2. REVIEW OF LITERATURE

The systematic studies on genetics of morphological markers of lentil (*Lens culinaris* Medik) have been negligible. However, the sporadic information was generated from isolated efforts and experimentations in India and other parts of the world and the major emphasis remained on inheritance of morphological markers. The inheritance of cotyledon colour was not studied comprehensively perhaps due to invisibility of this trait through testa. However, recently the molecular markers have been used for understanding the inheritance pattern of morphological markers and tagging of genes for disease resistance and economic traits.

The review of literature have been divided in the following three categories:

(i) inheritance pattern of morphological markers
(ii) genetics of quantitative traits
(iii) linkage between morphological markers

2.1 Inheritance pattern of morphological markers

2.1.1 Leaf pigmentation

The presence or absence of anthocyanin pigmentation on the leaves is easily visible in lentil. Emami and Sharma (1996) studied the inheritance of brown leaf pigmentation and found monogenic dominance
of pigmentation over non-pigmentation with 3 brown and 1 green ratio. The gene symbol \( B \) was proposed for this trait and \( b \) for recessive one.

### 2.1.2 Dark green foliage

Mishra et al. (2001) worked out the inheritance pattern of dark green and light green foliage colour. The study was based on 28 cross combinations between the parents having dark green foliage and light green foliage. The \( F_1 \) phenotype was dark green while the \( F_2 \) population segregated into 3 dark green foliage colour and one light green foliage. The results were good fit in 3:1 ratio with non significant \( \chi^2 \)-value. The gene symbol \( D_g \) was proposed for this trait.

### 2.1.3 Plant pubescence

The pubescence was studied in different parts of the lentil plant like leaf pubescence, stem pubescence, pod pubescence and peduncle pubescence. However, there is not even single contrasting report where the one part is pubescent and other part is non-pubescent within same plant; therefore it will be rather appropriate to denote plant pubescence than part pubescence and there by gene symbol \( Pub \) was proposed for this trait for dominant and \( pub \) for recessive form by Hoque (2001).

In earlier studies by Emami (1996) the inheritance of peduncle pubescence was reported as monogenic dominant. The \( F_2 \) ratio was good fit for 3 pubescent : 1 non-pubescent peduncle. The non-pubescent peduncle is therefore, caused by single recessive gene and the gene symbol was proposed \( Pdp \) for pubescent and \( pdp \) for non-pubescent peduncle.
Vandenbarg and Slinkard (1989) reported the dominance of pubescent pod over non-pubescent pod. They obtained the $F_2$ ratio of 3 pubescent : 1 non-pubescent pods, indicating that pod pubescent character is governed by single dominant gene. The non-pubescent pods is therefore caused by the recessive form of this gene. The proposed gene symbol was $G_ip$. Thus pubescent podded plants have $G_ipG_ip$ genotype while glabrous podded plants have $gip gip$ genotype.

2.1.4 Tendril formation

Tendril formation at the apex of lentil leaf is reported to be controlled by a dominant gene (Vandenbarg and Slinkard, 1989). The $F_2$ ratio was 3 tendrilled and 1 tendrilless and the gene symbol $Tnl$ was proposed for this trait. Therefore, homozygous tendrilled plant have genotype $Tnl Tnl$ and tendrilless have $tnl tnl$ genotype.

2.1.5 Stem pigmentation

Ladizinski (1979) for the first time studied the stem pigmentation character in lentil and reported that the stem pigmentation was completely dominant over green stem. He also observed that this dominance is governed by a single gene because the $F_2$ population in his experiment segregated in 3 pigmented : 1 green stem. He proposed gene symbol $Gs$ for this traits. The plants with genotype $gs$ do not produce pigmentation on the stem. Emami (1996) have also substantiated these results in his experiments.

2.1.6 Number of flowers per peduncle

This trait was studied by different workers and reported contrasting results. Gill and Malhotra (1980) observed that the inheritance of two
flowers per peduncle is controlled by a single dominant gene. They crossed a lentil strain having two flowers per peduncle with the strain having three flowers per peduncle and obtained the ratio 3 (two flowers per peduncle) : 1 (three flowers per peduncle). They proposed the gene symbol _F_ for two flowers per peduncle and _f_ for three flowers per peduncle trait. Contrary to this report Emami (1996) reported that the trait three flowers per peduncle was monogenic dominant over two flowers per peduncle. Hoque (2001) also worked on this trait and supported the results obtained by Emami (1996).

2.1.7 Flower colour

Lal and Srivastava (1975) reported _F_ 1 segregation ratio of 3 violet : 1 white when they crossed the strain having violet flower colour and white flower colour. They also got three violet and one pink ratio in another cross between plants with violet flower and plants with pink flower. Interestingly they obtained four types of phenotypes i.e. violet, pink, white and rose in the ratio 9:3:3:1. They cross pink and white flower genotypes which reveals that this trait is governed by two genes with complete dominance with out epistasis. Gene symbol for this trait was proposed _V_ for violet and _P_ for pink and thus the genotypes of the four classes are _VVPP_ (violet), _VvPP_ (white), _vvPP_ (pink) and _vvpp_ (rose).

Wilson and Hudson (1978) reported the _F_ 2 ratio of 9 violet : 6 intermediate : 1 white suggesting additive effects. They found that white flower may have pale pink and pale violet veins deep within the throat of the standard petal. They proposed gene symbols _V_ for violet and _W_ for white and genotypes of three classes i.e. _VWW_ (violet) _VVWw_ and _vwWW_ (intermediate) and _vwvw_ (white).
The results obtained by Gill and Malhotra (1980) in a cross between violet and white flowered plants suggested 3 violet : 1 white flower plant segregation ratio in F$_1$ generation. Ladizinsky (1979) also reported the monogenic dominance of blue flower colour over white flower colour in a cross between blue and white flowered plant.

2.1.8 Pod pigmentation

When a cross was made between the genotypes of green and red pod the result of F$_1$ generation was 3 red : 1 green pod indicating the dominance of red pod over green ones (Vandenbeng and Slikard, 1989). The gene symbol Grp was proposed to this trait. The red pod is produced by dominant homozygous condition (Grp Grp) while green pod by recessive condition (grp grp).

Emami (1996) also reported that red pigmented pod is monogenic dominant over green pod. He proposed gene symbol Rdp for this trait. Double recessive condition (rdp rdp) gave green pod phenotype. Another gene symbol (Pdp) has also been proposed for the presence of violet strap on the pod (Havey and Muchibauer, 1989).

2.1.9 Testa colour

Genetics of testa colour in lentil is complicated because of the impression of cotyledon colour on testa. The inheritance of this trait was worked out by different workers. Wilson and Hudson (1979) got the F$_2$ ratio of 1 black : 14 mottled : 1 beige in a cross between the genotypes with black and beige testa. They concluded that there are two factors that determine the inheritance of testa colour without showing the dominance to each other.
Vandenberg and Slinkard (1990) reported that the ground testa colour of lentil is controlled by two dominant genes at non-linked loci. This conclusion was based on their findings of 9:3:3:1 phenotypic ratio. Gray ground colour is determined by the dominant gene $G_{gc}$ and tan ground colour is determined by the dominant gene $T_{gc}$. They proposed the genotypic combination for different phenotypes as brown-$G_{gc} G_{gc} T_{gc} T_{gc}$; gray-$G_{gc} G_{gc} t_{gc} t_{gc}$; tan-$g_{gc} g_{gc} T_{gc} T_{gc}$ and green-$g_{gc} g_{gc} t_{gc} t_{gc}$.

Vaillancourt and Slinkard (1992) reported that black testa was monogenic dominant over non-black. Singh and Singh (1993) reported a ratio of 3 brown : 1 gray testa in $F_2$ population of cross between brown testa and gray testa. They proposed gene symbol $B$ for brown and $b$ for gray testa colour.

Vandenberg (1987) found that in some crosses one gene with codominance expression controlled the expression of black testa. However, in other crosses he reported two genes with dominance of non-black.

Emami and Sharma (2000) reported that black testa is dominant over non-black testa. The results were based on the analysis of $F_1$ and $F_2$ seeds. The $F_2$ population of the crosses between genotypes with brown and tan, brown and green segregated in the ratio of 3 brown : 1 tan and 3 brown : 1 green, respectively. These results indicated that brown testa colour is monogenic dominant over both, brown and green testa colour.

2.1.10 Testa spotting/mottling pattern

Ladizinski (1979) obtained plants in 3:1 ratio in $F_2$ generation with
spotted and unspotted testa and proposed the gene symbol \( Scp \) for testa spotting pattern and \( scp \) for unspotted testa pattern. Vandenberg and Slinkard (1990) have studied several crosses with different testa patterns. Crosses between genotypes with dotted testa with flecks (\( DF \)) and dotted without flecks segregated into 3 DF: 1 dotted with out flecks testa patterns in \( F_2 \) population. These results suggested that \( DF \) should also be included in the multiple allelic series at the \( Scp \) locus. However, they could not determine the dominance relationship of the \( DF \) allele with other \( Scp \) alleles reported by them. They also reported another distinct testa pattern, which was designated as Eston Mottle (\( EM \)). The crosses between genotypes with \( EM \) testa pattern and without pattern produce \( F_2 \) progenies that exhibited the \( EM \) phenotype.

Emami (1996) reported that testa pattern i.e. mottled or speckled or combination of both was completely dominant over non-spotting testa. The symbols \( Mot \) and \( Spl \) were proposed for mottled and speckled testa pattern, respectively.

Hoque (2001) also reported monogenic dominance of mottled testa pattern over non-mottled testa when he crossed the genotypes with mottled and non-mottled testa.

2.1.11 Cotyledon colour

Tschemak (1928) for the first time reported the genetics of cotyledon colour in lentil. Wilson et al. (1970) reported that the \( F_1 \)'s were red when reciprocal crosses between red and yellow were attempted. This indicated that the red cotyledon colour was determined by single dominant gene therefore red cotyledon colour was dominant over yellow.
The mode of inheritance of cotyledon colour was studied by Singh (1978), Slinkard (1978) and Sinha et al. (1987) independently. The red cotyledon colour was referred as orange by Singh and proposed gene symbol O for orange and o for yellow. Slinkard (1978) studied the inheritance of red, yellow and green cotyledon colours. On the basis of his study he proposed that the red cotyledon was completely dominant over both yellow and green. In the F₁ generation of cross between red and green cotyledon parents, the 9 red : 3 yellow : 4 green ratio was observed, indicating dihybrid ratio with a recessive colour inhibitor gene. The following symbol was given Yc (red cotyledon): yc (yellow cotyledon) and r-yC (inhibitor of cotyledon colour producing green cotyledons). In this scheme, r-yc does not inhibit expression of either yc or Yc alleles in its dominant state. Thus, the genotype of homozygous green cotyledon plants would be either yc yc r-yc r-yc or Yc Yc r-yc r-yc. In other words, orange or yellow cotyledon colours were produced only when the r-yc gene was dominant, e.g. r-yc Yc (orange) and r-yc yc yc (yellow)

Emami (1996) reported that the cotyledon colour of lentil gave different mode of inheritance when crossed in different parental combinations. When a cross was attempted between the genotypes with orange yellow cotyledon, it was observed that orange cotyledon was monogenically dominant over yellow cotyledon and gave 3 orange and 1 yellow ratio. In a cross between orange and light green cotyledon parents, the F₁ segregated into four phenotypic classes viz. orange, yellow, brown and light green with good fit to the ratio of 9:3:3:1. He concluded the involvement of two independent gene controlled cotyledon
colour in lentil. The gene symbol $Y$ and $B$ have been proposed for yellow and brown cotyledon colour, respectively. According to this study different phenotypic classes would be: $Y-B$ (orange), $Y-bb$ (yellow), $yyB$ (brown) and $yybb$ (light green).

By extensive study, inheritance of cotyledon colour of lentil was worked out by Hoque (2001). He confirmed the findings of Emami (1996) who reported that the orange cotyledon was monogenically dominant over yellow cotyledon. In a cross between genotypes with orange and yellow he observed that the $F_1$ seeds were orange while the $F_2$ population segregated into 3 orange and 1 yellow cotyledon. In another crosses between genotypes having orange and light green cotyledon the cotyledon of $F_1$ seeds were orange while the $F_2$ population segregated into orange : yellow : brown : light green with good fit into 9:3:3:1 ratio having non significant $\chi^2$-value. These observations revealed the digenic control of cotyledon colour in lentil. Hoque (2001) also studied another cross combination to work out the inheritance of cotyledon colours in lentil. When he crossed the genotypes with orange cotyledon and dark green cotyledon, he found that the orange cotyledon colour was dominant over dark green cotyledon with $F_2$ segregation in 3 orange and 1 dark green ratio.

To study the genetic interaction between light green and dark green cotyledons, crosses were attempted between the respective cotyledon colour genotypes (Hoque, 2001). The $F_1$ seeds were of orange cotyledon colour. The $F_2$ seeds segregated into five phenotypic classes for cotyledon colour viz. orange, brown, yellow, light green and dark green. These classes were good fit into the ratio of 27:9
(yellow) : 9 (brown) : 3 (light green) : 16 (dark green) with non significant
\( \chi^2 \)-value.

2.2 Genetics of quantitative traits

Estimation of genetic parameters for quantitative characters are
important as they help in defining efficient breeding methods. The traits
like, plant height, days to flowering and maturity, number of pods per
plant, seed weight etc. are important quantitative traits which have direct
effect on the yield. In lentil there is a measurable amount of heterosis
in \( F_1 \) hybrids in respect to quantitative traits.

Singh and Jain (1971), Sagar and Chandra (1980), Sandhu et al.
(1981), Bhajan et al. (1987) and Tyagi and Sharma (1989) observed
heterosis for number of branches per plant, pods per plants clusters
per plant, harvest index and earliness in flowering and maturity,
indicating non-additive genetic variance for these traits. Predominance
of non-additive genetic variance for seed yield per plants has also been
reported by Singh and Jain (1971) and Chauhan and Singh (1995).
Greater importance of additive genetic variance in the inheritance of
100 seed weight has been reported by Singh and Singh (1993) and
Chauhan and Singh (1995). The importance of both additive and non-
additive genetic variance for branches per plant has been reported by
Sagar and Chandra (1980), Sandhu et al. (1981) and Waldia and
Chhabra (1989).

High estimates of heritability were obtained for yield per plant, 100-
seed weight, plant height, days to flowering, germination percentage,
total plant weight (biomass) and maturity by Nandan and Pandya (1980).
Sindhu and Mishra (1982), Lakhani et al. (1986) and Singh et al. (1989). Low estimates of heritability were reported for grain yield, seed size, seeds per pod, pods per plant and number of primary branches by Sindhu and Mishra (1982), Ramgir et al. (1989) and Singh et al. (1989).

2.3 Linkage mapping

The potential use of genetic markers to establish linkage maps has increased dramatically over the last decade. Relatively well-developed linkage maps that include loci encoding various isozymes, restriction fragment length polymorphism (RFLP) and qualitative and quantitative traits loci are available in several crops, such as wheat (Hart and Gale, 1990), tomato ( Tanksley et al., 1982, Tanksley and Mutchler, 1990), pea ( Weeden and Wloko, 1990) and lentil ( Tahir et al., 1993) soybean ( Palmer and Kiang, 1990) and maize (Coe et al., 1990). An important use of these maps would be to develop marker base selection of plant breeding programmes.

An established linkage map can also provide useful information for the detection of analogous genes and linkage groups in related genera. Several linkage groups previously identified in pea were found to have their counterparts in lentil. For example, the association between the genes responsible for the production of anthocyanin at the base of the stem (D in the pea and GS in the lentil) and the gene encoding the plastid-specific form of aspartate amino transferase (Aat-P) has been shown in both the genera (Muehlbauer et al., 1989 and Weeden and Marx, 1987).
Fig. 2  Linkages among genetic markers found in recombinant inbred lines of lentin. Estimates of recombination in centimorgans are shown on left (Tahir and Muehlbauer, 1994)
Fig. 2 Linkages among genetic markers found in recombinant inbred lines of lentil. Estimates of recombination in centimorgans are shown on left (Tahir and Muchaibauer, 1994).
Fig. 2  Linkages among genetic markers found in recombinant inbred lines of lentil. Estimates of recombination in centimorgans are shown on left (Tahir and Muchlaufer, 1994)
The first report on linkage map in lentil was published by Zamir and Ladizinsky (1984). They reported two linkage groups that involved 5 loci. In the first group, linkage was detected between the gene for epicotyl colour (Gs) and Got 2 (14 cM) and also between Gs and Mc 1 (25 cM). The second linkage group involved two enzyme-coding genes Got 3 and Adh1 which could be located 21 cM apart from each other. Taamor et al. (1987) determined 5 linkage groups in a cross between L. culinaris and L. ervoides. Four loci (Aco 1, Pgm 2, Gs, Got 2) were shown to be linked with a translocation break point in one linkage group. Havy and Muehlbauer (1989) and Muehlbauer et al. (1989) crossed L. culinaris and L. orientalis and demonstrated the linkage between 6 morphological markers, 8 loci and 20 RFLP probes. Six out of 34 markers showed to be non linked while remaining 28 were separated into 9 linkage groups. Tahir et al. (1993) reviewed a total of 21 morphological and at least 91 polymorphic isozymes and RFLP markers and arranged them in ten tentative linkage groups based on pooled data derived from different studies and the regions of homology shared with pea (Fig. 1). Tahir and Muehlbauer (1994) identified six linkage groups which included 17 isozymes and four morphological traits loci (Fig. 2).

Emami (1996) worked out the linkage between three morphological markers. He located Ert and Bl at a distance of 34 cM. The linkage between Bl-Gs was first time reported with the distance of 14 cM. Taking the recombination fraction between Ert-Gs, Ert-Bl and Bl-Gs he concluded that these three genes are located at same chromosome in the order of Ert-Bl-Gs or Gs-Bl-Ert.
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Emami (1996) worked out the linkage between three morphological markers. He located Ert and BI at a distance of 34 cM. The linkage between BI-Gs was first time reported with the distance of 14 cM. Taking the recombination fraction between Ert-Gs, Eri-BI and BI-Gs he concluded that these three genes are located at same chromosome in the order of Ert-BI-Gs or Gs-BI-Ert.
Fig 3: Linkage map of Drosophila (Engel et al., 1992)
Eujayl et al. (1997) reported that to maximize the extent of polymorphism within a mapping population wide crosses are often made to know the segregation distortion. They attempted the cross between wild lentil (*Lens culinaris* sub sp. *orientalis*) and cultivated lentil (*Lens culinaris* Medik.) and RAPD markers were used for genetic mapping in F$_2$ populations. Eighty three per cent RAPD markers showed segregation distortion, which was also observed in isozyme and morphological loci. Seventy eight segregating loci were analysed for linkage at a LOD score >3.0, resulted in 28 RAPD, one RFLP, one morphological and three oligonucleotide markers, which were assigned to 9 linkage group spanning 206 cM of lentil genome. A genetic linkage map of *Lens* sp. was constructed with 177 markers (89 RAPD, 79 AFLP, 6 RFLP and 3 morphological markers) using recombinant inbred lines (Eujayl et al., 1998). This linkage map covered 1073 cM of the lentil genome with an average distance of 6.0 cM between adjacent markers. The morphological markers pod indehiscence, seed-coat pattern and flower colour loci were mapped (Fig. 3). Out of the total linked loci, 8.4 per cent showed segregation distortion. AFLP markers showed more segregation distortion than RAPD markers. They also reported that it was the most extensive genetic linkage map of lentil to date.

Hoque et al. (2001) studied the inheritance and linkage relationship between eight morphological and 9 RAPD markers. Out of nine polymorphic primers only two primers OPB-02 and OPB-06 showed the expected Mendelian pattern of inheritance. The linkage was found only between two gene pairs *Bl-Gs* and *Bl-Rdp* having the map distance 25.38 and 46.01 Kosambi unit, respectively. The summation of map
distance between BI-OPM 06_{x_1} and Gs-OPM 06_{x_1} is smaller than the map distance between the genes BI-Gs. Other gene pairs viz. BI-Tnl, BI-Blf, BI-Ola, BI-Lpd and BI-Y-B were non linked with non significant \chi^2-values.