CHAPTER 12

GENETICS AND CYTOGENETICS OF LENTIL

S. K. MISHRA[1], B. SHARMA[2] AND S. K. SHARMA[3]

[1,3] *National Bureau of Plant Genetic Resources, Pusa Campus, New Delhi 110012, INDIA*

[2] *Former Head, Division of Genetics, Indian Agricultural Research Institute, New Delhi 110012, INDIA*

E-mail: skmishra_gene@rediffmail.com

Abstract: Lentil (*Lens culinaris* Medik.) is an important winter season grain legume grown worldwide in semi-arid regions. Although lentil has been an important crop for centuries, very little attention has been paid in terms of genetic research until recently. A few centers around the world, including India, have started systematic work on genetic and linkage studies in lentil. Inheritance studies involving about three-dozen morphological markers have been completed. A comprehensive linkage map involving molecular markers and a few morphological markers has been developed. In the present paper, an effort has been made to comprehend the current status and recent advances made in terms of genetic, cytogenetic, linkage studies and other related aspects in lentil. The strategies for future research have also been outlined

1. INTRODUCTION

Lentil (*Lens culinaris* Medik.) is one of the most important cool season food legume crops grown worldwide in semi-arid regions. The crop is valued as a high-protein food and for its residues, which are used in animal feeding. The Indian subcontinent is the largest lentil producing region in the world, contributing about 42% of the total world production. Besides high yield potential, its in-built capabilities to withstand moisture stress as well as problematic soil conditions has imparted a very wide adaptability to this crop. In addition, lentil has a distinct export potential superior to most pulses of Indian origin.

Even though lentil has been an important food legume for centuries, very little effort has been made on genetic studies and gene mapping in this crop until recently. In fact genetic markers have not yet been identified in sufficient numbers to create a comprehensive programme on genome mapping. The current linkage maps proposed in lentil consist of small numbers of markers mainly isozymes and DNA markers,

S.S. Yadav et al. (eds.), Lentil: An Ancient Crop for Modern Times, 187–208.

covering a relatively small portion of the lentil genome. An effort, therefore, has been made in the present paper to review the current status of genetic, cytogenetic and other related aspects in lentil.

2. TAXONOMY

Lentil is known by as many as 30 common names in different parts of the world (Kay, 1979). It belongs to the genus *Lens* and tribe Vicieae. Cubero (1981) recognized five species in the genus *Lens (Lens culinaris*, *L. ervoides*, *L. montbretti*, *L. nigricans and L. orientalis.* Later another species *L. odomensis* was also included (Ladizinsky, 1986). Among these, *L. culinaris* Medik. has been regarded as the only cultivated species of lentil. Barulina (1930) sub-divided the cultivated lentil (*L. culinaris*) in to two types, macrosperma and microsperma, primarily based on seed characters. The macrosperma types were characterized by large seeds (6–9 mm diameter), yellow cotyledons, poor pigmentation on flowers and vegetative parts, whereas, the microsperma types were have small seeds (2–4 mm diameter), orange (red)/yellow cotyledons and pigmentation on flowers and vegetative parts. Although, Williams *et al*. (1974) do not support the separation of two types of lentil based on seed size, this concept is still largely accepted by lentil workers. Based on crossability behaviours, the genus *Lens* was classified in two biological species namely, *L. culinaris* and *L nigricans*. Ladizinsky (1979 b) studied seed protein profiles of lentil species from different geographical regions and concluded that *L. culinaris*, *L. orientalis* and *L. nigricans* were closely related whereas *L. ervoides* was different from these. Based on cytogenetic and crossability studies, Ladizinsky *et al*. (1984) recognized two species within the genus *Lens: L. culinaris* and *L. nigricans*. Ladizinsky (1986) while describing the new taxon *L. odemensis*, assigned all the five taxa (Pinkas *et al*. 1985) to the species level. Sharma *et al*. (1995) used RAPD markers to distinguish different lentil taxa representing wild and cultivated lentils. They observed that the ssp. *orientalis* is the closest to the cultivated lentil. On the other hand, *L. ervoides*, was the most divergent wild taxon followed by *L. nigricans*. The genetic similarity between the two latter species was of the same magnitude as between ssp. *orientalis* and cultivated lentil. Sharma *et al*. (1996) confirmed the above findings based on AFLP markers and Ahmad and McNeil (1996) compared a range of techniques for determining the interspecific relationships in lentil.. Van Oss *et al*. (1999) concluded that the genus *Lens* is comprised of seven taxa (*Lens culinaris* ssp. *culinaris*, *L. culinaris* ssp. *orientalis*, *L. odemensis*, *L. ervoides*, *L. nigricans*, *L. tomentosus*, *L. lamottei*). Ferguson *et al*. (1999) reassessed the classification of the genus *Lens* based on evidence relating to crossability behaviour and phylogenetic relationships to identify the morphological markers for taxon delimitation which was also supported by the isozyme and RAPD data. The following classification was proposed based on available information:

L. culinaris Medik
- ssp. *culinaris*
- ssp. *orientalis*

ssp. *tomentosus*
ssp. *odemensis*
Lens ervoides
Lens nigricans
Lens lamottei

On the basis of interspecific hybridization results, Sharma and Chahota (2004) concluded that the wild progenitor of the cultigens, *L. culinaris* ssp. *orientalis*, is a member of primary gene pool and *L. odemensis* of the secondary gene pool. They observed that using embryo rescue techniques, *L. ervoides* can be hybridized with the cultivated lentils and thus can become a member of secondary gene pool. However, *L. nigricans* was incompatible with the cultigen.

3. GEOGRAPHICAL DISTRIBUTION

Although, the geographical distribution of the genus *Lens* is mainly the Mediterranean region, significant variations exist in the distribution of individual species. The species *L. orientalis* has an eastern distribution from Turkey and Israel eastward to Uzbekistan whereas the species *L. nigricans* has the distribution mainly across the northern shores of the Mediterranean from Israel to Spain and into Algeria, Morocco and the Candy Islands. The wild form of the species *L. ervoides* has been reported in Uganda and Ethiopia. The previously recognized species *L. montbretti* is known to have very limited distribution around the headwaters of the Tigris and Euphrates.

4. CENTRES OF DIVERSITY

According to Vishnumittrre (1974), lentil was domesticated in India in the Neolithic Chalcolithic period. Based on phyto-geographic and archeological evidences, lentil belongs to the tribe Vicieae and primary areas of diversity are considered to be South-west Asia and the Mediterranean region. The archaeological evidences also suggest the lentil as one of the primary domesticates in the Near-East arc (Zohary, 1972). There are both wild and cultivated forms in the primary gene pool of lentil. Ladizinsky (1979 a) demonstrated that the species *L. nigricans* belongs to the secondary gene pool. The remaining other species are expected to form the tertiary gene pool. However, there are a few contradictions about the number of species and their inter-relationships (Ladizinsky, 1979 b). However, availability of large diversity is of great help in genetic improvement of lentil.

5. CYTOGENETICS

The cultivated lentil and their wild relatives are self-fertilizing diploids having chromosome number $2n = 2x = 14$. Variable chromosome numbers have been reported in inter-specific hybrids e.g. seven bi-valents in the intra-specific hybrids within the members of *L. culinaris* to five bivalents and one quadrivalent in the F1

hybrids derived from *L. culinaris* and *L. orientalis*. Ladizinsky (1979a) observed variable chromosome associations (univalents to multivalents) in the hybrids derived from *L. culinaris* and *L. nigricans*. Several workers have studied the karyotypes in cultivated lentil, *L. culinaris*, however, the karyotypes reported by different workers were similar. The length of chromosomes ranged from 3.0μ to 9.2 μ. Gupta and Singh (1981) reported two pairs of metacentric, two sub-metacentric and three pairs of acrocentric chromosomes. Ladizinsky (1979a, Ladizinsky *et al*., 1984) noticed that karyotype of *L. orientalis* was similar to *L. culinaris*. Gupta and Bahi (1983) observed that the karyotype of *L. culinaris* differed from *L. nigricans* by three interchanges.

6. GENETICS OF QUALITATIVE TRAITS

Leaf pigmentation: Pigmented leaf (brown) was reported to be completely dominant over non-pigmented (green) leaf and the gene symbol ***Bl*** has been proposed for pigmented leaf (Kumar, 2002; Mishra 2004).

Chlorina mutant: Vandenberg and Slinkard (1989) observed that a chlorina chlorophyll mutant was determined by a single recessive gene (***chl***) to its normal dominant allele (***Ch***l) which also confirmed later by Viallancourt and Slinkard (1992).

Xantha mutant: Vandenberg and Slinkard (1987) reported that xantha chlorophyll mutant was determined by a single recessive gene (***xan***) to its normal dominant allele (***Xan***) which was subsequently confirmed by Viallancourt and Slinkard (1992).

Foliage colour: Dark green foliage was found to be dominant over light green foliage and the gene symbol ***Dgl*** has been proposed for this trait (Kumar, 2002; Mishra, 2004).

Leaflet size: Inheritance of leaflet size was studied based on analysis of 8272 plants in F_2 generation derived from twenty-four crosses involving parents with broad leaflets and narrow leaflets. The results revealed the incomplete dominance of broad leaflets over narrow leaflets and the gene symbol ***Blf*** has been proposed for broad leaflets (Kumar *et al*., 2004; Mishra 2004).

Leaf shape: Oval leaf was reported to be monogenic dominant over normal leaf shape and the gene symbol ***Ol*** was proposed for oval leaf shape (Kumar, 2002; Mishra 2004).

Stipule size: Large stipule was found to be incompletely dominant over small stipule and the gene symbol ***Lst*** has been proposed for large stipule (Kumar, 2002).

No. of leaflets: A higher number of leaflets (6–8) was found to be monogenic dominant over a lower number of leaflets (3–4) and the gene symbol ***Hl*** has been proposed for a higher number of leaflets (Kumar, 2002; Mishra, 2004).

Growth habit: The prostate growth habit has been reported to be incompletely dominant over erect growth habit (Ladizinsky, 1979b) and the gene symbol ***Gh*** was proposed for prostrate growth habit. This dominance has since been confirmed by several other workers. Contrary to this, erect growth habit was reported to be completely dominant over prostrate growth habit and the gene symbol ***Ert*** was proposed for erect growth habit (Kumar, 2002; Mishra, 2004).

Epicotyl colour: Ladizinsky (1979c) reported that purple epicotyl was monogenic dominant over green epicotyl. The gene symbol ***Gs*** was proposed for purple epicotyl. However, the same gene symbol has been proposed by other workers (Viallancourt and Slinkard, 1992; Kumar, 2002 and Mishra, 2004) for stem pigmentation. They reported that pigmented stem was dominant over non-pigmented stem.

Tendril formation: Tendrilled plants were found to be monogenic dominant in their genetic control over non-tendrilled plants and the gene symbol ***tnl*** has been proposed for tendrilless leaf (Vandenberg and Slinkard, 1989; Viallancourt and Slinkard, 1992; Kumar 2002; Mishra, 2004).

Plant pubescence: Pubescent nature was found to monogenic dominant over non-pubescent plants and the gene symbol ***Pub*** has been proposed for pubescent nature (Kumar, 2002; Mishra, 2004).

Stem fasciation: Fasciated stem was recorded to be completely dominant over non-fasciated stem and the gene symbol ***Fa*** has been proposed for fasciated stem (Kumar, 2002; Mishra, 2004).

Globe plant type: This is an induced mutant having a compact appearance with globe like phenotype (Plate 1). Analysis of crosses between globe and the normal plant type revealed that the globe type is monogenically dominant over normal plant type. The gene symbol ***Glo*** has been proposed for globe plant type ((Kumar, 2002; Mishra *et al*., 2002; Mishra, 2004).

Plant height: Analysis of crosses between tall and dwarf plant types indicated that tall plant type behaved as monogenically dominant over dwarf plant type. The gene symbol ***Ph*** has proposed for tallness in lentil (Kumar, 2002; Mishra, 2004).

Flower colour: The flower colour in lentil has been a most variable character in lentil. Overall flower colour depends on the colour of the standard, wings and keel. Ladizinsky (1979c) suggested that the production of coloured (bluish) flower in lentil is governed by a single dominant gene, whereas, the white flower appears under recessive condition. Lal and Srivastava (1975) reported the existence of two genes for controlling the flower colour in lentil. They suggested the gene symbols ***VVPP, vvPP*** and ***VVpp*** for violet, pink and white flowers, respectively. Red flower colour was reported to be monogenically dominant over white flowers and the gene symbol ***P*** was proposed for coloured flowers (Kumar, 2002; Mishra, 2004).

Peduncle length: Long peduncle was reported to be under genetic control of a single dominant gene designated as ***Pdl*** (Kumar, 2002; Mishra, 2004). The short peduncles are produced under homozygous recessive condition.

Pod pubescence: The genetics of pubescence on different plant parts have been studied by different workers. Vandenberg and Slinkard (1989) reported that the production of glabrous pod was determined by a single recessive gene (***glp***) to the pubescent pod (***Glp***). A similar nature of inheritance of pod pubescence was confirmed by Viallancourt and Slinkard (1992). However, Kumar (2002) studied the inheritance of plant pubescence and concluded that a single dominant gene is responsible for production of pubescent-glabrous characters in lentil. He proposed the gene symbol ***Pub***, the recessive counterpart of which creates the glabrous plants.

Pod colour: Monogenic recessive nature of inheritance for green pod colour (***grp***) over red pod (***Grp***) was reported by Vandenberg and Slinkard (1989) which was later confirmed by Viallancourt and Slinkard (1992). Similar findings were noted by Kumar (2002) and Mishra (2004), but they proposed the gene symbol ***Rdp*** to represent red pod colour in lentil.

Pod dehiscence: Pod dehiscence is one of the most important characters contributing to yield losses in lentil. Ladizinsky (1979b) studied the inheritance of pod dehiscence between the crosses *L. culinaris* and *L. orientalis* and reported that pod-indehiscence was controlled by a single recessive gene (***pi***). However, the pod dehiscence is a dominant trait (***Pi***). Such reports were also confirmed by Viallancourt and Slinkard (1992).

Seed coat (testa colour): The seed coat (testa) colour is also an important trait especially for consumption and commercial utilization of lentil. Erskine and Witcombe (1984) classified the ground colour of testa into five groups viz. green, pink, brown, gray and black. This has made the inheritance pattern of seed coat colour more complex. Ladizinsky (1979b) studied the spotting pattern on seed coat and proposed the gene symbol ***Scp*** for seed coat colouration pattern whereas the unspotted seed coat will be produced under recessive homozygous condition (***scpscp***). Vandenberg (1987) and Vandenberg and Slinkard (1990) concluded that the testa colour in lentil is determined by two non-linked dominant genes. They suggested that gray ground colour of testa is determined by the dominant gene, ***Ggc,*** whereas, the tan ground colour is produced by other dominant gene ***Tgc***. The genotypic constitutions for different colours were as follows, ***GgcGgcTgcTgc*** (brown), ***GgcGgctgctgc*** (gray), ***ggcggcTgcTgc*** (tan) and ***ggcggctgctgc*** (green). Vandenberg (1987) reported that black seed coat is determined by one gene (***blsc 1***) in some crosses and by other gene (***blsc 2***) in some other crosses. However, Vallincourt and Slinkard concluded only one dominant gene determining the black seed coat (***Blsc***) in lentil. Emami and Sharma (2000) based on their studies involving the crosses with different testa (black, brown, tan, green) and cotyledon (orange, yellow, dark green) colours reported that although black testa was dominant over non-black testas, its penetrance is not complete, as the expression of testa colour is greatly influenced by the cotyledon colour. They suggested to carry-out detailed genetic analysis using appropriate genotypes for cotyledon and testa colours. The monogenic dominant nature of black testa has been confirmed. The gene symbol ***Blt*** has been proposed for black testa (Sharma *et al*. 2004; Mishra, 2004) although the mode of inheritance proposed remains the same. Monogenic dominant control was reported for mottling on seed coat (***Mot***) over non-mottling (***mot***) in lentil (Kumar, 2002; Mishra, 2004).

Cotyledon colour: Monogenic dominance of orange cotyledon is reported by several workers (Tschermak-Seysenegg, 1928; Wilson *et al*. 1970; Slinkard, 1978; Singh, 1978; Sinha *et al*. 1987, Emami, 1996). However, Emami and Sharma (1996a,b) discovered and confirmed the digenic control of cotyledon colour in lentil. They proposed orange colour is due to the interaction of two dominant genes viz., yellow (***Y***) and brown (***B***). The two genes can produce independently the yellow (***Y-bb***) and

brown (***yyB-***) pigments. However, the orange colour will be produced only when both the genes are present in dominant condition (***Y-B-***). Under double recessive conditions (***yybb***), the light green cotyledons are produced, as no pigments are synthesized. Emami and Sharma (2002) discovered a third gene designated as ***Dg*** which leads to the production of dark green cotyledons and this gene behaved as a monogenic recessive to the orange phenotype. This proposal was later confirmed with a voluminous set of data (Sharma *et al*., 2004; Mishra, 2004). Accordingly, a system of three genes (***Dg***-dark green, ***Y***-yellow, ***B***-brown) has been confirmed to control cotyledon colour in lentil. In the presence of dominant gene ***Dg***, the yellow cotyledon is produced by the gene ***YY***, whereas, the gene ***BB*** produces brown cotyledon. When all the genes are present in dominant condition (***Dg-Y-B-***), the orange (red) cotyledons are produced. However, when the gene for dark green colour is recessive (***dgdg***), irrespective of dominant or recessive genes for yellow/brown/orange cotyledons (***YY or yy; BB or bb; Y-B-***), the dark green cotyledons are developed. The light green cotyledons are produced when the genes for yellow and brown colours are both recessive (***Dg-gyybb***).

Hard seed coat: Ladizinsky (1985) reported that the hard seed coat is a monogenic dominant charatcter and assigned the gene symbol ***Hsc***. This finding has been confirmed by Vaillancourt (1989).

Days to flowering: Sarker *et al*. (1999) reported that the early flowering was determined by a single recessive gene (***sn***). However, the occurrence of early flowering transgressive segregants in F_2 could be attributed to the interaction of the gene ***sn*** and minor genes for earliness.

7. GENETICS OF DISEASE RESISTANCE

Wilt *[Fusarium oxysporumf. Sp. Lentis (Snyder and Hensen)]:* Kamboj *et al*. (1990) reported that the resistance to *Fusarium* wilt in lentil was controlled by two dominant duplicate genes in the variety Pant L 234 whereas it was controlled by two independent dominant genes having complementary effects in the susceptible varieties JL 446 and LP 286. The allelic tests revealed that the five genes were operating in the resistance to *Fusarium* wilt in their materials under study. However, Euzyl *et al*. (1998) reported that the resistance to wilt was conditioned by a single dominant gene after three seasons of testing the $F_{6.9}$, $F_{8.9}$ recombinant inbred lines (RILs) and $F_{2.4}$ progenies in a well-established wilt-sick plot. These populations were developed by crossing between resistant (ILL 5588) and susceptible (L 692-16-$1_{(s)}$) lines. They also proposed the gene symbol ***Fw*** for resistance.

Rust *(Uromyces fabae (Pers.) de Bary):* Rust resistance in lentil is reported to be controlled by a single dominant gene (Sinha and Yadav, 1989). Single, but different dominant genes for rust resistance in different varieties (Pant L 406, Pant L 639, LG 120, UPL 175) was reported by Singh and Singh (1990). Singh and Singh (1992) also reported that resistance is governed by a monogenic dominant gene based on F_2 and F_3 analysis of 21 crosses derived from the crossing of seven resistant and three susceptible parents. Chauhan *et al*. (1996) also observed a single dominant

behaviour of rust resistance. Duplicate dominant genes controlling rust resistance was reported by Lal *et al*. (1996). Kumar *et al*. (1997) have reported that resistance to rust in five genotypes (L 178, L 1534, L 2980, L 2991, HPLC 8868) is governed by a single dominant gene whereas in the genotype Precoz, it was found to be controlled by duplicate dominant genes. Kumar *et al*. (2001) studied inheritance of rust resistance in 23 crosses derived from eight resistant and ten susceptible lines in different combinations. They reported that two independent dominant and one recessive genes were imparting resistance to rust in the material under study. For the first time they reported gene symbol as $\boldsymbol{Urf}_1$ (Precoz, L 4603), $\boldsymbol{Urf}_2$ (Pant L 4, L 4147) and $\boldsymbol{urf}_3$ (DPL 21). Chahota *et al*. (2002) studied two crosses (Precoz × L 259; Precoz × Pant L 639) under greenhouse conditions and reported that the resistance was governed by duplicate dominant genes. Mishra *et al*. (2005) have reported the phenomenon of slow rusting in lentil based on evaluation of 305 lentil lines (255 lines from ICARDA, Syria and 50 indigenous lines) at a hot spot location. Mishra (2006) reported monogenic dominant control of rust resistance in lentil. However, the gene for resistance in the variety Precoz was different from that of PL 4 confirming partly the findings of Kumar *et al*. (2001).

Blight *(Ascochyta pisi/A. lentis/A. fabae)***:** Ahmad *et al*. (1997) reported that the host resistance was controlled by two complementary dominant genes in the wild species namely, *L. ervoides* and *L. odemensis*. Tay and Slinkard (1989) reported that each genotype Laird, ILL 5538 and ILL 5684 had single dominant genes for resistance. Ahmed and Morali (1998) could not observe the Mendelian segregation pattern for virulence in the materials studied.

8. GENETICS OF ABIOTIC STRESSES

Boron: Boron deficiency was identified in highly calcareous soils in India where genetic differences could be demonstrated in chickpea and pigeonpea (Singh *et al*., 1991). Among nutrient-imbalance issues in cool-season food legumes, boron (B) has received scant attention (Saxena *et al*., 1994). However, Sakal *et al*. (1988) demonstrated the differential response to boron application in lentil and noticed that the cultivars DL 77–2 and Pant L 406 were the most efficient for boron uptake while the variety L 9–12 being most B inefficient. Similar observations have also been reported from Srivastava *et al*. (2000). Yau (1999) identified the line ILL 5583 as tolerant to boron toxicity. Yau and Erskine (2000) and Hobson *et al*., (2006) studied the diversity of boron-toxicity tolerance in lentil growth and yield and reported highly significant differences in B-toxicity tolerance between 231 and 310 accessions respectively. On average, accessions from Afghanistan were the most tolerant, followed by those from India, Iraq, Syria, Europe Ethiopia and Nepal.

Iron: Erskine *et al*. (1993) observed significant differences in iron deficiency symptoms in lentil germplasm. Ali *et al*. (1997) studied the inheritance of iron-deficiency based on six crosses involving resistant and sensitive lines. They indicated the resistance was under monogenic dominant control and proposed the gene symbol *Fe* for resistance.

Salt: Ashraf and Waheed (1990) studied the effect of NaCl on germination and emergence of 131 lentil varieties in the greenhouse and reported five varieties producing significantly greater fresh and dry biomass than the others. Detailed study was carried-out by Katerji *et al*. (2001) by taking one sensitive and one tolerant variety from the above study. They concluded that the lentil is most sensitive to salinity and it can be grown on non-saline soils. Maher *et al.,* (2003) investigated over 300 lines for salt tolerance and found considerable variability. However, the main Australian commercial varieties were all low in salt tolerance. Ashraf and Waheed (1998) reported that both additive and non-additive effects were significant for yield components.

9. LINKAGE STUDIES

Genetic maps of agricultural crops are a valuable tool for plant geneticists and breeders. The maps can be used to improve breeding efficiency and tagging of genes by their association with the specific traits, and locating quantitative trait loci (QTL). The first report on linkage in lentil was published by Zamir and Ladizinsky (1984) with two linkage groups. Tadmor *et al*. (1987) determined five linkage groups (2 morphological and 8 isozyme markers) in a cross between *Lens culinaris* and *Lens ervoides*. Havey and Muehlbauer (1989) and Muehlbauer *et al*. (1989) proposed nine linkage groups involving 6 morphological, 8 isozyme loci and 20 RFLP probes using the mapping population derived from an inter-specific cross between *Lens culinaris* and *Lens orientalis*. Weeden *et al*. (1992) developed eleven linkage groups covering 560 cM distance using 64 markers (morphological, isozyme and DNA markers). The comparison between this proposed map with that of *Pisum sativum* revealed eight regions showing linkages among markers were conserved. Tahir *et al*. (1993) compared the data from different studies and proposed 10 tentative linkage groups involving 7 morphological, 25 isozyme, 38 RFLP and 6 other loci. Tahir and Muehlbauer (1994) identified six linkage groups, which included 4 morphological and 17 isozyme loci. Emami (1996) could establish linkage among growth habit, stem colouration and leaf colouration. Euzyl *et al*. (1998) worked extensively on linkage studies of *Len*s involving 177 markers (3 morphological, 89 RAPD, 79 AFLP, and 6 RFLP) using 86 recombinant inbred lines ($F_{6:8}$) obtained from a partially inter-specific cross and proposed seven linkage groups. The map covered 1073 cM of the lentil genome with an average distance of 6.0 cM between adjacent markers. Hoque (2001) constructed four linkage groups in lentil using 12 morphological and one RAPD markers. These markers could cover 217 Kosambi units of lentil genome with an average distance of 8.75 cM Mishra *et al*. (2002) proposed four linkage groups in lentil based on the linkage analysis involving sixteen gene pairs (morphological markers) using F_2 populations of inter-varietal crosses of *Lens culinaris*. They analyzed 496 combinations of different markers. Kumar (2002) constructed four linkage groups in lentil based on morphological markers. Rubeena *et al*. (2003) constructed the first intra-specific linkage map in lentil using 114 markers (100 RAPD, 11 ISSR and 3 RGA) in an F_2 population

derived from the cross ILL 5588 x ILL 7537). They proposed nine linkage groups comprising between 6 to 18 markers each with the total coverage of 784.1 cM. The utility of ISSR and RGA markers for mapping in lentil was explored and the primers with an AC repeat motif were found to be more useful. Kahraman *et al*. (2004) proposed nine linkage groups using 175 markers. Average distance between linked markers was 9.1 cM, however, it ranged from 0.3 –21.1 cM. A framework of 130 markers covering 1192 cM distance of lentil genome was used for the analysis of quantitative trait loci (QTLs). Mishra (2004) proposed nine linkage groups in lentil involving 16 morphological markers (including rust resistance) and 11 RAPD primers covering 740.2 cM of the genome. Recently, Mishra (2006) could identify a RAPD marker OPP 15 to be linked with the rust resistance gene (*Urf*) at a map distance of 26.1 cM. Although, the distance is not very close, it can be a beginning point for identification of more closely linked markers for utilization in marker assisted selection.

10. GENETICS OF QUANTITATIVE TRAITS

Genetic divergence: Genetic divergence is the measure of genetic distance among the cultivars or germplasm lines. This divergence may be due to geographic barriers or any other reasons, which may restrict the gene flow, resulting in the formation of distinct groups. In crop improvement programmes, selection of parents for hybridization is a crucial step for harnessing the useful variability for economic purposes. Therefore, breeders and geneticists essentially require information on nature and magnitude of genetic diversity in the materials available at their disposal. The Mahalanobis D^2 technique is a novel and widely used method to work out the genetic divergence. Biswas and Das (1985) estimated genetic diversity over two environments for ten characters in lentil accessions collected from Bangladesh and India and reported that the population from the two countries were divergent from each other. However, the clustering pattern was influenced by the parentage and geographical origin in a few cases while this was not true in others. Balyan and Singh (1986) grouped 48 genotypes of lentil into 12 clusters based on the analysis of nine characters. Based on Nei's average gene diversity, Harvey and Muehlbauer (1989) established that the wild lentils (*L. orientalis* and *L. odemensis*) had greater variability for RFLP and were more close to the cultivated lentil (*L. culinaris*). However, a narrow range of diversity could be obtained within the accessions of *L. ervoides* and *L. nigricans*. Chahota *et al*. (1994) classified 40 genotypes of small seeded lentil (microsperma) into six clusters based on Mahalanobis' D^2 Statistic and Canonical analysis considering 15 traits. The low level of diversity in the cultivated taxon as compared to the wild species was reported in lentil based on allozyme polymorphic survey for 11 loci in 439 accessions (Ferguson and Robertson, 1996). Rathi *et al*. (1998) grouped 21 genotypes into eight clusters based on analysis of six yield and yield contributing traits. They reported that the number of primary branches per plant contributed most towards the total genetic divergence followed by yield per plant. The clustering pattern predicted that the genetic diversity is not

necessarily parallel to the geographical diversity. Singh *et al*. (2001) reported eight clusters based on the multivariate analysis of 58 diverse strains of lentil. Jeena and Singh (2001) carried out Hierarchal cluster analysis using 30 genotypes of lentil (28 wild accessions and 2 cultivated) for qualitative (HCA 1), quantitative (HCA 2) and both qualitative and quantitative (HCA 3) traits. The results indicated wide genetic divergence as each analysis yielded four, three and three clusters, respectively. Jeena and Singh (2002) evaluated 61 lentil accessions representing four wild species viz., *L. nigricans* (2), *L. odemensis* (16), *L. ervoides* (24) and *L. orientalis* (19). Based on the analysis of data on 20 quantitative traits, all the accessions could be grouped into four clusters. Interestingly, 58 accessions could be grouped into Cluster 1 while rest of the clusters were mono-genotypic. The study clearly indicated that the genetic diversity was not related to the geographical diversity and species differences. Solanki *et al*. (2002) reported 72 genotypes to be classified into eight and nine clusters under normal and late sown conditions, respectively. Singh *et al*. (2002) reported the genotype x environment interaction on determination of clustering pattern. They carried out D^2 analysis involving 40 genotypes for two consecutive years and grouped them into six and seven clusters, respectively. Rakesh *et al*. (2005) grouped 44 genotypes in to five clusters based on the analysis of data on 15 important characters at two locations. Yadav *et al*. (2005) worked-out genetic divergence based on analysis of data on 50 genotypes under two environments and reported that the genetic diversity was not paralleled to the geographical diversity. Recently, Poonam (2006) grouped 100 lentil genotypes of diverse origin into ten clusters based on analysis of 12 quantitative traits. Out of these 100 accessions, sixty genotypes were also subjected for divergence analysis using ten RAPD primers. Although, these genotypes could be grouped into ten close-knit clusters, there was no parallelism between the two types of the clustering pattern.

Correlation: Adequate knowledge about degree and direction of the association of characters is a pre-requisite for operating an efficient selection programme. Exhaustive studies on interrelationship of characters among themselves and also between yield and yield components have been carried–out. A positive association between seed size and pod size reported by Sharma and Sharma (1978) can be useful in selecting the variability for seed size. Significantly positive genotypic and phenotypic correlations between seed and straw yields have been recorded both in small seeded (*microsperma*) and bold seeded (*macrosperma*) accessions of lentil (Erskine, 1983) indicating the possibility of continued selection for higher seed yield would not adversely affect the straw yield. Sarwar *et al*. (1984) reported positive correlation of seed yield with number of pods per plant, number of primary and secondary branches per plant in the Indigenous as well as in the exotic germplasm. Erskine *et al*. (1985) recorded negative genetic correlation between seed yield and protein content whereas it was positive between cooking time and seed size (Hamdi *et al*. 1991). Although there was positive correlations of seed size with seed impermeability and seed germination. However, the seed impermeability and germination were negatively correlated (Shahi *et al*. 1986). Positive correlations

of seed yield per plant with number of primary branches per plant, plant height, number of seeds per plant and 100-seed weight were observed in lentil (Murari *et al*. 1988). Profuse branching and number of pods per plant were positively correlated with seed yield (Zaman *et al*. 1989). A positive and highly significant correlation coefficient was found between seed yield per plant and number of pods per plant (Nigam *et al*. 1990). Hamdi *et al*. (1991) reported positive correlation between seed yield and straw yield. Multiple correlation and regression analysis revealed that the combination of two or three variables such as plant height, number of branches per plant, number of pods per plant was the best method for improving the seed yield. Singh and Singh (1991) observed that plant height was always correlated positively with seed yield per plant in both *microsperma* and *macrosperma* lentils. Seed yield per plant was positively correlated with all the yield components except 100-seed weight in Indigenous lentil germplasm (Pandey *et al*., 1992). Esmail *et al*. (1994) reported that seed yield was positively and significantly correlated with plant height, number of branches per plant, number of seeds per pod and number of pods per plant, however, it was negatively correlated with flowering duration. Both genotypic and phenotypic positive correlations of seed yield with plant height, number of primary branches per plant, number of pods per plant, protein and methionine contents were observed in 13 parents and their 31 F_1*s* (Kumar *et al*., 1995). Seed yield per plant was positively correlated with harvest index (Chauhan and Singh, 2001). Rakesh *et al*. (2005) reported the correlation among yield and yield components (15 characters) in 44 germplasm accessions of lentil. The analysis indicated that that the values of genotypic correlations were slightly higher, in general, than the phenotypic correlations.

Path coefficient: Pods per plant had higher direct effect on seed yield in both Indigenous and exotic germplasm. However, in exotic germplasm, 100 -seed weight showed a high direct effect on seed yield (Sarwar *et al*., 1984). Luthra *et al*. (1990) reported that biological yield was the main contributor towards seed yield while other characters showed variation in their relative contribution towards seed yield. The path analysis indicated that the number of pods per plant had high positive direct effect on seed yield per plant based on analysis of thirteen hundred germplasm accessions of Indigenous origin (Pandey *et al*., 1992). However, days to flowering, plant height and number of primary branches per plant had high positive indirect effects via number of pods per plant. Plant height, number of primary branches per plant and number of pods per plant could emerge as direct yield contributors while number of secondary branches per plant, number of pods per plant, and number of seeds per pod influenced the seed yield indirectly via number of primary branches per plant (Kumar *et al*., 1995).

11. HERITABILITY AND GENETIC ADVANCE

Heritability is an important parameter in the genetic studies of quantitative characters. It is considered as an index of transmissibility of the character(s) from parents to their off-springs. The heritability in a broadsense is the ratio of genetic

variance to the total (phenotypic) variance. Thus, the population expressing larger proportion of genetic variability for particular character or group of characters will be more amenable to selection. Although, heritability is an important biometrical estimate, it should be used in conjunction with genetic advance for better understanding and use (Johnson *et al*., 1955). High heritability coupled with high genetic advance may be the most desirable situation for practical utility. Dixit and Dubey (1985) reported the highest heritability estimate for days to flowering. However, moderate heritability (59.7%) coupled with highest genetic advance in percent of mean (72.9%) was observed for seed yield. Erskine *et al*. (1985) reported highest heritability estimate for average seed weight (98%) followed by cooking time (82%). Lakshmi *et al*. (1986) recorded higher heritability coupled with high genetic advance for germination percentage, hard seed percentage and 100-seed weight. Ali and Johnson (2000) worked-out heritability estimates for winter hardiness under natural and controlled condition. The estimates of narrow sense heritability estimates ranged from 0.32 to 0.71 under field conditions whereas under controlled condition it was maximized at 1.00. Omvir and Gupta (2000) studied heritability in microsperma x macrosperma derived lines. They reported low heritability estimates in poor environments, however, it was higher in the best environment. Rathi *et al*. (2002) reported high heritability estimates along with higher genetic advance for 1000-grain weight. Dayachand (2007) reported higher estimates of broadsense heritability in combination with high genetic advance for days to maturity.

12. COMBINING ABILITY

The success of any breeding programme depends on choice of parents for developing segregating population for selection. Although, *per se* performance has been an important criteria for selection of the parents, good performing parents do not always produce desirable segregants. The information regarding combining ability of the parents for yield and yield related traits has been an important criteria in designing the appropriate breeding methodology. The importance of general combining ability (GCA) variance has been reported for days to flowering (Malhotra *et al*., 1973, Haddad *et al*., 1982, Singh and Gupta, 1994); for plant height (Malhotra *et al*., 1973,Waldia and Chhabra, 1989); for secondary branches per plant (Singh *et al*., 1975), for primary branches per plant (Singh and Gupta, 1994), for seeds per pod (Gupta and Singh, 1994, Rathi *et al*., 1994) and for 100-seed weight (Singh and Singh, 1993, Chauhan and Singh, 1993). Preponderance of the non-additive portion of genetic variance for seed yield per plant has been reported by several workers (Singh and Jain, 1971; Chauhan and Singh, 1993). Singh and Singh (2003) carried out combining ability analysis based on an 8x8 diallel. They reported that the parents DPL 62 and K 75 were good general combiners for days to flower, days to maturity, plant height, primary branches per plant, secondary branches per plant, number of pods per plant, 1000-seed weight and grain yield per plant whereas L 830 was good general combiner for earliness.

The specific combining ability (SCA) effect represents the non-additive gene action which is non-fixable in nature. In none of the studies, did a single cross have significant SCA effect for all the characters, SCA effects are found to vary in magnitude with the change of environment. Thus a particular parent may be a good combiner for specific traits. It is also not necessary that the crosses exhibiting positive significant SCA effect involve parents with high × high GCA effects. In most of the cases high SCA crosses result from the high × low, low × high, high × average, average × high GCA combinations. In few rare cases, high × high or low × low GCA combinations may show significant SCA effects. Singh and Singh (1990) reported that both GCA and SCA effects were significant fro all the characters under study across the generations.

13. HETEROSIS

Singh and Jain (1971) reported very low to very high magnitude of heterosis for different characters based the performance of F_1 hybrids developed from 11 parents. They observed that the heterosis for grain yield was mainly due to heterosis in yield contributing characters and genetic diversity among the parents. Goyal *et al*. (1976) recorded highest better parent heterosis for pods per plant (166%) followed by seed yield (146%). Sagar and Chadra (1980) reported highest mid-parent heterosis for yield per plant in nine crosses of lentil. Kamboj (1986) reported heterosis for eight quantitative characters in ten crosses involving five parents. All the hybrids exhibited moderate to high manifestation of standard heterosis except for 100-seed weight for which estimates were negative and high. Erskine *et al*. (1991) worked-out the magnitude of heterosis based on the performance of 50 hybrids over two years under rainfed conditions and concluded that heterosis over better parent was non-significant for grain yield. Interestingly, the magnitude of heterosis was higher in the hybrids involving low yielding parents whereas it was least in the crosses involving high yielding parents. Singh and Singh (1992) reported that heterosis over better parent was maximum for No. of clusters per plant (66.6%) followed by pods per plant (65.3%) and seed yield per plant (15.3%). Kumar *et al*.(1996) recorded high manifestation of heterosis over better parent and standard variety for yield per plant. Dayachand (2007) also reported high magnitude of heterosis over better parent for seed yield per plant.

14. VARIABILITY AND GENETIC RESOURCES

Variability is the hub of any breeding programme**.** The success of a breeding programme depends upon the nature and magnitude of variability present in the materials. The higher the variability, the greater the chances of attaining better success in selection and vice-versa. Also, among three components of genetic variability namely, additive, dominance and epistatic, the additive component, which is fixable, is of greatest importance in selection breeding. Several studies have been conducted to assess the variability in the germplasm/genetic stocks regarding yield

and its components, biotic and abiotic stresses and nutritional parameters (Rajput and Sarwar, 1989; El Attar, 1991; Pandey *et al*., 1992; Esmail *et al*., 1994; Kumar *et al*., 1995; Chauhan and Singh, 1998; Kumar *et al*. 1999; Chakraborty *et al*. 2000, Solanki and Sharma, 2001; Rathi *et al*., 2002; Hamdi *et al*., 2003; Mishra *et al*., 2005; Poonam, 2006 etc.) and a wide range of variability have been reported. Systematic efforts are also being made for augmentation of germplasm through Indigenous collections and acquisition from other countries especially from CGIAR centers. ICARDA, Syria has been the major contributor for enrichment of lentil germplasm. Several potential donors have been identified for different economic traits (Mishra *et al*., 2005, Sardana, *et al*., 2005, Singh *et al*., 2006) in lentil.

15. ROLE OF GENETICS IN VALUE ADDITION

Cotyledon colour has been one of the most important characters for consumer preference. Normally, the lentil variety having orange (red) cotyledon colour is recognized as lentil especially in India. The same is true with yellow cotyledons in a few countries. Occurrence of brown, light green and dark green cotyledons in lentil has rarely been recognized. The recent studies on detailed genetic studies of cotyledon colour have amply demonstrated the trigenic control of cotyledon colour (detailed under the sub-head genetics of qualitative characters). Therefore, genetic manipulation can easily be made for developing varieties with specific cotyledon colour as per consumer demand. The seed size is another parameter which affects the market value of lentil. The genetic studies on inheritance of seed size have direct bearing on varietal development. The protein content and amino acid profile are also important biochemical parameters for deciding the quality of lentil. Reports on heterosis for protein and methionine contents, although old, are of potential value for exploitation in breeding programmes (Kumar *et al*., 1994). Genetic studies on cooking quality (Erskine *et al*., 1985) are of special importance for value addition in lentil.

16. RECENT ACHIEVEMENTS

Although, lentil has been an important winter season legume, very little attention was paid in terms of genetic research until recently. However, recognizing its potential to thrive well under adverse agro-edaphic situations, considerable work has been started in a few institutions engaged in lentil research and development with tangible results. Recent studies conducted at the Division of Genetics, Indian Agricultural Research Institute, New Delhi on inheritance and linkage studies involving morphological and molecular markers has paved the way for further research. A large number of multi-marker lines have been developed for their use in future genetic analysis. The joint collaborative efforts of ICARDA, Syria and University of Keil, Germany has led to the development of genetic linkage map using lentil based on micro-satellite, AFLP, RAPD and morphological markers

(ICARDA Annual Report, 2005). Molecular tagging of genes for resistance against biotic and abiotic stresses is a recent initiative.

17. FUTURE OUTLOOK

As discussed above, considerable work on genetic studies has been underway in lentil. There is an immediate need to form a network of researchers working on lentil genome mapping after comprehending the progress made so far. Although several linkage maps have been proposed mostly involving molecular markers, it is essentially required to involve more morphological markers and traits of economic importance for their tagging or establishing tight linkage for practical use in marker assisted selection. The seven linkage groups are still to be identified and defined. This can only be completed if systematic studies are made involving geneticists, cytogeneticists, plant breeders, biotechnologists, plant physiologists and plant protection scientists in a multi-disciplinary mode. There is also a need to create more markers through induced mutagenesis for developing a comprehensive linkage map. The inheritance studies on resistance/tolerance to biotic and abiotic stresses will be useful in designing appropriate breeding methodology based on the regional requirements. Molecular tagging of genes for resistance against biotic and abiotic stresses should receive first priority in order to exploit them in practical breeding programmes with increased selection efficiency and better precision.

REFERENCES

Ahmad, M., Russell, A. C. and McNeil, D. L. 1997. Identification and genetic characterization of different resistance sources to *Ascochyta* blight within the genus *Lens*. *Euphytica*, **97**: 311–315.

Ahmad, M. and McNeil, D. L. 1996. Comparison of crossability, RAPD, SDS-PAGE and morphological markers for revealing genetic relationships within and among Lens species. *Theoretical and Applied Genetics*. **93** (5/6): 788–793.

Ahmed, S. and Morrall, R. A. A. 1998. Inheritance of virulence in *Ascochyta lentis* on lentil. *Lens Newsletter*, **25**(1&2): 67–70.

Ali, A., Riaz- ul-Haque, M. and Bhatti, M. S. 1997. Inheritance of resistance to iron-deficiency chlorosis in lentil. *Lens Newsletter*, **24**(1& 2): 28–29.

Ali, A. and Johnson, D. L. 2000. Heritability estimates for winter hardiness in lentil under natural and controlled conditions. *Plant Breeding*, **119**(3): 283–285.

Annual Report. 2005. International Centre for Agricultural Research in the Dry Areas, Aleppo, Syria. pp.156.

Ashraf, M. and Waheed, A. 1990. Screening of landraces/exotic accessions of lentil (*Lens culinaris*) for salt tolerance at two growth stages. *Plant and Soil*, **128**: 167–176.

Ashraf, M. and Waheed, A. 1998. Genetic basis of salt (NaCl) tolerance in lentil. *Lens Newsletter*, **25**(1&2): 15–22.

Balyan, H. S. and Singh, S. 1986. Genetic divergence in lentil. *Lens Newsletter*, **13** (1): 3–4.

Barulina, E. I. 1930. Lentils of USSR and Other Countries: A Botanico Agronomical Monograph. *Trudy Prikl. Bot. Genet. (Suppl.)*, **40**: 265–304. (cf. S. K. Sharma and R. K. Chahota. 2004. Current status of interspecific hybridization in genus *Lens*. *Journal of Lentil Research*, **1**: 15–18).

Biswas, P. K. and Das, P. K.1985. Genetic divergence in lentil (*Lens culinaris* Medik.). *Annals of Agricultural Research*, **6**: 179–182.

Chahota, R. K., Sharma, S. K. and Lal, C. 1994. Genetic divergence in microsperma lentil. *Legume Research*, **17**(2): 132–134.

Chahota, R. K., Gupta, V. P. and Sharma, S. K. 2002. Inheritance of rust resistance in lentil (*Lens culinaris* Medik.). *Indian Journal of Genetics and Plant Breeding*, **62**(3): 226–227.

Chakraborty, M. and Haque, M. F. 2000. Genetic variability and component analysis in lentil. *Journal of Research*, *Birsa Agricultural University*, **12**(2): 199–204.

Chauhan, M. P. and Singh, I. S. 1993. Genetics of seed size in lentil (*Lens culinaris* Medik.). Abstr. National Sym. On Plant Breeding Strategies for India in 2000 A.D. and Beyond, 25–27 December, Aurangabad, India, Indian Society of Genetics and Plant Breeding, New Delhi: 220–221.

Chauhan, M. P. and Singh, I. S. 1998. Genetic variability, heritability and expected genetic advance for seed yield and other characters over two years in lentil. *Lens Newsletter*, **25**(1): 3–6.

Chauhan, M. P. and Singh, I. S. 2001. Relationship between seed yield and its component characters in lentil (*Lens culinaris* Medik.). *Legume Research*, **24**(4): 278–280.

Chauhan, M. P., Singh, I. S., Singh, R. S. 1996. Genetics of rust resistance in lentil *Lens culinaris*). *Indian Phytopathology*, **49**(4): 387–388.

Cubero, J. J.1981. Origin, Taxonomy and Domestication. *In*: Lentils (eds. C. Webb and G. Hawtin), CAB, London, U. K.: 15–38.

Daychand. 2007. Genetic Analysis of Yield and Yield Components in Lentil (*Lens culinaris* Medik.). Ph.D. Thesis, to be submitted to CCS University, Meerut, India.

Dixit, P. and Dubey, D. K.1985. Heritability and genetic advance in induced mutants of lentil (*Lens culinaris* Medik.). *Indian Journal of Genetics and Plant Breeding*, **45**(3): 520–524.

El Attar, A. H. 1991. Genetic variability among some exotic lentil germplasm in Egypt. *Bulletin of Faculty of Agriculture*, University of Cairo, **42**(3): 993–1000.

Emami, Mahmoud Khodambbashi. 1996. Genetic Mapping in Lentil *(Lens culinaris* Medik.). Ph. D. Thesis, IARI, New Delhi, India.

Emami, M. Khodambashi and Sharma, B. 1996 a. Digenic control of cotyledon colour in lentil. *Indian Journal of Genetics and Plant Breeding* , **56** (3): 357–361.

Emami, M. Khodambashi and Sharma, B. 1996 b. Confirmation of digenic inheritance of cotyledon colour in lentil (*Lens culinaris* Medik.). *Indian Journal of Genetics and Plant Breeding* , **56** (4): 563–568.

Emami, M. K. and Sharma, B. 2000. Inheritance of black testa colour in lentil (*Lens culinaris* Medik.). *Euphytica*, **115:** 43–47.

Erskine, W. 1983. Relationship between the yield of seed and straw in lentil. *Field Crops Research*, **7**:115–121.

Erskine, W., Williams, P. C. and Nakkoul, H. 1985. Genetic and environmental variation in the seed size, protein, yield and cooking quality of lentils. *Field Crops Research*, **12**: 153–161.

Erskine, W. and Witcombe, J. R. 1984. Lentil Germplasm Catalogue. ICARDA, Aleppo, Syria: pp. 48.

Erskine, W., Saxena, N. P. and Saxena, M. C. 1993. Iron deficiency in lentil: Yield loss and geographical distribution in a germplasm collection. *Plant & Soil*, **151**: 249–254.

Esmail, A. M., Mohamed, A. A., Hamdi, A. and Rabie, E. M. 1994.Genetic variability and heritability for agronomic traits in segregating populations of lentil (*Lens culinaris* Medik.). *Annals of Agricultural Science*, Moshtohor, **32** (3): 1107–1118.

Euzyl, I., Baum, M. and Powell, W., Erskine, W. and Pehu, E. 1998. A genetic linkage map of lentil (*Lens* sp.) based on RAPD and AFLP markers using recombinant inbred lines. *Theoretical and Applied Genetics*, **97**: 83–89.

Ferguson, M. E. and Robertson, L. D. 1996. Genetic diversity and taxonomic relationships within the genus *Lens* as revealed by allozyme polymorphism. *Euphytica*, **91**: 163–172.

Ferguson, M. E., Maxted, N., Slagreen, M. W. and Robertson, L. D. 1999. A reassessment of the taxonomy of *Lens* Mill. (Leguninosae, Papilionodeae, Vicieae). *Bot. J. Linn. Soc*., 133: 41–49 (cf. S. K. Sharma and R. K. Chahota. 2004. Current status of interspecific hybridization in genus *Len*s. *Journal of Lentil Research*, **1**: 15–18).

Goyal, S. N., Jaimini, S. N. and Tikka, S. B.1976. Heterosis in lentil. *Lens Newsletter*, **3**:1–3.

Gupta, P.K. and Bahi, J. R. 1983. Cytogenetics and origin of some pulse crops *In*: Cytogenetics of Crop Plants (eds. M. S. Swaminathan, P. K. Gupta and U. Sinha). Mac Millan, India: 405–440.

Haddad, N. I., Bogyo, T. P. and Muehlbauer, F. J. 1982. Genetic variance of six agronomic characters in three lentil (*Lens culinaris* Medik.) crosses. *Euphytica*, **31**: 113–120.

Hamdi, A., Erskine, W. and Gates, P. 1991. Relationships among economic characters in lentil. *Euphytica*, **57**:109–116.

Hamdi, A., El-Ghareib, A. A., Shafey, S. A. and Ibrahim, M. A. M. 2003. Genetic variability, heritability and expected genetic advance for earliness and seed yield from selection in lentil. *Ministry of Agriculture Giza*, *Egypt*, **81**(1): 125–138.

Havey, M. J. and Muehlbauer, F. J. 1989. Linkages between restriction fragment length, isozyme and morphological markers in lentil. *Theoretical and Applied Genetics*, **77**: 395–401.

Hobson, K., Armstrong, R., Nicolas, M., Connor, D. and Materne, M. 2006. Response of lentil (*Lens culinaris*) germplasm to high concentrations of soil boron. *Euphytica*, **151**(3): 371–382.

Hoque, Md. Ekramul. 2001. Inheritance and Gene Mapping Based on Morphological and Molecular Markers in Lentil (*Lens culinaris* Medik.). Ph.D. Thesis, IARI, New Delhi, India.

Jeena, A. S. and Singh, I. S. 2001. Estimation of genetic diversity in lentil germplasm. *Crop Improvement*, **28**(1): 81–88.

Jeena A. S. and Singh, I. S. 2002. Genetic divergence analysis in wild lentils. *Legume Research*, **25**(3): 175–179.

Johanson, H. W., Robinson, H. F. and Comstock, R. E. 1955. Estimation of genetic and environmental variability in soybean. *Agronomy Journal*, **47:** 314–318.

Kahraman, A., Kusmenoglu, I., Aydin, N., Aydogan, A., Erskine, W. and Muehlbauer, F. J. 2004. QTL mapping of winter hardiness genes in lentil. *Crop Science*, **44**: 13–22.

Kamboj, R. K. 1986. Genetics of Resistance to Wilt (*Fusarium oxysporum* f. sp. *lentis*) and Certain Quantitative Traits in Lentil (*Lens culinaris* Medik.). Ph. D. Thesis, G. B. P. U. A. &T., Pantnagar, India.

Kamboj, R. K., Pandey, M. P. and Chaube, H. S. 1990. Inheritance of resistance to *Fusarium* wilt in Indian lentil germplasm. *Euphytica*, **105**: 113–117.

Katerji, N., Hoorn van, J. W., Hamdy, A., Mastrolli, M., Oweis, T. and Erskine, W. 2001. Response of two varieties of lentil to soil salinity. *Agricultural Water Management*, **47**: 179–190.

Kay, D. E. 1979. Food Legumes Trp. Products Institute, Crop and Products Digest No. 3, Her Majesty's Stationary Office, London, pp. 210–223.

Kumar, A., Singh, D. P. and Singh, B. B. 1995. Genetic variability of yield and its components in lentil (*Lens culinaris* Medik.). *Indian Journal of Pulses Research*, **8**(1): 60–66.

Kumar, A., Singh, D. P., Singh, B. B. Kumar, A. 1996. Combining ability analysis in lentil. *Indian Journal of Genetics and Plant Breeding*, **56**(2): 173–176.

Kumar, Rakesh, Kumar, D. and Kumar, S. 1999. Genetic variability in lentil (*Lens culinaris* Medik.). *Annals of Agricultural Research*, **4**(1): 75–77.

Kumar, R., Mishra, S. K. and Sharma, B. 2001. Genetics of rust resistance in lentil (*Lens culinaris* Medik.). *Indian Journal of Genetics and Plant Breeding*, **61**(3): 238–241.

Kumar, Yogesh. 2002. Inheritance and Linkage of Genes for Morphological Traits in Lentil (*Lens culinaris* Medik.). Ph.D. Thesis, CCS University, Meerut, India.

Kumar, Yogesh, Sharma, B., Mishra, S. K., Tyagi, M. C. and Singh, S. P. 2004. Inheritance of leaflet size in lentil (*Lens culinaris* Medik.). *Journal of Lentil Research*, **1**(1): 26–29.

Ladizinsky, G. 1979 a. The origin of lentil and its wild genepool. *Euphytica*, **28:** 179–187.

Ladizinsky, G. 1979 b. The genetics of several morphological markers in lentil. *Journal of Heredity*, **70**: 135–137.

Ladizinsky, G. 1985. The genetics of hard seed coat in the genus *Lens*. *Euphytica*, **34**: 539–543.

Ladizinsky, G. 1986. A new *Lens* from the Middle-East. *Notes from the Royal Botanic Gardens*, *Edinburgh*, **43**:489–492.

Ladizinsky, G., Braun, D., Goshen, D. and Muehlbauer, F.J. 1984. The biological species of the genus *Lens* L. *Botanical Gazette*, **145**: 253–261. (cf. S. K. Sharma and R. K. Chahota. 2004. Current status of interspecific hybridization in genus *Len*s. *Journal of Lentil Research*, **1**: 15–18).

Lakhani, J. P., Holkar, S. and Misra, R. 1986. Genetics of seedling vigour and hard seed in lentil. *Lens Newsletter*, **13**(2): 10–12.

Lal, S. and Srivastava, R. S. 1975. Inheritance of flower colour in lentils. *Indian Journal of Genetics and Plant Breeding*, **35**: 29–30.

Lal, C., Sharma, S. K. and Chahota, R. K. 1996. Inheritance of rust resistance in lentil. *Indian Journal of Genetics and Plant Breeding* , **56**(3): 350–351.

Luthra, S. K. and Sharma, P. C. 1990. Correlation and path analysis in lentil (*Lens culinaris*). *Lens Newsletter*, **17**(2): 5–8.

Maher, L., Armstrong, R. and Connor, D. 2003. Salt tolerant lentils – a possibility for the future? In Solutions for a better environment: Proceedings of the 11th Australian Agronomy Conference, Geelong, Victoria, Australia, 2–6 February 2003: 0–4

Malhotra, R. S., Balyan, H. S. annd Gupta, P. K. 1978. Crossing techniques in lentil. *Lens Newsletter*, **5**: 7–8.

Mishra, Gyan Prakash. 2006. Inheritance of Rust Resistance and Identification of Molecular Markers for Rust Resistance in Lentil (*Lens culinaris* Medik.). Ph.D. Thesis, IARI, New Delhi, India.

Mishra. S. K. 2004. Final Technical Report on Development of Comprehensive Genetic Linkage Map in Lentil (*Lens culinaris* Medik.). Submitted to NATP(ICAR), Krishi Bhawan, New Delhi, India.

Mishra, S. K., Sharma, B. and Tyagi, M. C. 2002. Final Technical Report on Linkage Studies in Lentil (*Lens culinaris* Medik.). Submitted to ICAR, Krishi Bhawan, New Delhi, India.

Mishra, S. K., Sarker, A., Singh, B. B. and Basandrai, A. 2005. Slow rusting and its potential donors for resistance in lentil (*Lens culinaris* Medik.) *Indian Journal of Genetics and Plant Breeding*, **65**(4): 319–320.

Mishra, S. K., Singh, B. B., Basandrai, A. K., Sarker, A. and Dayachand. 2005. Screening of ICARDA's lentil material for rust resistance in India. *Indian Journal of Plant Genetic Resources*, **18**(1): 49–50.

Murari, K., Pandey, S. L., and Kumar, V. 1988. Simple correlation and multiple regression studies in lentil. *Legume Research*, **11**(2): 101–102.

Muehlbauer, F. J., Weeden, N. F. and Hoffman, D. L. 1989. Inheritance and linkage relationship of morphological and isozyme loci in lentil (*Lens* Miller). *Journal of Heredity*, **80**: 298–303.

Nigam, S. A., Rabie, H. A., Mohamed, M. A. and Mohamed, H. A. 1990. Correlation studies and path analysis in lentil. *Journal of Agricultural Research* (Egypt), **12**(1): 313–331.

Omvir and Gupta, V. P. 2000. Genotype x environment interaction and heritability for quantitative characters in macrosperma x microsperma derived lines of lentil. *Legume Research*, **23**(3): 201–205.

Pandey, A., Singh, D. P. and Singh, B. B. 1992. Evaluation of Indigenous Germplasm for Yield and Yield Components in Lentil (*Lens culinaris* Medik.). N. D. University of Agriculture & Technology, Faizabad, India, Research Bulletin No.1: pp. 45.

Pinkas, R. Zamir, D. and Ladizinsky, G. 1985. Allozyme divergence and evolution in the genus *Lens*. *Plant Systematic Evololution*, **151**: 131. (cf. S. K. Sharma and R. K. Chahota. 2004. Current status of interspecific hybridization in genus *Len*s. *Journal of Lentil Research*, **1**: 15–18).

Poonam. 2006.Chracterization of Lentil Germplasm Through Morphological and Metric Traits and Molecular Markers. Ph.D. Thesis, Bundelkhand University, Jhansi, India.

Rajput, M. and Sarwar, G. 1989. Genetic variability, correlation studies and their implications in selection of high yielding genotypes in lentil. *Lens Newsletter*, **16**(2): 5–8.

Rakesh Kumar, Sharma, S. K., Luthra, O. P. and Sharma, S. 2005. Phenotypic stability of lentil genotypes under different environments. *Annals of Biology*, **21**(2): 155–158.

Rathi, A. S., Sindhu, J. S., Katiyar, R. P. and Katiyar, S. L. 1994. Genetic architecture for grain yield and its components in lentil. Abstr. International Sym. on Pulses Research, 2–4 April, 1994, New Delhi, Indian Society of Pulses Research and Development, Kanpur.

Rathi, A. S., Sindhu, J. S. and Srivastava, S. B. L. 1998. Genetic divergence in lentil. *Indian Journal of Pulses Research*, **11**(2): 137–139.

Rathi, A. S., Sindhu, J. S. and Singh, V. S. 2002. Variability, heritability and genetic advance in lentil. *Legume Research*, **25**(2): 113–116.

Rubeena, R., Ford, P. and Tylor, W. J. 2003. Construction of an intraspecific linkage map of lentil (*Lens culinaris* spp. *culinaris*). *Theoretical Applied Genetics*, **107**: 910–916.

Sagar, P. S. and Chandra, S. 1980. Breeding behaviour and genetic variation for yield in crosses of lentil (*Lens esculenta*.). *Indian Journal of Agricultural Research*, **14**(3): 159–163.

Sakal, R. Singh, A. P. and Singh, R. B. 1988. Differential reaction of lentil varieties to boron application in calcareous soil. *Lens Newsletter*, **15**(1): 27–29.

Sardana, S., Dhillon, B. S.,Singh, Mahendra and Mishra, S. K. 2005. Pulses germplasm: collection, conservation and utilization. *In*: Pulses (eds. G. Singh, H. S. Shekhon and J. S. Kolar), Agrotech Publishing Company, Udaipur, India, pp. 95–144.

Sarker, A., Erskine, W., Sharma, B. and Tyagi, M. C. 1999. Inheritance and linkage relationships of days to flowering and morphological loci in lentil (*Lens culinaris* Medikus subsp. c*ulinaris*). *The American Genetic Association*, **90**: 270–275.

Sarwar, D. M., Khatoon, F. and Gowda, C. L. L. 1984. Comparative correlation and path analysis in local and exotic germplasm in lentil. *Indian Journal of Genetics and Plant Breeding*, **44**: 201–205.

Saxena, N. P., Saxena, M. C., Ruckenbauer, P., Rana, R. S., El-Fouly, M. M. and Shabana, R. 1994. Screening techniques and sources of tolerance to salinity and mineral nutrient imbalances in cool season food legumes. *In*: Expanding the Production and Use of Cool Season Food Legumes (eds. F. J. Muehlbauer and W. J. Kaiser). Kluwer Academic Publishers, Dordrecht, The Netherlands: 457–471.

Shahi, J. P., Singh, J., Agarwal, I. and Lal, M. S. 1986. Studies on variability for seed size, permeability of seed coat to water and germination in lentil. *Lens Newsletter*, **13**: 14–15.

Sharma, B. and Emami, M. K. 2002. Discovery of new gene causing dark green cotyledons and pathway of pigment synthesis in lentil (*Lens culinaris* Medik.). *Euphytica*, **124**(3): 349–353.

Sharma, B., Tyagi, M. C., Mishra, S. K. and Kumar, Yogesh. 2004. Three-gene control of cotyledon colour in lentil (*Lens culinaris* Medik.). *Journal of Lentil Research*, **1**(1): 1–10.

Sharma, B., Tyagi, M. C., Mishra, S. K. and Kumar, Yogesh. 2004. Confirmation of the inheritance pattern of black testa colour in lentil. *Journal of Lentil Research*, **1**(1): 19–20.

Sharma, S. K. and Sharma, B. 1978. Induced variability for pod and seed size in lentil. *Current Science*, **47**(21): 806–807.

Sharma, S. K., Dawson, I. K. and Waugh, R. 1995. Relationship among cultivated and wild lentils revealed by RAPD analysis. *Theoretical and Applied Genetics*, **91**: 647–654.

Sharma, S. K., Knox, M. R. and Ellis, T. H. N. 1996. AFLP analysis of the diversity and phylogeny of *Lens* and its comparison with RAPD analysis. *Theoretical and Applied Genetics*, **93**: 751–758.

Sharma, S. K. and Chahota, R. K.2004. Current status of interspecific hybridization in genus *Lens*. *Journal of Lentil Research*, **1**: 15–18.

Singh, A. P., Krishna, R., Kumar, R. and Singh, M. P. 2001. Assaying divergence in lentil (*Lens culinaris* Medik.). *Crop Research* (Hisar): **22**(3): 469–473.

Singh, A. P., Sakal, R., Sinha, R. B. and Bhogal, N. S. 1991. Relative response of selected chickpea and pigeonpea cultivars to boron application. *Annals of Agricultural Research,* **12**: 20–25.

Singh, B. B., Mishra, S. K., Sardana, S. and Dixit, G. P. 2006. Lentil and pea. In: Plant Genetic Resources: Foodgrain Crops (eds. B. S. Dhillon, S. Saxena, A. Agarwal and R. K. Tyagi). Narosa Publishing House Pvt. Ltd., New Delhi: 240–254.

Singh, D. P. and Singh, B. B. 1991.Evaluation of exotic germplasm in lentil. *Narendra Deva Journal of Agricultural Research*, **6**(2): 304–306.

Singh, K. B. and Jain, R. P. 1971. Heterosis in lentil (*Lens culinaris* Medik.). *Indian Journal of Agricultural Sciences*, **41**: 678–681.

Singh, I. P. and Singh, J. D. 2003. Combining ability analysis in lentil. *Indian Journal of Pulses Research*, **16**(2): 95–97.

Singh, J. P. and Singh, I. S. 1990. Genetics of rust resistance in lentil (*Lens culinaris). Indian Journal of Pulses Research*, **3**(2): 132–135.

Singh, J. P. and Singh, I. S. 1992. Genetics of rust resistance in lentil (*Lens culinaris*). *Indian Journal of Agricultural Sciences*, **62**: 337–338.

Singh, J. P. and Singh, I. S. 1993. Combining ability in lentil. *Indian Journal of Pulses Research*, **6**(1): 25–30.

Singh, T. and Gupta, K. K. 1994. Genetic diversity for yield and related traits in lentil (*Lens culinaris* Medik.). *Plant Archives*, **4**(1): 39–43.

Singh, T. P. Inheritance of cotyledon colour in lentil. 1978. *Indian Journal of Genetics and Plant Breeding*, **38**: 11–12.

Singh, T. P., Singh, K. B. and Malhotra, R. S. 1975. Heterosis and combining ability in lentil. *Indian Journal of Agricultural Sciences*, **45**(6): 259–263.

Singh, Tejbir, Gupta, K. K. and Singh, T. 2004. Genetic diversity for seed yield and related traits in lentil (*Lens culinaris* Medik.). *Plant Archives*, **4**(1): 39–43.

Sinha, R. P., Chaudhary, S. K. and Sharma, R. N. 1987. Inheritance of cotyledon colour in lentil. *Lens Newsletter*, **14**(1&2): 3.

Sinha, R. P. and Yadav, B. P. 1989. Inheritance of resistance to rust in lentil. *Lens Newsletter*, **16**: 41.

Slinkard, A. E. 1978. Inheritance of cotyledon colour in lentil. *Journal of Heredity*, **69**: 139–140.

Solanki, I. S. and Sharma, B. 2001. N-nitroso-N-ethyl Urea induced genetic variability for quantitative characters in lentil (*Lens culinaris* Medik.). *National Journal of Plant Improvement*, **3**: 102–106.

Solanki, I. S., Kumar, K., Malik, B. P.S. and Kumar, R. 2002. Study of genetic divergence under normal and late sown conditions in lentil. *Crop Improvement*, **27**(2): 232–235.

Srivastava, S. P., Bhandari, T. M. S., Yadav, C. R., Joshi, M. and Erskine, W. 2000. Boron deficiency in lentil: Yield loss and geographic distribution in a germplasm collection. *Plant and Soil*, **219**: 147–151.

Tadmor, Y., Zamir, D., and Ladizinsky, G. Genetic mapping of an ancient translocation in the genus *Lens*. *Theoretical and Applied Genetics*, **73**: 883–892.

Tahir, M., Simon, C. J. and Muehlbauer, F. J. 1993. Gene map of lentil: a review. *Lens Newsletter*, **20**(2): 3–10.

Tahir, M. and Muehlbauer, F. J. 1994. Gene mapping in lentil with recombinant inbred lines. *Journal of Heredity*, **85**(4): 306–310.

Tay, J. and Slinkard, A. E. 1989. Transgressive segregation for *Ascochyta* resistance in lentil. *Canadian Journal of Plant Sciences*, **69**: 547.

Tschermak-Seysenegg, E. 1928. Lentil and field bean crosses. *Sityringsber Akad.Wiss. Wein Math. Nat. Ki. I. Abs.,* **137**(3/4): 171–181.(cf. F. J. Muehlbauer, F. J. and A. E. Slinkard, 1987. Breeding methodology. *In:* Lentil (eds. C. Webb and G. Hawtin). CAB-ICARDA, Fernham, England: 69–90.

Vaillancourt, R. 1989. Inheritance and Linkage of Morphological Markers and Isozymes in Lentil. Ph.D. Thesis, University of Saskachewan, Saskatoon, Canada (cf. R. E. Vaillancout and A. E. Slinkard. 1993. Linkage of morphological and isozyme loci in lentil, *Lens culinaris* L. *Canadian Journal of Plant Sciences*, **73**: 917–926).

Vaillancourt, R. and Slinkard, A. E. 1992. Inheritance of new genetic markers in lentil. *Euphytica*, **64**: 227–236.

Van Oss, H., Arnon, Y. and Ladizinsky, G. 1997. Chloroplast DNA variation and evolution in the genus L. Mill. *Theoretical and Applied Genetics*, **94**: 452–457.

Vandenberg, A. 1987. Inheritance and Linkage of Several Quantitative Traits in Lentil. Ph.D. Thesis, University of Saskachewan, Saskatoon, Canada (cf. R. E. Vaillancourt and A. E. Slinkard, 1992, Inheritance of new genetic markers in lentil. *Euphytica*, **64**: 227–236.).

Vandenberg, A. and Slinkard, A. E. 1987. Inheritance of a xantha cholophyll deficiency in lentil. *Journal of Heredity*, **78**: 130.

Vandenberg, A. and Slinkard, A. E. 1989. Inheritance of four new quantitative genes in lentil. *Journal of Heredity*, **80**: 320–322.

Vandenberg, A. and Slinkard, A. E. 1990. Genetics of seed coat colour and pattern in lentil. *Journal of Heredity*, **81**: 484–488.

Vishnumittrre, A. 1974**.** The beginning of agriculture. Paleobotanical evidences in India. *In:* Evolutionary studies in World Crop Diversity and Change in Indian Sub-continent (ed. J. B. Hutchinson). Cambridge, U. K.

Waldia, R. S. and Chhabra, A. K. 1989. Inheritance of some quantitative traits in lentil. *Lens Newsletter*, **16**(1): 6–7.

Williams, T.T., Sanchez, A. M. C. and Jackson, M. T. 1974. Studies on lentils and their variation: the taxonomy of the species. *SABRAO Journal*, **6**: 133–145.

Wilson, V. E., Law, A. G. and Warner, R. L. 1970. Inheritance of cotyledon colour in *Lens culinaris* Medik. *Crop Science*, **10**: 205–207.

Weeden, N. F., Muehlbauer, F. J. and Ladizinsky, G. 1992. Extensive conservation of linkage relationships between pea and lentil genetic maps. *Journal of Heredity*, **83**: 123–129.

Yadav, S. S., Phogot, D. S., Solanki, I. S. and Malik, B. P. S. 2005. Character association and path co-efficient analysis under two environments in lentil. *Indian Journal of Pulses Research*, **18**(2): 147–149.

Yau, S. K. 1999. Boron toxicity in lentil: yield loss and variation between contrasting lines. *Lens Newsletter*, **26**(1&2): 14–17.

Yau, Sui-Kwong and Erskine, W. 2000. Diversity of boron-toxicity tolerance in lentil growth and yield. *Genetic Resources and Crop Evolution*, **47**: 55–61.

Zaman, M. W., Mian, M.A.K. and Rahman, M. M. 1989. Variability and correlation studies in local germplasm of lentil in Bangladesh. *Lens Newsletter*, **16**(1): 17–19.

Zamir, D. and Ladizinsky, G. 1984. Genetics of allozyme variants and linkage groups in lentil. *Euphytica*, **33**: 329–336.

Zohari, D. 1972. The wild progenitor and place of the cultivated lentil. *Lens culinaris*. *Economic Botany*, **26**: 326–332.