and EC 1045xN193 for oil content. These crosses also exhibited considerable inbreeding depression in F$_2$ generation. Significant and desirable heterosis along with significant inbreeding depression was also reported for the characters viz., days to 50 per cent flowering, number of branches per plant, days to maturity and 1000-seed weight.

Rao (2006) observed heterosis and inbreeding depression in positive direction for most of the characters. Maximum heterosis was recorded for seed weight per plant followed by number of capsules per plant and number of seeds per plant.

2.3 Studies on inheritance of diseases and other qualitative traits

The component of resistance and their phenotypic and genetic characteristics can be determined only by genetic analysis. On the basis of mode of inheritance three main kinds of resistance have been identified: (a) monogenic resistance, in which resistance is controlled by a single gene, (b) oligogenic resistance, where resistance is governed by few genes and (c) polygenic resistance, where resistance is controlled by many genes. Genes with large effect on the expression of resistance are said to be major genes and genes which individually have only a small effect on the expression of resistance are called minor genes (Russel, 1978).

Sharma et al. (1972) reported that none of the 104 varieties evaluated were resistant against *Oidium lini* but 45 were considered moderately resistant and the remaining varieties were moderately susceptible.
Singh and Kaurav (1973) studied 69 varieties and crosses, and found that the variety EC 9832 was completely unaffected and its crosses with Hira, T-397, No.55, R1 and Sabour showed only traces of infection against powdery mildew.

Dutt *et al.* (1975) evaluated genetic stock of linseed against powdery mildew and found that three stocks *viz.*., EC 5622, K 5835 and E 15663, out of 225 flax varieties tested against *Oidium lini* to be resistant under natural epiphytotic conditions.

Shukla and Mishra (1983) studied 1143 indigenous and exotic linseed varieties in field and laboratory for resistance to a mixture of seven known races of *Melampsora lini* and found that out of these 130 were free from infection.

Prasad *et al.* (1988) studied seeds of 2822 flax germplasm representing indigenous and exotic strains and reported that one per cent (27 cultivars) were free from rust and powdery mildew alone, whereas maximum number of germplasm entries were susceptible to powdery mildew than to rust.

Rozhmina (1988) studied varieties in four sets of diallel crosses involving eight sources of resistance to *F. oxysporum f.sp lini* and reported that the local population of *F. oxysporum* G4496, G5224, G4729, K6746 and the variety Dvina was controlled by a single dominant gene, while resistance in R260 was controlled by two dominant genes.

Singh *et al.* (1989) studied the inheritance of powdery mildew resistance in linseed using four resistant and three susceptible cultivars to *Oidium lini*. They found that all F1 plants were resistant to powdery mildew and F2 population segregated in the ratio of 3:1.

Goray *et al.* (1989) studied Inheritance of wilt resistance in linseed and segregation analysis indicated that inheritance of resistance was dominant and monogenic.

Agarwal *et al.* (1993) investigated F2 segregation ratios from nine intervarietal crosses involving the wilt resistant cultivars (RLC6 and R552) and four susceptible commercial varieties and reported that resistance to *Fusarium oxysporum f.sp. lini* is mostly determined by recessive alleles.
Sinha et al. (1993) evaluated 313 germplasm lines of flax for their reaction to rust and powdery mildew over three years. They found that variety surbhi gave resistance reaction to both rust and powdery mildew. While 22 lines including varieties like Hira, Mukta, and Neelum showed resistance towards rust.

Popescu et al. (1995) inferred from tests in the wilt nursery on 21 F₁ hybrids from a half-diallel set of crosses involving seven parental varieties differing in resistance to *F. oxysporum* f.sp. *lini*. Both additive and dominance types of gene effects were involved in the control of resistance, but additive effects predominated. The group of genes or dominant gene involved showed partial dominance acting in a favourable direction.

Spielmeyer et al. (1998) investigated inheritance of resistance to *Fusarium* wilt (*Fusarium oxysporum* f.sp. *lini*) from a recombinant doubled haploid (DH) population which was derived from the haploid component of polyembryonic F₂ seeds originating from a cross between a wilt resistant, twinning LinolaTM line and the wilt susceptible Australian flax cultivar Glenelg. They found that most of the phenotypic variation was attributable to the segregation of two independent genes with additive effects.

Portyankin and Karachan (1999) studied resistance of a set of fibre flax cultivars, out of which Kievsky, Kalininsky, Ustiensky, Torzhoksky 85, Nika, Niva, Rodnik, Mogilevsky-2, T-17 and K-65 were resistant to *Fusarium* wilt.

Sood (2004) observed that three parents *viz.*., Janaki, Surbhi and Flak-1 and seven cross combinations *i.e.*. KL-233 X Surbhi, KL-233 X KL-224, LCK-9816 X KL-224, LC-2232 X Flak-1, KL-178 X Flak-1, KL-233 X KL-221 and KL-187 X KL-221 were resistant to powdery mildew.

Ashry et al. (2002) evaluated flax genotypes for powdery mildew resistance and reported that selection for fibre type flax would result in an increase in powdery mildew resistance, while selection for seed type flax would result in a decrease in such a resistance.
Rashid and Duguid (2003) investigated the genetics of resistance to powdery mildew in flax and reported a single dominant gene designated PM1 for resistance to powdery mildew.

Mittapalli and Rowland (2003) determined the allelic gene relationship of the dominant yellow gene, the variegated recessive gene and various spontaneous and unknown recessive yellow genes in flax. The F$_1$ plants were observed to be brown seeded in variegated x brown crosses and yellow x brown crosses confirming dominance of brown seed colour over variegated and yellow seed colour.

Sood et al. (2007b) observed that none of the parents or their cross combinations were completely free from disease in both the environments. They observed that among two cross combinations involving common resistant parent, B-509 x LC-9826 and LC-2323 x LCK-9826 were moderately resistant.

2.4 Molecular studies

Different molecular markers can be cumulatively integrated to form genetic linkage map in a crop species. The high-density linkage maps increase the probability of identifying markers linked to gene(s) located in a chromosomal region of interest. Once the polymorphic fragments are identified between the parents, linkage analysis must be performed using different kinds of segregating populations which show the recombination as it occur between genes on the same chromosome during gametogenesis, such populations are F$_2$ population or F$_2$ derived F$_3$ population, backcross population, doubled haploid or recombinant inbred lines for mapping molecular markers (Paterson, 1996).

Chen et al. (2001) studied inheritance patterns of rust resistance and molecular markers in microspore derived population of flax. They concluded that two rust resistance genes and three out of six molecular markers were inherited in expected Mendelian ratios. For other three molecular markers, distorted segregation due to over representation of genomic fragmentation from more responsive parent was found.
Fu- Yong et al. (2002) used RAPD markers to assess genetic diversity and relationships in 34 genotypes. Genetic variation was generally low and 53 variable RAPD loci were observed for the 61 accessions, the landraces had a lower proportion of fixed recessive RAPD loci (0.427) than all other flax cultivars studied (0.529). They concluded that Canadian flax cultivars had a lower proportion of recessive loci (0.465) than the selected world flax cultivars (0.512).

Fu et al. (2003) evaluated genetic relationship of 54 North American flax cultivars by means of RAPD markers. The variations observed at the 84 polymorphic RAPD loci were relatively moderate with respect to primer, polymorphism and cultivar.

Aly et al. (2004) evaluated flax genotypes for powdery mildew resistance under field conditions in Giza, Egypt for two growing seasons and observed significant differences in disease severity. They opined that RAPD analysis may provide a supplementary assay to field tests to distinguish between powdery mildew resistant or susceptible genotypes.

Bo et al. (2008) identified molecular markers linked to the flax rust-resistance gene M4, RAPD analysis of NM4 (a near-isogenic line containing the M4 gene) and the recurrent parent Bison was performed using 540 decamer primers. They concluded that the amplification of different resistant germplasm proved that the marker is specific for the M4 gene and this marker has been used successfully in MAS in the flax breeding program.