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Breeding strategies to improve lentil for diverse agro-ecological environments

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Abstract

Lentil is an important cool season pulse crops and it is cultivated world-wide in diverse agro ecological conditions. Several varieties have been developed adopting conventional breeding methodologies. Significant progress in genetic improvement for yield has been made by using different breeding strategies including molecular marker based precise breeding strategy in lentil. However, lentil production and productivity has not increased to its potential due to several biotic and abiotic stresses affect its growth and development. Utilization of wild species may provide useful genes for broadening the genetic base of lentil in respect of disease resistance, abiotic stresses and desirable agronomic traits. In present article, we have reviewed the breeding strategies used for improving lentil genotypes adapted under diverse agro-climatic conditions.

Kew words: Genetics, short duration, seed size, herbicide, heat tolerance, root traits, lentil

Introduction

Lentil (*Lens culinaris* ssp. *culinaris* Medikus) is a diploid (2n=2x=14) self-pollinating legume crop with a genome size of approximately 4 Gbp (Arumuganathan and Earle 1991). It is the second most important cool season food legume after chickpea. Being grown for over 8,000 years (Dhuppar et al. 2012; Aditya and Kumar 2011), it is considered as one of the early domesticated species (Cokkizgin and Munqez 2013). Globally, lentil is cultivated as rainfed crop in more than 52 countries covering about 3.85 m ha area with a production of 3.59 m t (Erskine et al. 2011). Canada, India, Turkey, Australia, U.S.A., Nepal, China, and Ethiopia are the major contributors (Reda 2015). It is commonly used as food and feed because of its protein rich grains (24-28%) with abundance of lysine, minerals and vitamins. Being a legume crop, its ability to fix atmospheric nitrogen and better carbon sequestration to improve soil health is undeniable.

The *microsperma* types of lentil are small seeded, 2 to 6 mm diameter with 1000-seed weight up to 25 g, mostly red cotyledon, being cultivated in South Asia and Sub-Saharan Africa while *macrosperma* types are large seeded (6 to 9 mm diameter), with 1000-seed weight of 25 to 70 g and mostly yellow cotyledon; native to WANA region (West Asia and North Africa) and Southern Europe. In Northern America, green and red lentils are also grown to meet the demand of international market. In India, 65% of lentil area is under *microsperma* type (Punjab, Haryana, Uttar Pradesh and Bihar) and remaining 35% area comes under *macrosperma* type (Madhya Pradesh and adjoining districts of Uttar Pradesh) (Tickoo et al. 2005).

During the last three decades, breeding efforts were made to increase productivity of lentils using conventional breeding methods to develop varieties with high and stable yield for diverse agro-climatic conditions. However, the current productivity of lentils is still well below its potential. The application of molecular tools has potential to embark on precision breeding for making desired genetic improvement in lentil. The present review deals with breeding strategies used in the past and also outlines future initiatives for accelerated genetic improvement in lentil.

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Agro-ecological environments for lentil cultivation

Lentil has ability to adapt to a wide range of agro-ecologies (Joseph et al. 2014). During domestication, lentil spread from its center of origin to other parts of world and in the process of evolution, selection pressure from various climatic factors such as temperature, day length, and precipitation coupled with edaphic factors and biotic stresses has led to selection for those traits which play a major role in adaptation (Materne and Siddique 2009). As a result, it is less sensitive towards various climate features (Cokkizgin and Munqez 2013) and usually well adapted to various soil types ranging from sand to clay loam (Ozdemir 2002). As a rainfed crop, it has ability to grow successfully in areas with 280 to 300 mm rainfall (Brennan et al. 2002) as well as in areas from cool temperate steppe to subtropical dry conditions (McVicar et al. 2010). Therefore, different types of lentils are now grown in warm temperate, subtropical and high altitude of the tropics as a cool season crop. In Ethiopia, it is mainly grown in those areas, where rainfall is usually high (Jarso et al. 2009). However, the planting of lentil is varied from one region to another depending on the amount and distribution of rainfall, temperature, topography and elevation of the area (Regassa et al. 2006). In India, lentil is grown across different agro-ecological regions and its planting varies from 15th October to 15th November (Sekhon et al. 1986) but extended till 30th November in foot hills and northern parts of the country. However, high temperature (>27C), high humidity with excessive rain fall, water logging and alkaline, saline and acidic soils (Abraham 2015; Brennan et al.2002) affects the planting. Late planting after the harvest of rice, however, restricts vegetative growth and quite often leads to forced maturity with severe yield loss (Saxena and Hawtin 1981).

Trends in production and productivity

The major geographical regions of lentil production are South Asia and China (44.3%), North America (41%), Central and West Asia and North Africa i.e., CWANA (6.7%), Sub-Saharan Africa (3.5%) and Australia (2.5%). In south Asia, lentil is cultivated on 1.8 m ha area with 1.1 mt production exclusively as a post rainy season crop on residual moisture, whereas in CWANA region including Turkey, Syria, Iran and Morocco, it is a winter and spring crop occupying 0.59 m ha area with production of 0.48 m t. Ethiopia is the major producer with 0.11 m.t. India ranks second after Canada with a total production of 1.03 m t. World lentil production has risen steadily by nearly four times (375 %) from an average of 0.92 mt in 1961-63 to 4.89 mt in 2014-15. This trend has been possible primarily due to expansion of area from 1.64 m ha in 1961-63 to 4.52 m ha in 2014-15. Concomitantly, the average productivity is also enhanced from 560kg ha^{-1} in 1961-63 to 1080kg ha^{-1} by 2014-15 (FAOSTAT 2016). However, in India, the lentil occupies about 1.49 m ha area with production of 1.03 million tons but productivity remains low at 741 kg/ha. The average lentil yield in India is still low as compared to global productivity (1016 kg/ha). With rising demand from growing population, there is a need to increase national productivity to the extent of 1500 kg/ha. Past studies showed large yield gaps between research fields and farmer's field and this gap has to bridged by increasing the level of both production and the productivity.

Genetic resources

Genetic variability is prerequisite for executing any breeding strategy for developing improved plant types adapted to diverse agro-ecological environments. Globally, ICARDA holds one of the largest collections (~12,000 accessions) of lentil and has provided 1,03,197 seed samples to scientists in 52 countries since its establishment. The use of diverse germplasm in breeding lentil cultivars is still limited as only a few common lines have repeatedly been used in hybridization resulting into narrow genetic base. Development of regional core sets of the germplasm has been suggested for harnessing the wider adaptability and genetic enhancement of yield of chickpea (Upadhyaya et al. 2001 and lentil (Kumar 2015). In this respect different core sets, namely, a core of 234 accessions from the USA, (Simon and Hannan, 1995); a candidate set of 237 accessions from 1525 Indian accessions has been developed after assessing the magnitude of genetic variability (Kumar 2015). A core collection by ICRADA showed sufficient variation for phenological and morphological traits (Tullu et al. 2001). In Bangladesh, 110 lentil germplasm, including landraces and popular varieties were studied in detail for morphological and quantitative traits and identified phenologically adapted exotic lines to diversify the gene pool and broaden the genetic base. In this context, several useful traits can be targeted for genetic enhancement of lentil cultivars (Fig. 1). For enhancing the utilization of lentil germplasm, a Focused Identification of Germplasm Strategy (FIGS) has been developed (Kumar et al. 2013). In this strategy, germplasm for a target trait is identified from that region where it is frequently occurred. The strategy

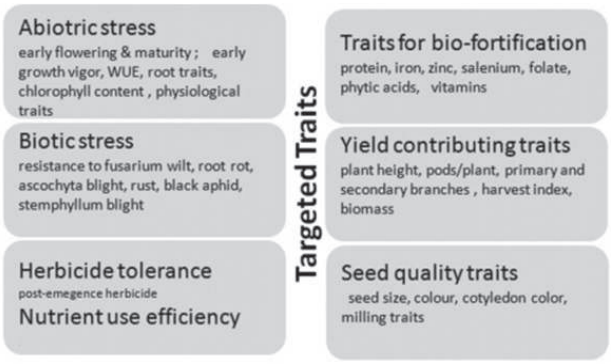

Fig. 1. Traits used in lentil breeding strategies for diverse agro-climatic conditions

has been useful in identification of genotypes having desirable traits such as tolerance to biotic and abiotic stresses, superior grain quality and nutritional traits, improved grain size and early maturity. Thus the development of core sets of diverse origin after their screening at multi-locations for useful traits may lead to their utilization for the improvement in yield and productivity.

Genomic resources and their utilization in marker-trait analysis

Significant progress has been made in the development of genomic resources in lentil during the past years. Thousands of molecular markers such as RAPD, SSR, AFLP, RFLP, SNP, including transcriptome sequences, EST sequences and whole genome sequences have been developed to be used in lentil (Havey and Muehlbauer 1989; Weeden et al. 1992b; Eujayl et al. 1998a; Hamwieh et al. 2009; Kaur et al. 2011; Kumar et al. 2014, 2015). However, in recent years, next generation sequencing platforms have accelerated development of SNP markers. For example, 44,879 SNP markers have been identified in lentil using Illumina Genome Analyzer (Sharpe et al. 2013). The recent discovery of high-density SNP markers has facilitated the establishment of ultra HTP genotyping technologies such as Illumina GoldenGate (GG), which can accommodate more than 1000 SNP's in GG platforms (Kaur et al. 2014; Sharpe et al. 2013). They are cost effective methods and through the use of allele-specific PCR markers we can include small to moderate amount of SNPs of any specific applications (Fedoruk et al. 2013; Sharpe et al. 2013). The transcriptome assemblies also provide excellent opportunities to identify EST derived SSR and SNP markers and intron-targeted primer (ITP). Transcriptome sequencing led to the discovery of a large-scale unigene assembly and SSR marker discovery (Kaur et al. 2011). Next generation sequencing also has accelerated development of ESTs and now in lentil about 10163 ESTs are available in public domain. The next generation sequencing techniques has made easy the sequencing of lentil genome (23x coverage). The lentil genome assembly v1.0, based on the Canadian variety CDC Redberry, was released in January 2016 (Bett et al. 2016). The assembly consists of 7 pseudomolecules anchored through the use of 6 high-density genetic linkage maps, with the total assembled bases representing approximately half of the 4.3 Gb lentil genome.

The first genetic mapping (linkage analysis) began in lentil in 1984 (Zamir and Ladizinsky 1984), the first map comprising DNA based markers was produced by Havey and Muehlbauer by (1989). Subsequent molecular maps have been developed in lentil and used for marker trait association analysis (Kumar et al. 2015). These maps were constructed using RAPD, AFLP, RFLP, ISSR, ITAP resistance gene analogs and morphological markers using RIL populations derived from inter or intra specific crosses (Eujayl et al. 1998a; Rubeen et al. 2003; Rubeen et al. 2006; Durán et al. 2004; Hamwieh et al. 2005; Gupta et al. 2012 a, b).

These molecular maps have been used to study the association of molecular markers with desirable traits in lentil. During the past years, marker-trait association have been studied a number traits and identified genes/QTLs controlling Fusarium wilt resistance (Fw) ((Eujayl et al. 1998b; Hamwieh et al. 2005) and anthracnose disease resistance (Lct-2) (Tullu et al. 2003), plant height and floweting time (Duran et al. 2004), winter surival (Kahraman et al. 2004). The mapping of ascochyta blight resistance using an F_2 population derived from ILL7537 x ILL6002 identified three QTLs accounting for 47% (*QTL*-1 and *QTL*-2) and 10% (*QTL*-3) of disease variation. Recently, QTLs conferring resistance to Stemphylium blight and rust diseases using RIL populations were identified in lentil (Saha et al. 2010a; Saha et al. 2010b). Though the use of F_2 populations in identification of QTLs has been done widely in lentil, their use in marker-trait analysis has led to identification of only major QTLs. Thus, several minor QTLs were overlooked in such populations and identification of environmental responsive QTLs was difficult. Because quantitative traits are influenced by both genetic and environmental effects, RILs or near isogenic lines (NILs) are more suitable populations to accurately dissect their

components. For ascochyta blight, three QTLs each were detected for resistance at seedling and pod/ maturity stages (Gupta et al. 2012a). Together these accounted for 34 and 61% of the total estimated phenotypic variation and demonstrated that resistance at different growth stages is potentially conditioned by different genomic regions. For nutritional traits, QTL analysis resulted in identification of 4 QTLs for Fe uptake that can be used in molecular breeding towards the development of biofortified cultivars (Aldemir et al. 2014). Recently, Rahaman et al. (2013) assessed selnium in the field and further, QTL mapping has been conducted for selenium concentration in RIL mapping population developed from the cross PI 320937 (119 ìg/kg × Eston (883 ìg/kg). In this study, four QTL regions and 36 putative QTL markers, with LOD scores ranging from 3.00 to 4.97, distributed across two linkage groups (LG2 and LG5) have been identified to be associated with seed Se concentration. These QTLs have explained 6.3-16.9% of the phenotypic variation (Ates et al. 2016). Fedoruk et al. (2013), first used the AM in lentil to identify QTL for seed size and seed shape. As the properly designed AM panels have a greater frequency of alleles, encompass the genetic variation of a crop, may facilitate time and cost saving as compared to MAS in lentil. The ûanking markers identified may be useful for MAS and pyramiding of potentially different resistance genes into elite backgrounds that are resistant throughout the cropping season.

Generation of new variability through induced mutation

Induced mutations are highly useful to create variability, when a desired trait may not be available in the existing germplasm and/or suitable screening methods are available that can be adopted to evaluate large mutagenised populations. Seven mutant cultivars including three each in India (Ranjan, Arun and HUL) and Bangladesh (Bina Masur 1, Bina Masur 2 and Bina Masur 3) and one, NIAB Massor 2006 in Pakistan have been developed. Induced mutation was used in Canada to develop a lentil line with tolerance to imidazolinone herbicides. The trait was patented (US Patent 7232942) and licensed for use in Clearfield® lentil varieties, which are now widely grown in Canada and USA. The trait has been transferred to cultivars of all market classes, resulting in the release of a series of herbicide tolerant cultivars (Muehlbauer et al. 2009). Mutant lentil lines with resistance to imidazolinone have also been developed in Australia (Materne et al. 2011). Experience with lentil mutagenesis has shown that *macrosperma* cultivars are more prone to mutagens than the *microsperma* genotypes.

Genetic studies

Genetic analysis is primarily aimed to understand the nature and mode of inheritance for different traits in order to utilize the information in crop improvement. In this context several researchers have worked out the genetics of several quantitative or qualitative traits. The compiled information is presented in Table 1. Two important traits namely, pod dehiscence and seed dormancy involved in the domestication process are under the control of a single recessive gene. Seed size showed more complex inheritance pattern. Mode of inheritance of a number of traits including seed colour (*Scp*), epicotyl colour (*Gs*), growth habit (*Gh*), flower colour, and pod dehiscence has been studied in a wide cross (*L. culinaris.* ssp*. culinaris* × *L. culinaris.* ssp. o*rientalis*) (Ladizinsky 1979), whereas the hard seed coat in ssp. *orientalis* is governed by a single recessive gene. Tahir and Muehlbauer (1994) observed that the traits, epicotyl colour, pod indehiscence, and growth habit have been involved in the domestication syndrome of lentil. These traits were associated with those genes or factors that provided a selective advantage to cultivated lentil. Genetics of resistance to most severe diseases like rust, wilt and *Ascochyta* blight are controlled by a few independent genes. For instance, wilt resistance is controlled by five dominant genes, while rust resistance is governed by a single dominant gene and duplicate dominant genes. Kumar et al. (2013) demonstrated that early growth vigour is controlled by a single recessive gene but the occurrence of transgressive segregants for seedling length in segregating populations indicated that some minor genes are also involed. It is suggested that to understand the nature of genetics of early growth vigor, it is desirable to develop early maturing genotypes having ability of rapid ground coverage. Recently, inheritance studies carried out in a number of interspecific crosses (9 wild x cultivated genotypes) showed that each trait *viz*., growth habit, flower colour, cotyledon colour and pod dehiscence are controlled by a single gene (Singh et al. 2014).

Development of short duration varieties

Lentil is a cool season crop and its podding stage invariably encounters terminal moisture and heat stresses leading to forced maturity and lower yield. With rising global temperature due to climate change the possibilities of forced maturity may occur during

Table 1. Genetic studies for morphological traits in lentil

Characters	Genetic control	References
Growth habit	Monogenic recessive	Emami and Sharma 1999a
Red foliage	monogenic recessive	Ladizinsky 1979; Emami and Sharma 1996a; Vandenberg and Slinkard 1989; Havey and Muehlbauer 1989; Emami 1996
Light green foliage	Monogenic dominant	Kumar 2002
Oval leaflet shape	Monogenic dominant	Kumar et al. 2006
Acute leaflet shape	Monogenic recessive	
Leaflet number	Monogenic dominant	Kumar et al. 2005a
Tendril formation	Monogenic recessive	Vandenberg and Slinkard 1989; Vaillancourt and Slinkard 1992; Emami 1996
Plant pubescence	Monogenic dominant	Vandenberg and Slinkard 1989; Emami 1996; Kumar 2002
Plant height	Monogenic dominant	Tahir et al. 1994
Stipule size	Incomplete dominance	Kumar 2002
Earliness	Monogenic recessive	Sarker et al. 1998, 1999
Flower colour	Monogenic dominant	Lal and Srivastava 1975; Ladizinsky 1979; Kumar 2002; Wilson and Hudson, 1978; Gill and Malhotra 1980
Two-flower/peduncle and three flower/peduncle	Monogenic dominant and recessive	Gill and Malhotra 1980; Emami 1996; Kumar 2002
Pod size	Incomplete dominance	Kumar et al. 2005b
Pod dehiscenc	Monogenic dominant	Ladizinsky 1979, 1985; Vaillancourt and Slinkard 1992
Seed coat colour black > brown > grey > green	Three Independent genes and monogenic dominant	Vandenberg and Slinkard, 1990
Tannin in seed coat	Monogenic dominant	Vaillancourt et al. 1986
Seed coat spotting	Monogenic dominant	Ladizinsky 1979; Vandenberg and Slinkard 1990; Emami 1996
Seed size	Polygenic with partial dominance	Abbo et al. 1991
Hard seededness	Monogenic dominant	Ladizinsky 1985; Vaillancourt and Slinkard 1992
Orange cotyledon	Digenic dominant	Emami and Sharma 1996 b, c; Vaillancourt and Slinkard 1993
Yellow cotyledon colour	Digenic dominant	
Green cotyledon colour	Digenic recessive	
Winter hardiness	Polygenic	Kahraman et al. 1999
Fusarium wilt	Monogenic dominant	Eujayl et al. 1988
	Five independent genes	Kamboj et al. 1990
Rust	Duplicate dominant	Lal et al. 1996
	Monogenic dominant	Kumar et al. 1997
Ascochyta blight	Monogenic dominant	Ford et al. 1999
Early growth vigour	Single recessive and minor genes	Kumar et al. 2013
Growth habit, flower colour, cotyledon colour and pod recessive	Monogenic dominant/ dehiscence	Singh et al. 2014

Source: modified from Kumar et al. (2012)

Table 2. Marker-trait association studies conducted in lentil

Trait	Gene/QTL	Marker	Phenotypic variation explained (%)	Reference
Ascochyta blight resistance	*QTL*	RAPD	90	Ford et al. 1999
	Ra/2	RAPD, SCAR	-	Chowdhury et al. 2001; Tar'an et al. 2003a
	QTLs	AFLP	up to 50	Rubeena et al. 2006
Anthracnose resistance	*LCt-2*	AFLP, RAPD	-	Tullu et al. 2003; Tar'an et al. 2003a
Fusarium wilt resistance	*Fw*	RAPD, SSR	-	Eujayl et al. 1998b, Hamwieh et al. 2005
Ascochyta blight	*QTL*	-	~50	Taylor et al. 2006
Winter hardiness	*Frt*	RAPD, SSR	-	Eujayl et al. 1999
	QTL	RAPD, SSR, AFLP	33.4	Kahraman et al. 2004
Earliness and plant height	QTL	RAPD, SSR, AFLP	31-46	Tullu et al. 2008
Plant structure, growth habit and yield, seed diameter, seed weight	QTL	RAPDs, ISSRs, AFLPs, SSRs	18.2-90.4	Fratini et al. 2007
Winter hardiness	QTL	RAPD, ISSR and AFLPm	20.5	Kahraman et al. 2010
Stemphylium blight resistance	QTLs	SSRs, SRAPs, RAPDs	46	Saha et al. 2010a
Rust resistance	*R*	STS, SSRs, RFPLs, RAPDs, CAPS and dCAPS		Saha et al. 2010b
Seed thickness, diameter, seed plumpness, days to 50% flowering	*QTL*	SSR and seed color loci	8.4-60	Fedoruk et al. 2013
Hundred seed weight, plant height, seed diameter	*QTL*	SSR, SRAP, RAPD	15.3-32.6	Saha et al. 2013
Boron tolerance	*QTL*	SNP	71	Kaur et al. 2014
Rust	*R*	SSR	-	Mekonnen et al. 2014
Rust	*R*	SSR	-	Dixit et al. 2016
Flowering time	*QTL*	SSR	57	Kahriman et al. 2015
Seed weight and size	*QTL*	SNP	27.5-48.4	Verma et al. 2015
Salenium content	*QTL*	SNP	6.3-16.9	Ates et al. 2016
Drought tolerance	*QTL*	SSR	69.7	Singh et al. 2016
Root and shoot traits reacted to drought tolerance	*QTL*	SNP, SRAP	27.6-28.9%	Idrissi et al. 2016

Source: modified from Kumar et al. (2012); Kumar et al. (2015)

the coming years, which may drastically reduce the yield particularly under delayed sowing after late harvesting of rice. Currently, about 11.7 million ha area after harvesting of rice remains fallow because present cultivars do not fit in a window of 100-110 days for growing lentil. Therefore, the development of early maturing lines with high and stable yield is a major breeding goal in lentil. An early maturing genotypes may escape from drought/flooding and also allows the cultivation of multiple crops in a year. Breeding of short duration varieties may also be helpful in avoiding moisture limiting and heat stress situations at the reproductive stage which leads to forced maturity (Erskine et al. 1994; Shrestha et al. 2006)

Manipulation of flowering time

A number of studies have been conducted to know genetics of flowering time in lentil in order to exploit early flowering trait in breeding program (Sarker et al. 1999; Tullu et al. 2008; Kahriman et al. 2015). The conventional genetic linkage analysis showed that flowering time is determined by a single recessive gene (Sarker et al. 1999) while marker trait association analysis using biparental population identified a number of QTLs controlling the flowering in lentil (Tahir et al. 1994; Tullu et al. 2008). Recently super early genotypes with <90 days maturity have been identified from wild taxa, which may serve as donor for breeding early maturing varieties (Kumar 2015). A good progress has been made in development of short duration varieties with high yield such as BARI M4, BARI M5, BARI M6 and BARI M7 in Bangladesh and these varieties being early escape from terminal heat stress.

Manipulation of crop duration and high biomass

Generally shorter growing period reduces plant biomass and seed size affecting yield drastically. Therefore, breeding high yielding large seeded genotypes with short duration is a challenging task. However, the earlier studies showed that the simultaneous improvement of yield and earliness is possible because high heritability has been estimated for important traits including crop growth rate, efficient partitioning of photosynthetic assimilates and reproductive duration (Jogloy et al. 2010). The positive relationship between grain yield and length of the reproductive period has also been observed (Erskine et al. 1990). Longer reproductive duration provide sufficient time to synthesize greater sink size. However, a recent study showed negative correlation of reproductive duration with yield indicating that genotypes with short duration can produce high yield, if they are efficient in partitioning the photosynthetic assimilates into economic yield (Kumar and Srivastava 2015). They observed that 35-40 days of reproductive period can be sufficient to develop a genotype with high yield. Since early flowering genotypes also have early maturity, the recombination breeding for combining the early flowering with above reproductive period could be an effective breeding strategy for developing high yielding and early maturing genotypes. Earlier, Shrestha et al. (2005) reported that derivatives from crosses between South and West Asian lentils produce rapid canopy cover, early phenology and show high harvest index. Manipulation of these traits including the prolonged flowering and podding period, may lead to increased dry matter production, more number of pods, high harvest index, efficient water use and large seeds and the evolved genotypes may adapt to drought and heat stress conditions.

Plant type for mechanical harvesting

Manual harvesting of lentil is becoming increasingly costly due to higher labor cost at the peak harvesting time. Moreover, delay in harvesting of lentil causes significant yield losses due to pod shattering. This problem can be overcome by using combine-harvesters but their use for harvesting of present cultivars leads to loss of pods and grains because of plant height. Hence, the development of erect plant type with lodging resistance may be restructured to suit mechanical harvesting, which may reduce the pod shattering (Kumar et al. 2013). Genetic variability for these traits is available in the germplasm. For example, mutants with upright growth habit have been identified and used in breeding the improved lines (Erskine and Goodrich 1991). ICARDA has identified a number of lines having >30 cm height with more ground clearance (>15 cm) without reduction in the pod bearing length and number of pods. These lines have strong stem and tolerance to lodging, pod shattering and pod drop (Kumar et al. 2013). ICARDA has also developed economic machine harvest systems involving a flattened seed bed, cultivars with improved standing ability and the use of cutter bars. On-farm trials and demonstrations confirmed the value of the mechanization package. The variety Idlib 2 is most suitable for machine harvest (El-Ashkar et al. 2003).

Breeding for seed size

The lentils cultivated in India are of *microsperma* type. They have been categorized into small seeded (<2.5 g/100 seed weight) and large seeded (> 2.5 g/100 seed weight) types adapted to different agro-climatic conditions. The large-seeded types have a longer reproductive growth period compared to small seeded type. Generally, these differences are from 2 to 8 days. This extended period is required to fill its greater seed mass per pod and the large-seeded type produces usually taller plants with more straw (Kumar et al. 2013). They further reported that small seeded type show better adaptability to dry environments, while large seeded type are better adapted to wetter environments (Erskine 1996). The large seeded lentils are preferentially grown by farmers in central India, whereas small seeded lentils are grown north-eastern part of the country. Abbo et al. (1991) reported that the seed size in lentil is a polygenic trait and is controlled

by several genes. To develop genotypes with large seed a breeding strategy involving several parents in hybridization and intense selection may be followed to accumulate a number of genes in suitable genetic background. Studies have also been conducted to identify the genes/QTLs that control seed size in lentil (Fedoruk et al. 2013; Verma et al. 2015). Several QTLs, each accounting for large genetic variation, have been identified for seed size and seed weight. Thus, the information accrued would help in designing the selection strategies for developing the improved cultivars with small and large seed size.

Breeding for biotic stresses

Lentil is affected by several diseases that are prevalent in different agroclimatic conditions. *Fusarium* wilt caused by *Fusarium oxysporum* f. sp. *lentis* is widespread particularly in rainfed areas. Losses due to vascular wilt usually vary from 5 to 12% but may reach in epidemic situations up to 72% in Syria (Bayaa et al. 1986) and to a complete crop failure in India (Khare 1981). Pathogenic variability has not yet been established though geographical differences in pathogenicity do occur (Erskine and Bayya 1996). In order to identify the genetic resources, the screening of ~20,000 lines in a well-established wilt sick plot has resulted in identification of 325 accessions with resistance (Kumar et al. 2010). Two wild accessions, ILWL113 and ILWL138 belonging to *Lens culinaris* ssp. *orientalis* and *L. culinaris* ssp. *ervoides*, respectively showed a high level of resistance to wilt (Bayya et al. 1995). These resistance sources are being used in wilt resistance breeding program. In spite of good progress in breeding wilt resistant varieties in lentil, its impact could not be translated into a success story due to their susceptibility to pathogens causing other root rot diseases such as collar rot (*Sclerotium rolfsii* Sacc.) and dry and wet root rot (*Rhizoctonia*). Due to lack of efficient screening techniques, stable resistance for these pathogens has not yet been identified. The foliar disease *Ascochyta* blight incited by *A. lentis* is a serious disease of lentil especially Canada, Australia, Latin America, Ethiopia, Pakistan, North-west plains of India, the USA and highlands of WANA region (Johansen et al. 1994; Erskine et al.1994; Ahmed and Morrall 1996). Resistance to *Ascochyta* blight has been identified in germplasm (Iqbal et al. 1990; Singh et al. 1982) including the wild species, *Lens orientalis*, *L. odemensis*, *L. nigricans* and *L. ervoides* (Bayya and Erskine 1994). Other biotic stresses of lentil include, Anthracnose (*C. truncatum*), botrytis grey mold (*Botrytis fabae*, *B. cinerea*), Stemphylium blight (*Stemphylium botryosum*), lentil rust (*U. fabae*) and *Sclerotinia* white mold (*S. sclerotiorum*) (Muehlbauer et al. 2006). Rust is a serious yield constraint in Bangladesh, Ethiopia, India, Morocco, Nepal, Pakistan and South America. Yield losses to the extent of 60-69% have been reported in India (Singh et al. 1986) and up to 100% in Ethiopia. Identified resistant source, Precoz (Singh and Sandhu 1988) has been utilized in breeding of a number of rust resistant varieties in India and Bangladesh (Kumar et al. 2013). Stemphylium blight is appearing commonly in Bangladesh and India causing a huge reduction in yield. Disease intensity as high as 83% was observed on an unsprayed local cultivar in Bihar of India, causing >90% yield loss (Sinha and Singh 1993). However, limited efforts are being made to screen lentil germplasm against this pathogen.

Breeding for abiotic stresses

Heat and drought

Heat and drought are major abiotic stresses lentil encounters in dry areas affecting yield potential. Escape and avoidance of stresses during critical stages play crucial role in overcoming the heat and drought stresses in lentil. Developing crop varieties with short duration is one of the major strategy. Some of the traits such as early growth vigour, rapid ground cover, and leaf and root characteristics including size, morphology, depth, length, and density are found to be associated with drought tolerance. These traits either determine the transpiration demand of a plant or help to improve the water use efficacy of crop plant. As a result crop plants are able to avoid drought stress. Long roots along with prolific lateral root development (high dry root weight) are known to enhance the capacity of a plant to extract water from deeper soil strata and to take up nutrients (Gahoonia et al. 2005). A significant correlation was observed between deep root system and shoot growth and seed yield (Sarker et al. 2005) and between root and shoot traits such as dry shoot biomass and chlorophyll content (Kumar et al. 2012). Non-availability of simple repeatable large-scale screening technique for physiological traits has restricted their use as selection criteria for drought tolerance in breeding program. In this direction, some techniques, e.g., SPAD chlorophyll meter, NDVI index and carbon isotope discrimination have been developed for studying the drought physiology. These methods help to study the water use efficiency of crop plant under the drought conditions. Therefore, in lentil, genetic variability for SPAD value was studied (Kumar

et al. 2012). Similarly, significant genetic variability for root traits have also found among lentil germplasm in a number studies (Kumar et al. 2012; Mia et al. 1996). The studies suggested that above ground traits can be reliably used for indirect selection of underground traits (root) in breeding programs (Idrissi et al. 2015), who also emphasized on a well-developed root system and early biomass development for drought tolerance. With the use of modern biotechnological techniques, such as molecular mapping and tagging, has eased the identification of different genes/QTLs controlling root traits. Singh et al. (2016) recently identified a molecular marker associated with *Sdt* locus controlling seedling survival drought tolerance in lentil and a QTL-hotspot genomic region controlling a number of root and shoot characteristics (Idrissi et al. 2016), which imparted in drought tolerance.

Lentil crop encounters a few days of exposure to high temperatures (30-35°C) at reproductive stage, causing heavy yield losses due to flower drop and pod abortion (Summerfield et al. 1985; Sarker et al. 1999; Roberts et al. 1986). In lentil, limited studies have been conducted for heat tolerance. More emphasis has been given on the development of early maturing genotypes to avoid heat stress. Based on number of filled pods at higher temperature has been used as a criterion for selecting heat tolerant lentil genotypes, IG 3745, IG 4258 and IG 5146 (Kumar et al. 2016a). Pollen viability has also been demonstrated as an effective criterion for heat tolerance in chickpea and soybean (Devasirvatham et al. 2012; Djanaguirama et al. 2013).

Tolerance to aluminium toxicity

Area under acidic soils with a problem of aluminium (Al) toxicity is prevalent in several countries including India (Singh et al. 2012). The Al toxicity affects 40-70% of the world arable lands which in turn causes 25-80% yield losses in crops grown on soils containing excessive Al (Singh et al. 2011). The Al is present in the form of insoluble alumina-silicates or oxides in soils. At low pH level of soils (5.0) Al gets solubilised in the form of phytotoxic Al^{3+} ions. This phytotoxic Al^{3+} state is very toxic in lentil displaying rapid inhibition of root growth which is visible within hours or even minutes of exposure to Al^{3+} (Kochian et al. 2005). The problem to Al toxicity can be solved through the use of lime which raises the soil pH, however it is not a permanent solution since it is costly and not always practical. Therefore breeding lentil varieties resistant to is sustainable solution. The most reliable screening parameters are root re-growth (RRG) and callose accumulation in roots under hydroponic assay (Singh et al. 2016), it is independent as the technique of Al concentration in soil which is interactive with environmental factors (Butare et al. 2012). The screening under hydroponics as well as in field conditions is expected to help in characterization of resistance in terms of seed yield and its contributing traits. Callose induction in roots during Al toxicity is also known to mediate by Al^{3+} stress even under short-term exposure to Al (Sivaguru et al. 2006). The production of reactive oxygen species (ROS) has also been reported under Al stress environments (Singh et al. 2016). The antioxidative enzyme activities of superoxide dismutase, catalase, ascorbate peroxidase and guaiacol peroxidase facilitate the removal of excessive ROS and check lipid peroxidation (Apel and Hirt 2004).

Salinity stress tolerance

The problem of salinity occurring worldwide, severely limits plant growth and productivity due to ion toxicity and reducing osmotic potential especially in arid and semi-arid regions. Among other cereal and pulse crops Lentil is also sensitive to salinity stress. Several soil and water management practices are being used for amelioration of soil salinity in affected areas, however, it is costly approach for small farmers. Therefore, the development of salt-tolerant genotypes is the most effective strategy for increasing yield under salinity affected areas. The screening techniques such as germination, visual salt injury, seedling survival, reduction in seedling growth, biomass accumulation, Na+, Cl, K+ contents, proline, H_2O_2 production and antioxidant activities have been widely used for evaluation of salt tolerance in different crops including lentil. Germination, seedling survival, growth and biomass were found to be affected by salinity stress in crop plants (Ebbisa and Getachew 2015; Abdel-Haleem and El-Shaieny 2015). However, germination stage is less sensitive to salinity than early vegetative growth stage (Al-Mutata 2003). The effect of salinity leads to major reduction in growth and also reduction in vascular tissue dimension observed in roots of Chloris gayana Kunth (Céccoli et al. 2011). The severe ion imbalance takes place due to entry of both Na+ and Cl into the cells leads which might cause significant physiological disorder (s). Although, the mechanisms such as regulation of Na^+ and Cl ions uptake, xylem loading, retrieval from xylem, extrusion from roots and intracellular compartmentation in the vacuole and osmolyte accumulation make plants to escape from

Na^+ and Cl toxicity. The increased concentration of Na^+ and Cl enhances production of ROS (reactive oxygen species) inhibiting the uptake of K^+ ions leading to low productivity and at times death (James et al. 2011; Singh et al. (2016) reported that there is no reduction in germination of tolerant wild accessions and breeding lines at any salinity levels but moderately tolerant and sensitive cultigens decreasing germination at 40 to 120 mM NaCl level.

Tolerance to alkalinity stress

The plant growth and productivity is greatly affected by soil alkalinity throughout the world. More than half of the saline soils throughout the globe contain sodic alkaline salts (FAO; http://www.fao.org/ag/agl/agll/spush/intro.htm). About 6.73 million ha area is alkalinity affected soils (2.1% of the country) has been reported earlier (Mandal et al. 2009). The 2.8 million ha area is alkaline in nature and laying in the Indo-gangetic plains. The alkaline soil is dominated by excess sodium on exchange sites and a high concentration of carbonate/bicarbonate anions which adversely affect the physical and nutritional properties of the soil. These ions in excess concentration in soil lead to drastic reduction for plant growth and development.

Alkalinity in soil leads to induction of leaf chlorosis and stunted growth due to high uptake of Na^+ and low uptake of nutrients in wheat (Millar et al. 2007). The screening of germplasm at seedling stage is simple (Javid et al. 2012) whereas it is difficult at vegetative and reproductive stages as it is greatly affected by environmental effects. The technique of hydroponics is more effective than soil-based bioassays because it provide consistent control over pH in Brassica **(**Javid et al. 2012). The availability of impressive genotypic variation for low accumulation of Na^+ along with more K^+ contents indicates that the introduction of low Na^+ along with high K^+ accumulation into genotypes may be considered for determining alkaline tolerance. Thus differences in tolerance of these two categories, in terms of accumulation of Na^+ and K^+ and seed yield are clearly established. This type of contrasting responses in tolerance provides very suitable materials in the quest to understand the genetics, molecular and physiological mechanisms of alkaline stress tolerance.

Lentil is sensitive to alkaline stress and the best pH range for selection for alkaline stress tolerance between 9.0 and 9.1. Further the range of variation for seed yield decreased with the increase in soil pH indicating the existence of limited range of variability. The wild accessions namely, ILWL-15, ILWL-192 and ILWL-20 and tolerant breeding lines, PDL-1 and PSL-9 under alkaline stress showed higher seedling survivability, lesser reduction in seedling growth, biomass and seed yield may ascribed to the regulation of Na^+ contents, low H_2O_2 production and more uptake of K^+ (Personal communications D. Singh). Adaptation of lentil to alkaline conditions is different among genotypes with diverse genetic backgrounds.

Winter hardiness

Lentil crop suffers from low temperature at seedling stage but India does not face much problem of frost and severe winter, however, the low temperature is major problem in the highlands of CWANA region and central Anatolia where temperatures go down below 4C. Efforts have been made to identify genetic resources for tolerance to low temperature. Ali et al. (1999) screened lentil cultivars under different temperature regimes and identified cold hardy genotypes. Evaluation of 3,592 accessions under field conditions in Central Anatolia showed large genetic variability for cold tolerance with as many as 238 accessions exhibiting tolerance (Hamdi et al. 1996; Solanki et al. 2011). The prolonged low temperature causes slower growth and injuries to flowers leading to degeneration and dropping of flowers (Solanki et al. 2011), which consequently resulted in reduced grain yield (Muehlbauer et al. 2006). Solanki et al. (2011) reported that different genes are responsible to control tolerance to low temperature at different stages including bud opening, flower growth, fertilization, pod initiation and pod development. Quantitative inheritance to low temperature tolerance in lentil has earlier been reported (Kahraman et al. 2004). They identified many QTLs for winter survival in lentil through marker trait analysis. The RAPD markers linked to frost resistance were also identified in lentil (Eujayl et al. 1999). Therefore, accumulation of genes responsible for winter survival will probably require stringent field testing and marker assisted selection.

Herbicide tolerance

Parasitic and nonparasitic weeds are also major production constraints of lentil. Non-parasitic weeds compete for light and nutrients, often leading to yield losses up to 40% in legume crops (Tepe et al. 2005; Ali and Gupta 2012). As manual weeding is becoming costly due to competing on- and off-farm activities and high labor wages, development of herbicide resistant variety can be important alternative strategy

in lentil. Herbicide tolerant varieties have earlier been developed in Canada and Australia (Slinkard et al. 2007). These efforts can lead an expansion of lentil area under conservation agriculture. Besides common weeds, parasitic weeds like Orobanche have also emerged as a threat to lentil production in some Mediterranean countries (Rubiales et al. 2006). The evaluation of lentil germplasm accessions in the infested field did not show genetic resistance to Orobanche (Erskine et al. 1994). However, only potential resistant sources with significant reduction in infestation density have been reported in Spanish germplasm (Fernandez-Aparicio et al. 2008) and wild species including *Lens ervoides*, *L. odemensis* and *L. orientalis* (Fernandez-Aparicio et al. 2009).

Exploitation of alien genes of wild and exotic germplasm

The narrow genetic base of indigenous *microsperma* germplasm (i.e. pilosae type) is one of the major reason for yield stagnation in lentil. Repeated use of same genotypes in breeding programs (Ferguson et al. 1998; Kumar et al. 2004) has led to poor progress. Diverse germplasm and wild relatives are the reservoir of useful genes, which are not available in the cultivated gene pool (Tanksley and McCouch 1997; Kumar et al. 2011). Over the years, 587 accessions of wild relatives belonging to *Lens culinaris* ssp. *orientalis* and *L. odemensis* (primary gene pool), *L. ervoides* and *L. nigricans* (secondary gene pool), and *L. lamottei* and *L. tomentosus* (tertiary gene pool) from 26 countries were collected and conversed in ICARDA gene bank. The use of indigenous and native genes from exotic lines and genes from wild relatives is one of the options for broadening the genetic base of lentil in South Asia (Erskine et al. 1998). Several studies have indicated that wild species have good cross compatibility with cultivated species (Fratini et al. 2004; Fratini and Ruiz 2006). Therefore, the introgression of alien genes from wild relatives can be successfully achieved (Gupta and Sharma 2007; Singh et al. 2016) as the *L. culinaris* ssp. *orientalis* and *L. odemensis* are cross-compatible with cultivated species (Muehlbauer et al. 2006). However, the fertility of the F_1 hybrids derived from interspecific hybridization depends on the differential affinity between the chromosomes of wild parent (Ladizinsky 1979; Ladizinsky et al. 1984) and the cultivated species. As a result, resistance to a few diseases and insect pests from wild relatives and unadapted germplasm has been successfully transferred in to suitable genetic background (Stalker 1980; Ladizinsky et al. 1988; Hajjar and Hodgkin 2007; Singh et al. 2013; Kumar et al. 2014). The useful genetic variability for days to 50 % flowering, secondary branches, no. of pods/plant, biological yield/plant, grain yield/plant and 100 seed weight (Kumar et al. 2014).

Wild species, *Lens nigricans* and *L. ervoides* do not readily cross with the cultivated ones due to embryo abortion in F_1 hybrids (Abbo and Ladizinsky 1994; Gupta and Sharma 2005). Therefore, advances made in *in-vitro* techniques provided feasibility for introgression of alien gene from wild species (Tullu et al. 2013). *Lens ervoides* having resistance to anthracnose has been exploited in Canada by transferring resistance genes into cultivated backgrounds with the help of embryo rescue techniques (Fiala et al. 2009; Tullu et al. 2011). This species is also a good source of resistance to other diseases and some agronomic traits such as growth habit, biomass production, and seed traits. Development of a number of recombinant inbred lines from crossing of cv “Eston” (*L. culinaris*) with PI72815 and L01-827 (*L. ervoides*) resulted in transgressive segregations for various agronomic traits including an 8 % increase in seed size (Tullu et al. 2011; Singh et al. 2013). An early flowering exotic line, Precoz, introduced in India, has been frequently used in Indian lentil breeding program for improving earliness, seed size and rust resistance (Erskine et al. 1998). Involving Precoz in the breeding has led to the development of a number of superior lines. Molecular and phenotypic analysis of these derivatives showed that use of exotic line in breeding program has broaden the genetic base of cultivated gene pool (Kumar et al. 2014). As a result a high yielding and large seeded variety IPL 316 has been developed.

Breeding for nutrient use efficiency

Lentil is generally cultivated in soil having deficiency for key minerals such as iron (Fe) and boron (B) especially in countries like India and Ethiopia. However, these stresses remain of local importance. For example, Fe-deficiency is a common soil disorder especially in high pH soils, causing18-25% yield losses in susceptible genotypes in India and up to 47% in Syria (Ali et al. 2000; Erskine et al. 1993). Similarly, B-deficiency has been observed in the eastern *Terai* plains of Nepal, eastern India and northern Bangladesh. Tolerance among lentil genotypes have been observed against these stresses and identified a number genotypes that showed tolerance after screening of lentil germplasm to Fe-deficiency, B-deficiency

(Srivastava et al. 2000), and B-toxicity (Yau and Erskine 2000; Hobson et al. 2006). This variability is needed to use in breeding program for developing genotypes having high yield potential in soils with imbalance minerals.

Improving quality traits

Lentil seeds are rich in proteins, micronutrients, vitamins and many phytochemicals. The studies have shown a good amount of genetic variability for nutritional qualities in lentil germplasm (Kumar et al. 2016b). In brief, studies showed that protein concentration ranged 22 to 31 % in all type of lentils (Bhatty et al. 1976; Boyle et al. 2010). Significant genetic variability ranging from 42-132 ppm for Fe and 23-78 ppm for Zn has been recorded in a large collection of lentil germplasm (Anon. 2014). Moreover, lentil germplasm showed variability for folate concentration (216 to 290 ìg/100 g) (Jha et al. 2015).), Se (Selenomethionine) (Thavarajah et al. 2008; Raham et al. 2013; Thavarajah et al. 2015), â carotene (2 to 12 ìg/g) (Thavarajah and Thavarajah 2011), folate concentration (114 ± 3 to 330 ±7µg/100g) and total dietary fibers (de Almeida Costa et al. 2006). It has been observed that high concentration of both of these compounds in Mediterranean landraces as compared to the breeding lines and released varieties of lentil (Singh et al. 2013) and other macro nutrients (Karakoy et al. 2012; Kumar et al. 2016b). Prebiotic carbohydrates, which are important components of healthy diets supporting healthful hindgut microflora, showed significant variation among lentil genotypes (Chung et al. 2008; Tahir et al. 2011; Johnson et al. 2013a). Genotypic differences were also observed for antioxidant and enzyme inhibitory activities of the phenolics, total phenolic content (4.46 to 8.34 mg CAE/ g dry weight), total flavonoid and condensed tannin content among lentil genotypes (Zhang et al. 2015). The moderate level of heritability estimates of Fe and Zn concentrations (64-68%) has indicated that there is a possibility for breeding of high Fe and Zn containing lentil genotypes (Thavarajah et al. 2009a). Breeding for nutritional traits has been complicated as the concentration of nutrients in a genotype is influenced by G (Genotype) × E (Environment), G × Location (L), G × Year (Y) and Y × L interactions in lentil (Thavarajah et al. 2009, 2010, 2015; Jha et al. 2015).

Genetic variability available for nutritional traits has provided opportunity to breeders for biofortification to enrich cultivars. ICARDA has taken initiative through Harvest Plus Challenge Program under CGIAR system to improve lentil in respect of nutrients (Hotz and McClafferty 2007). As a result, a number of varieties with high iron and zinc concentration with good agronomic attributes have been identified (Kumar et al. 2016b). Presence of phytic acid in lentil seeds limits bioavailability of micronutrients to human body and it is suggested to develop such cultivars with reduced amount of phytic acid in lentil seeds. However, on the other hand, low level of phytic acid in seeds had adverse effect on seeding germination (Urbano et al. 2000; Raboy 2002). These limitations have restricted the nutritional improvement of such traits through genetic means and hence for the optimum concentration of respective traits could be accomplished using biotechnological tools.

Conclusion

In spite of the progress made in the development of improved cultivars adopting conventional breeding methodologies, it has not been commensurated to the demand of growing population. It is essential, therefore, to focus on such a breeding strategy, which could help the development of high yielding and stable cultivars for diverse agro ecological conditions. To extend cultivation in rice fallows short duration cultivars that could fit into <100 day growing window need to be selected. Since the harvest losses are significant and it is labour intensive crop, the restructuring of plant type with lodging resistance, erect growth habit and tolerance to pod shattering suiting mechanical harvesting is needed. Wild species of *Lens* possess several useful genes, which can be utilized to improve agronomic traits in lentil. Pre-breeding lines involving wild relatives have been developed, which can serve as useful genetic resources. have been developed from crossing of wild relatives with cultivated lines. Wild species have also been utilized for pest and disease resistance e.g., *Fusarium* wilt, anthrcnose etc. Considerable progress has been made in development of genomic resources facilitating marker assisted selection and mapping of genes/QTLs for disease resistance and different agronomic traits of economic importance. The progress made so far is useful to develop high yielding, stable, disease and pest resistant genotypes in order to revolutionize the lentil production. The higher production and on-farm productivity level will play a crucial role in alleviating protein malnutrition for the growing Indian population.

Declaration

The authors declare no conflict of interest.

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