Chapter 4
Toward Climate-Resilient Lentils: Challenges and Opportunities

Dorin Gupta, Rama Harinath Reddy Dadu, Prabhakaran Sambasivam, Ido Bar, Mohar Singh, Navya beera and Sajitha Biju

Abstract Lentil among legumes has a significant place in crop production and rotation, and the nutritional security of growing human population. Current lentil cultivars have a narrow genetic base and are challenged with many biotic and abiotic stresses. The pressures from changing climate necessitate more efforts to find durable resistance sources for biotic and abiotic stresses. Distant landraces and wild lentil species which are less explored are known to possess such genes to develop resilient cultivars, one of the best adaptation strategies for climate change. The research efforts are currently focusing on enhancing lentil grain yield and resilience to climate change through introgression of desired genes from other gene pools. The current lentil-breeding efforts have concentrated upon conventional plant breeding techniques for the inclusion of the cultivated lentil gene pool only. Unlike other crops, genomics-assisted breeding remains one of the areas to be further explored to speed-up the climate-smart high-yielding cultivars development process, which is reliant on the extensive genomic resources. Several lentil linkage maps have been developed and quantitative trait loci for tolerance to biotic and abiotic stresses have been identified. However, advances in molecular markers, next-generation sequencing, genomewide sequencing, and bioinformatics will further help to precisely identify genes of interest that can be best utilized to breed climate-resilient cultivars for higher production and quality through genetic engineering and plant breeding.

Keywords Lentil · Wild · Gene pool · Climate-smart traits · Genomics

D. Gupta (✉) · R. H. R. Dadu · S. Biju
Faculty of Veterinary and Agricultural Sciences, University of Melbourne, Dookie, VIC, Australia
e-mail: doring@unimelb.edu.au; gupta.dorin@gmail.com

P. Sambasivam · I. Bar
School of Natural Sciences, Environmental Futures Research Institute, Griffith University, Nathan, QLD, Australia

M. Singh
ICAR-National Bureau of Plant Genetic Resources Regional Station, Shimla, India

N. beera
Institute of Biotechnology, Telangana State Agricultural University, Hyderabad, India

C. Kole (ed.), *Genomic Designing of Climate-Smart Pulse Crops*,
https://doi.org/10.1007/978-3-319-96932-9_4

4.1 Introduction

Lentil (*Lens culinaris* Medikus) like other food legumes offers a range of benefits from soil to human health and has become an integral part of current farming system as a valuable cash crop. However, lentil is still one of the neglected crops especially in developing countries, which has potential to be grown in more drier areas being fairly drought tolerant and highly nutritious. Legumes are accepted in farming system around the world but not to the extent as cereal crops. However, legumes including lentil which can fix atmospheric nitrogen and can minimize the nitrogen input requirements, provide pest breaks and weed control for subsequent cereal crop when used in crop rotations. Lentil offers many health benefits due to its low fat, high prebiotic carbohydrates, high fiber, and low glycemic index (Srivastava and Vasishtha 2012; Thavarajah 2017). Lentil grain provides 22–25% dietary protein (one-quarter of total caloric value), carbohydrates, vitamins, and a good balance of minerals (K, Mg, Fe, Zn), along with high contents of essential amino acids such as lysine and tryptophan (Erskine et al. 1990; Johnson et al. 2013; Faris et al. 2013; Ray et al. 2014). Staple cereals are high in sulfur-based amino acids which are lacking in lentils, therefore, when eaten together, cereal-lentil based diet can provide complete profile of the essential amino acids. Due to its high protein content, this grain is also regarded as cost-effective alternative to animal-based protein, especially in the Indian subcontinent where plant-based diet predominates due to religious believes, and less affordability of fresh meat. Lentil ranks sixth among important annual grain legumes with 5.4 million hectare worldwide area under cultivation leading to an annual production of 6.3 million tons (FAO 2016). It is grown in Canada, Australia, Southern Europe, Eastern, and Northern Africa, the drier regions of the Middle East and the Indian subcontinent during cooler season of the year. Lentil productivity has not seen tremendous rise over the past years and even has not crossed the mark of one ton per hectare globally (FAO 2016). Climate change will have a significant impact on global food production and food security of growing human population as clearly highlighted by Intergovernmental Panel on Climate Change (IPCC), if we look deeper, major implications will be through reduced soil fertility, reflection of reduced microbial activity and diversity, and carbon sequestration leading to less than optimal plant growth and yields (Dhankher and Foyer 2018). The future projections of drastic climatic events such as frequent droughts and floods, higher or lower temperatures, salt, and heavy metal stresses leading to higher incidences of pest infestations will significantly affect crop yields. Adaptation through diversified new crops and cultivars could be one of the strategies to combat climate change and sustain food production. Further, to be climate resilient, crop production system requires tailored solutions through inclusion of past and current knowledge about crops, beneficial crop rotations, their unique genetic make-up, and specific traits to be targeted for their inclusion in modern cultivars to cope and produce enough under various stresses. Lentil being one of the hardy crops can potentially yield higher, to meet the demands of quality food for growing human population. However, since past many years, crop is being grown on marginal lands especially in the developing

countries due to preferential cereal-based cropping, which led to the loss of genes of higher productivity (Bejiga and Degago 2000). Along with cultivation on marginal lands which generally have low soil fertility, the crop is mostly grown as rainfed and is subjected to mainly terminal drought and heat stress (abiotic) and various fungal and bacterial diseases—Ascochyta blight, rust Stemphylium blight, collar rot, root rot, white mold, Fusarium wilt, and anthracnose (Kumar et al. 2013; Sharpe et al. 2013a). At parallel, current improved cultivars are bred to yield higher but not primarily to cope with various stresses, if resistant to one or the disease exists, it is not very durable and traits responsible for tolerance to various abiotic stresses are not introgressed as priory traits. These cultivars have narrow genetic base owing to handful desired cultivated germplasm parentage (Singh et al. 2014) whereas, not much has been explored in wild lentil relatives which are more diverse (Ford et al. 1997; Duran et al. 2004; Gupta and Sharma 2007; Singh et al. 2014). Therefore, these cultivars cannot yield higher due to their vulnerability to major biotic and abiotic stresses under climatic uncertainties and narrow genetic base. Farmers adopt new crop cultivars and change their practices to cope with changing environments. However, the pace of environmental change will be difficult to match along with the expected expansion of crops to new environments and lands suggesting strong need for research efforts to develop climate-resilient crops (Dhankher and Foyer 2018). In lentil, the identification and inclusion of climate resilient useful and diverse traits/genes to broaden the genetic base of the existing lentil cultivars from closely or distant relatives should be prioritized. Therefore, this chapter aims at understanding lentil's untapped sources of genetic variation, traits of importance, role of conventional, genomics, and modern molecular technologies for better use of such identified traits and their inclusion in breeding programs to breed and develop climate-resilient lentil cultivars.

4.2 Prioritizing Climate-Smart (CS) Traits

To sustain crop yields under uncertain environments, higher yielding climate-smart crop cultivars should possess multiple resistance and/or tolerance to stresses (biotic and abiotic). One of the major differences between two types of major stress categories is that the mechanisms controlling abiotic stresses are governed by multiple genes, therefore targeting germplasm in breeding programs which shows the potential for common defense mechanisms can address multiple stress tolerance in plants. The adaptation to climate change can be sought through the development of new cultivars with multiple tolerance to abiotic stresses such as heat, cold, frost, drought and salinity, and resistance to various diseases and pests. At parallel lentil, cultivars should possess adapted phenology (maturation times and responses) and different agro-morphological traits which will offset the new challenges of changes in growing season (shorten/longer than usual).

4.2.1 Flowering Time

The transition from vegetative to reproductive growth is an important trait and a major component of crop adaptation, particularly in rainfed environments (Subbarao et al. 1995; Gao et al. 2014). The timing of flowering is dependent upon the genotype, the seasonal temperature profile, photoperiod, light, nutrient levels, and vernalization responses of the plant. If flowering occurs prematurely under stressful environments, seed set and grain filling may be compromised. If flowering is delayed, the plant risks succumbing to terminal drought stress before producing any seed. A complex network of genetic pathways allows the plants to detect and integrate external or internal signals to initiate the floral transition (Bluemel et al. 2015). In indeterminate species like lentil, early flowering may enable the plants to prolong the reproductive phase, especially when the flowering duration is delimited by terminal drought stress that terminates seed set. The transition to flowering stage in lentil is proposed to be a function of both photoperiod and temperature, longer days and warmer temperatures accelerate flowering (Summerfield et al. 1985; Roberts et al. 1986; Barghi et al. 2013). Yuan et al. (2017) showed that the overall days to flowering of lentil genotypes were mainly influenced by the red/far-red (R/FR)-induced light quality change. While most of the wild lentil genotypes had reduced responses and flowering time, the cultivated lentil showed consistent, accelerated flowering in response to the low R/FR light environment together with three wild lentil genotypes (*L. orientalis* IG 72611, *L. tomentosus* IG 72830, and *L. ervoides* IG 72815). These genotypes would represent key genetic resources for developing lentil cultivars with better adaptation to variable light environments.

The role and importance of vernalization in floral induction for lentils, however, remains largely undefined. Summerfield et al. (1985) in his analysis of six lentil genotypes reported a variation in vernalization response with respect to flowering time, vernalized plants flowered earlier in all instances compared to nonvernalized plants. Roberts et al. (1986) in contrast proposed that the effect of vernalization on floral induction was negligible. It has also been suggested that for sensitive genotypes, vernalization exposure reduced the critical or nominal base photoperiod, required for floral induction (Summerfield et al. 1985; Roberts et al. 1986). Photoperiod-sensitive and insensitive phases can be identified through experiments in which individual plants can reciprocally be transferred in a time series from long to short days and vice versa in growth chambers. This will help to develop cultivars with shorter pre-inductive photoperiod-insensitive and sensitive phases to fit short growing seasonal regions. Exploitation of genetic variability for flowering time can assist in the development of high yielding early maturing cultivars that are able to adapt to changing environmental conditions. Exotic and indigenous lentil germplasm were screened to identify early flowering genotypes (Erskine et al. 1998; Asghar et al. 2010; Kumar and Solanki 2014; Kumar et al. 2014b; Singh et al. 2014). Sarker et al. (1999a, b) identified single recessive gene (*sn*) control for early flowering in lentil. The variants of early flowering at this locus could be useful for the development of early flowering

cultivars for water-limited environments and can help to diversify the lentil genetic base.

4.2.2 Root Characters

Root characters are one of the important agronomic traits, which play vital roles in crop adaptation and productivity under stressed environments. Developing crops with better root systems is a promising strategy to ensure productivity in both optimum and stressed environments. A deep and proliferative root system extracts sufficient water and nutrients under stressed conditions. Well-developed root systems are linked to drought tolerance as an avoidance mechanism guaranteeing productivity of lentil under water-limited environments (Idrissi et al. 2015a, 2016; Sarker et al. 2005; Verslues et al. 2006; Gaur et al. 2008; Vadez et al. 2008). Drought-tolerant genotypes tend to elongate their rooting depth significantly more than sensitive ones under drought stress in lentil (Sarker et al. 2005). Specific rooting patterns can be associated with drought avoidance mechanisms that can be used in lentil breeding programs. Modifications in the root architecture allow the plants to increase their water extraction capacity and drought tolerance.

Gorim and Vandenberg (2017a) found significant differences for root traits and fine root distribution between and within selected wild lentil species and cultivated lentil. The authors also observed variability in nodule number and nodule shape within and between genotypes. Some genotypes used water more efficiently for either biomass or seed production. The allocation of resources to seed production also varied between genotypes. These findings could have an impact on the design of future lentil breeding CS traits in the context of strategies for managing changes in rainfall amount and distribution for lentil growing regions. The distribution pattern of root traits and nodulation at different soil depths in both wild and cultivated lentil genotypes were also analyzed by Gorim and Vandenberg (2017b). Their findings suggest that wild lentil genotypes from a particular gene pool might have similarity for root traits and nodule distribution in the soil. Furthermore, wild genotypes with deep root systems allocated their resources mostly toward biomass production implying that when interspecific hybridization and introgression become part of a long-term breeding strategy for lentil, it will be necessary to develop appropriate selection strategies for simultaneous selection of yield and root traits under stressed environments.

4.2.3 Heat Tolerance

Lentil is similar to other cool-season legumes in its susceptibility to rising temperatures (Summerfield et al. 1985; Ahmed et al. 1992; Porch and Jahn 2001; Croser et al. 2003; Choudhury et al. 2012; Bhandari et al. 2016; Sehgal et al. 2017). It

requires cooler temperatures during the vegetative growth and warmer temperatures at maturity; the optimum temperature for lentil growth is 18–30 °C (Choudhury et al. 2012). Susceptibility of vegetative and reproductive stage in lentil crop to heat stress has been described by (Delahunty et al. 2015; Bhandari et al. 2016; Kumar et al. 2016a, b and Sita et al. 2017). Temperatures greater than 24.4 °C reduced the germination rate in lentil (Covell et al. 1986). Temperatures above 32/20 °C (max/min) during flowering and pod filling in lentil drastically reduced seed yield and resulted in 20–70% yield reductions, equating to $1000/ha loss, through flower drop and pod abortion (Delahunty et al. 2015; Kumar et al. 2016a, b). Heat stress in lentil causes a reduction in germination percentage, abnormal seedling growth, nodules degeneration, early flowering, reduction in plant biomass, loss in cell membrane stability and photosynthetic efficiency, and increase in lipid peroxidation, (Ellis and Barret 1994; Muehlbauer et al. 2006; Chakraborty and Pradhan 2010; Sehgal et al. 2017). Higher expression of ascorbate peroxidase (APX) has been linked with heat tolerance in lentil (Chakraborty and Pradhan 2010). Heat tolerance in lentil is attributed to superior pollen function and higher expression of leaf antioxidants (Sita et al. 2017). Heat stress especially when combined with drought stress, even for a few days during flowering and pod filling drastically reduces seed yield in lentil because of accelerated development, forced maturity, shortened reproductive period, and damage to reproductive organs leading to flower drop, pollen sterility, pod abortion, and reduced seed set (Siddique 1999; Boote et al. 2005; Choudhury et al. 2012; Gaur et al. 2015; Bhandari et al. 2016).

Even though only limited studies were conducted to screen lentil germplasm for heat tolerance in both laboratory and field conditions, genetic variations for heat tolerance have been identified in lentil and are listed in Table 4.1.

4.2.4 Cold/Frost Tolerance

Lentil is prone to radiant frost when compared with other legumes and are less prone to frost than peas but more susceptible than chickpeas (Murray et al. 1988). Frost tolerance for lentil at flowering is –2 to –3 °C. Lentil is least tolerant to frost injury at flowering due to the exposed nature of the flowers and the small size of pods. Frost injury symptoms in lentil include flower and pod abortion, damage to seed, and injuries to vegetative tissues. During the pod filling stage, frost can damage the seed coat and the developing seed. In severe frost events, leaves are damaged and stem wilts. Plant at the early vegetative stage can quickly recover from underground axillary buds, however, at the vegetative maturity stage or beyond, the plants will most likely die because axillary bud initiation will most likely not occur as the plant is moving into reproductive stage. Frost damage can also result in an increased vulnerability to entry of pathogen causing diseases like anthracnose and botrytis gray mold. Yield losses from frost damage can be severe for a high-value crop like lentil. Since 1980, considerable research efforts have been put into breeding and characterizing the genetics of frost tolerance of lentil (Erskine et al. 1981; Summerfield et al. 1985;

Table 4.1 Genetic variation for tolerance to heat, frost, and waterlogging in lentil

Type of stress	Accession	Selection criteria	References
Heat	IPL81, IPL406	Heat tolerance index (TI) and antioxidant activities	Chakraborty and Pradhan (2010)
	Ranjan, IC201710, IC208329, 14-4-1	Cell membrane thermostability	Choudhury et al. (2012)
	Qazvin	Cell membrane thermostability	Barghi et al. (2013)
	72578, 70548, 71457, 73838	Seed yield	Delahunty et al. (2015)
	ILL2181, ILL82, ILL5151, ILL5416 ILL4587, ILL956 ILL 598, FLIP2009-55L, ILL2507, LL4248	Pollen viability, grain yield	Gaur et al. (2015)
	FLIP2009-55L, IG2507, IG4258	Pollen viability	Kumar et al. (2016a, b)
	IG3745, IG4258, IG5146	Number of filled pods at higher temperature	Kumar et al. (2016a, b)
	LL931	Seed weight	Bhandari et al. (2016)
	GP2961, PL234, LKH2	Biological yield, grain yield, number of pods per plant, pod yield, and number of seeds per pod	Kumar et al. (2019)
	IG2507, IG3263, IG3297, IG3312, IG3327, IG3546, IG3330, IG3745, IG4258, FLIP2009	Pollen germination, pollen viability, ovular viability, pod number, nodulation, antioxidants, sucrose	Sita et al. (2017)
Frost/cold	LC9978057, LC9977006 LC9977116, LC9978013 ILL759, ILL1878, ILL4400 ILL7155, ILL8146, ILL8611, ILL9832, Kafcas, Cifei, Ubek	Winter survival rates, visual rate, damage percentage of survival	Hamdi et al. (1996)
	ILL5865, Balochistan local	Controlled freezing test	Ali et al. (1999)

(continued)

Table 4.1 (continued)

Type of stress	Accession	Selection criteria	References
	LL1878, ILL662, ILL857, ILL975, ILL1878	Winter hardiness	Sarker et al. (2002)
	Morton, WA8649041, WA8649090	Winter survival rates	Kahraman et al. (2004a)
	ILL662, ILL857, ILL975	Rapid ground cover Early vigor	Sarker et al. (2002)
Waterlogging/ flooding/ submergence	ILL6439, ILL6778, ILL6793	Stomatal conductance and biomass	Ashraf and Christi (1993)

Murray et al. 1988; Spaeth and Muehlbauer 1991; Kusmenoglu and Aydin 1995; Ali et al. 1999). More recently, several research studies have also been carried out in the aspects of winter hardiness and frost injury in lentil (Kahraman et al. 2004b; Barrios et al. 2007, 2010, 2016). Identified genetic variation for tolerance to frost is listed in Table 4.1.

4.2.5 Drought Tolerance

Lentil is considered as moderately tolerant to drought when compared to other legumes (Reda 2015). Even though lentil is a hardy crop requiring less water for its growth compared to other legumes, the plant productivity can decrease from 6 to 70% under drought conditions and can even lead to total crop failure (Saxena 1993; Johansen et al. 1994; Babayeva et al. 2014). Drought stress at reproductive stage led to 24% grain yield reduction and was 70% when drought occurred at pod development stage (Shrestha et al. 2006; Allahmoradi et al. 2013). Drought stress occurring at flowering or podding stage affects vegetative and reproductive growth leading to reduced leaf area (48–55%), total dry matter (32–50%), flower production (22–55%), and number of pods and seeds (27–66%), with significantly higher flower drop and aborted pods (Table 4.2) (Shrestha et al. 2006). Drought stress can also lead to fluctuation in concentration of photosynthetic pigments, osmoregulation, and antioxidant metabolism in lentil (Aksoy 2008; Öktem et al. 2008; Gokcay 2012; Muscolo et al. 2014; Mishra et al. 2016; Biju et al. 2017). The variable annual rainfall patterns threaten the sustainability of lentil production by increasing the frequency of drought periods during the cropping season (Dai 2011). Ninety percent of the world's lentil is produced in areas relying upon conserved, receding soil moisture and therefore, crop productivity is largely dependent on the efficient utilization of available soil moisture (Kumar and Van Rheenen 2000).

Lentil withstands drought stress through drought tolerance and drought avoidance mechanisms. Drought tolerance mechanisms in lentil include dense pubescence

Table 4.2 Identified sources of resistance to drought stress in lentil from literature

Accession	Selection criteria	References
ILL6439, ILL6451	Osmotic adjustment	Ashraf et al. (1992)
ILL1983, ILL2501, ILL2526	Seed yield	Hamdi et al. (1992)
MI30B, MI52, MI563	Leaf water traits	Salam and Islam (1994)
ILL1861, ILL784	Seed yield	Hamdi and Erskine (1996)
ILL590, ILL7200	Short duration, rapid biomass, leaf area development, high photosynthetically active radiation	Clements et al. (1997)
HUL35	Osmotic adjustment	Singh (2001)
ILL6002	Stem length, taproot length, number of lateral roots	Sarker et al. (2005)
TN1768	High yield	Salehi et al. (2008)
Naeen, Shiraz7	Stress tolerance index (STI), geometric mean productivity (GMP)	Rad et al. (2010)
TN1084, KC210034	GMP, harmonic mean (HM), STI, stress susceptibility index (SSI)	Siahsar et al. (2010)
Seyran	Antioxidant enzyme activities (APX, CAT, GR, and SOD), protein profiles	Gokcay (2012)
Cabralia inta	Shoot length, germination stress index (GSI)	Salehi (2012)
Land race	RWC, Fv/Fm, proline, stomatal resistance	Allahmoradi et al. (2013)
ILL10700, ILL10823, FLIP96-51	Seedling survivability, drought tolerance score, root and shoot length, fresh and dry weight of roots and shoots	Singh et al. (2013a)
Eston, Castelluccio	Seed germination, water content, root length	Muscolo et al. (2014)
ILL123613, ILL123466, ILL123613, ILL123466, ILL134466, ILL123684, ILL123679, ILL123648, ILL123629	Drought tolerance index (DTI)	Babayeva et al. (2014)
Eston, Castelluccio	Seed germination, RWC, root length, proline content, total soluble sugars	Muscolo et al. (2014)

(continued)

Table 4.2 (continued)

Accession	Selection criteria	References
PDL1, PDL2	Seed yield	Singh et al. (2016a, b)
Ranjan	Length of shoot and root, fresh weight of shoot and root and dry weight of shoot and root	Dash et al. (2017)
HUL57	Nodulation, yield traits, DSI, STI, mean productivity (MP)	Mishra et al. (2014, 2016, 2018)
Digger, Cumra, Indianhead, ILL5588, ILL6002, ILL5582	Crop water stress index (CWSI), canopy temperature depression (CTD), Root Shoot ratio, RWC, harvest index, and drought tolerance efficiency	Biju et al. (2018)
Binamasur10	Seed yield	www.icarda.org

of leaf, regulated stomatal closure, osmotic adjustment, increased antioxidant responses, and enhancement in yield components. Drought-avoidance strategy is shown by short duration genotypes of lentil such as BARI M4, BARI M5, BARI M6, Precoz, Idlib 3, and Bakaria at the reproductive stage as an adaptation to drought stress through early flowering, rapid root growth, and early growth vigor with high yield potential (Erskine and Saxena 1993; Silim et al. 1993a, b; Erskine et al. 1994; Shrestha et al. 2005). Shoot traits such as canopy structure, stem length, leaf surface, stomatal characteristics, and leaf movements also have significant roles in drought avoidance as reported in the lentil mutant line MI-30 (Salam and Islam 1994). Specific rooting patterns such as root-shoot ratio (RS ratio), can also be associated with drought avoidance mechanisms that can be used in lentil breeding programs (Idrissi et al. 2016; Biju et al. 2017). Drought escape was believed to be relatively insignificant in wild lentil genotypes when compared to cultivated ones (Hamdi and Erskine 1996). Contrary to this finding, recently, Gorim and Vandenberg 2017a) has identified the different drought mechanisms in wild lentil genotypes across species by assessing both above ground plant characteristics and their root systems. They found that wild lentil genotypes employed diverse strategies such as delayed flowering, reduced transpiration rates, reduced plant height, and deep root systems to either escape, evade, or tolerate drought conditions, based on the environmental conditions at their centers of origin. Interestingly, in some cases, more than one drought strategies were observed within the same genotype. The success of increasing lentil production in drier areas prone to terminal drought mainly depends upon the development of short-season cultivars that enable the crop to escape adverse soil–water scarcity (Siddique et al. 2001). Early sowing of lentil in Southwestern Australia and Northern Syria develops a large green canopy and rapid ground cover which absorbs a significant proportion of photosynthetically active radiation (PAR) early in season when vapour pressure deficits (VPD) or atmospheric demand for water are low and

uses more water in post flowering phase thus producing good yield and biomass (Siddique et al. 1998; Chen et al. 2006). Hence, the selection for early flowering lines with pliability for the maturity that provides a massive yield under high moisture availability, is therefore required for severely drought-prone areas. The International Centre for Agricultural Research in Dry Areas (ICARDA) developed early maturing lentil genotypes with good yield and is deposited with 'International Drought Tolerant Nursery' to be shared with the national and international programs.

Changes in several morphological, physiological, and biochemical traits such as seedling survivability, seedling vigor, plant height, total root length, taproot length and number of lateral roots, total root weight, early flowering, maturity, pod number per plant, seed number per pod, grain yield, harvest index, relative water content, water use efficiency, stomatal conductance, and antioxidant activity have been used in screening genotypes for drought tolerance in lentil (Sarker et al. 2005; Shrestha et al. 2006; Chakherchaman et al. 2009; Kumar et al. 2012, 2013; Singh et al. 2017a; Biju et al. 2018). Well-developed vigorous shoot and root system at early seedling stage are important for drought tolerance (Mia et al. 1996; Aswaf and Blair 2012; Kumar et al. 2012; Idrissi et al. 2013, 2015a). Deep and well-developed roots will increase the uptake of water and nutrients in a low moisture soil under drought conditions (Wu and Cheng 2014). Thus, the selection of deep rooting is recommended to increase the yield of legumes including lentil under drought conditions (Buddenhagen and Richards 1988).

The extent of membrane damage and the enzymatic antioxidant activity appears to be a useful method for evaluating the level of plant drought stress. Simple screening tests like electrolyte leakage measurements after stress can be used for drought tolerance in cool-season food legumes. Cell leakage studies were performed in different lentil genotypes and found that drought-tolerant lentil genotypes exhibit lower cell membrane injury along with higher seedling growth, water use efficiency, and osmotic regulation (Stoddard et al. 2006). Similarly, germination stress index (GSI) and cell membrane stability (CMS) index can also be used as a good criterion prior to conducting a field screening for drought tolerance in lentil at a large scale (Salehi et al. 2008). Polyethylene glycol (PEG) based in vitro screening for drought tolerance at seedling stage has been proven to be another suitable method to effectively screen large sets of germplasm with good accuracy by analyzing the traits like germination percentage, germination rate, germination index, seedling length, root and shoot length of seedlings, seedling dry weight, relative water content, proline, and total soluble sugars (Salehi 2012; Muscolo et al. 2014; Keshtiban et al. 2015; Dash et al. 2017; Biju et al. 2017). A new phenotyping technique for drought tolerance assessment in lentil using hydroponics has been developed to screen many genotypes at seedling stage (Singh et al. 2013a). However, most of these methods are slow, laborious, time consuming, expensive, and influenced by environmental conditions. Most recently, it has been reported that canopy temperature (Tc) and crop water stress index (CWSI), both assessed using infrared thermal images, along with root-shoot (RS) ratio, relative water content (RWC), harvest index (HI), and other drought tolerance indices are useful in defining the drought stress tolerance variability within lentil genotypes (Biju et al. 2018). The water conservation traits, such as

early partial stomatal closure under soil drying, and limited transpiration under high atmospheric vapor-pressure deficit have recently been proven to be useful in other legumes under drought stress (Devi et al. 2010; Zaman-Allah et al. 2011; Belko et al. 2012; Seversike et al. 2013; Ghanem et al. 2017) and these traits can be used in lentil for defining drought stress along with physiological screenings and mechanistic crop simulation modeling. Table 4.2 shows the identified sources of resistance to drought stress in lentil.

Early on partially closed stomata under moisture stress and high VPD will enable less transpiration loss and could be traits of importance for drought stress tolerance in lentil.

4.2.6 Flooding and Submergence Tolerance

Flooding and submergence are adverse environmental conditions, which severely constrain the growth and yield of legume crops growing in the fine-textured and duplex soils (Solaiman et al. 2007; El-Enany et al. 2013; Kang et al. 2017). Lentil is the most sensitive of all legumes to waterlogging (Solaiman et al. 2007; Singh et al. 2013a) and transient waterlogging is an important hindrance for lentil production, especially during the early developmental stages (Materne and Siddique 2009). Waterlogging in lentil affects yield at any growth stage during the growing season causing most damage (Materne and Siddique 2009). Waterlogging during germination can cause unsuccessful germination, late emergence, and suppression of root growth (Jayasundara et al. 1997). Flooding at vegetative stage can induce root system damage and led extensive leaf senescence and desiccation (Nessa et al. 2007). Lentil is most susceptible to waterlogging at flowering period causing flowers and pods to abort. The response of lentil to waterlogging is like its response to low light and low temperatures, all result in stunted growth and leaf senescence (turning yellowish to red), wither and eventually die. Lentil germplasm with waterlogging tolerance associated with their geographic origin was studied by Wiraguna et al. (2017) and reported that genotypes from Bangladesh are adapted to waterlogged soil at germination. Waterlogging-tolerant genotypes were characterized by its low biomass, higher stomatal conductance, early flowering and maturity, and high root porosity (Ashraf and Chishti 1993; Malik et al. 2015; Erskine et al. 2016). Formation of lysigenous cavities and aerenchyma are waterlogging responses found in lentil (Hamdi, 1987). Some management practices used to reduce the effects of waterlogging in lentil involve sowing time, paddock selection, seeding rate, and drainage (Toker and Mutlu 2011). Studies revealing the biochemical and physiological responses for waterlogging tolerance and possible measures to combat this abiotic stress in lentil still deserves more attention.

4.2.7 Salinity Tolerance

Salinity is a major abiotic stress for lentil production, especially under drought conditions in shallow subsoils of alkaline soils especially in the arid and semiarid regions of Australia, Canada, North Africa, and South Asia (Muehlbauer et al. 2006; Nuttall and Armstrong 2010). Lentil is considered as an extremely sensitive species to salinity than other legumes such as faba bean and soybean (Ashraf and Waheed 1990, 1993; Katerji et al. 2001, 2003; Sidari et al. 2008), whereas it has greater salinity tolerance than chickpea and field pea (Siddique 1999). Yield reduction due to salinity stress has been reported in lentil to be as high as 20% at an electrical conductivity (EC) of 2 dS/m and 90–100% at an EC of 3 dS/m by negatively affecting yield attributes (Ayoub 1977; Van Hoorn et al. 2001; Golezani and Yengabad 2012). In lentil, responses to salinity stress vary with both growth stage, salinity level, and environmental factors such as soil–water status, temperature relative humidity, and available nutrients (Lachaâl et al. 2002). Like all other legumes, lentil is more susceptible to salinity stress during seedling establishment and later growth stages (Ayoub 1977; Rahimi et al. 2009; Farooq et al. 2017). Lentil roots are highly sensitive to saline soils with limited root growth, root depth, and moisture extraction capabilities which, in turn, can badly affect the nodulation and nitrogen fixation probably by limiting the root hair growth and rhizobium infection (Rai and Singh 1999; Van Hoorn et al. 2001). Delays in seed germination, reduced seed germination percentage, reduced seed viability, and decreased seedling growth also occurs with increasing levels of salinity in lentil (AL-Quraan et al. 2014). Salinity intensifies anthocyanin pigmentation in leaves and stems in lentil resulting in necrosis of the outer margins and yellowing of the older leaves which ultimately leads to the death and withering of leaves due to excess accumulation of ions. Salinity also reduces flower production and pod setting in lentil (Van Hoorn et al. 2001). Increasing level of exchangeable sodium percentage (10–25%) under salinity stress decreased plant height, leaf area, leaf dry weight, total biomass production, chlorophyll a and b content, nitrate and nitrite reductase enzymes activities, DNA and RNA content and finally, the grain yield of lentil (Tewari and Singh 1991; Singh et al. 1993). Salinity stress also restricts lentil growth and morphology by adversely affecting various physiological and biochemical attributes such as photosynthesis (AL-Quraan et al. 2014), membrane damage (Hossain et al. 2017), ion homeostasis (Turan et al. 2007; Hossain et al. 2017), oxidative damage (Al-Quraan and Al-Omari 2017; Hossain et al. 2017), antioxidant responses (Bandeoglu et al. 2004), γ-aminobutyric acid (GABA) accumulation (Al-Quraan and Al-Omari 2017), osmolyte accumulation, and proline metabolism (Turan et al. 2007; Hossain et al. 2017) (Table 4.3). Recently, it has been reported that the excessive accumulation of betaine and choline in lentil plants might play a pivotal role in salt tolerance inducing osmotic adjustment or osmoregulation which causes a fall in water potential (Varshney and Singh 2017).

Table 4.3 Identified sources of resistance to salinity stress in lentil

Accession	Selection criteria	References
DL443, PantL406	Nitrogen fixation, grain yield	Rai et al. (1985)
ILL5845, ILL6451, ILL6788, ILL6793, ILL6796	Seed germination, biomass	Ashraf and Waheed (1990)
NEL2704	Seed germination, plant growth, grain yield	Mamo et al. (1996)
ILL6976	Biomass, soluble sugars, efficiency of potassium utilization	Asraf and Zafar (1997)
LC53, DLg103, Sehore74-3, LC50	Nodulation, seed germination, seed yield, plant height, root length, plant growth	Rai and Singh (1999)
ILL8006	Water use efficiency	Hamdi et al. (2000)
Masoor93, Mansehra89	Na/K ratio	Yasin et al. (2002)
LG128, ILL3534	Grain yield	Maher et al. (2003)
ILL5582	Proline, superoxide dismutase activity	Cicerali (2004)
DL443, Pant L406, ILL3534 LG 128, ILL6796	Grain yield and biomass	Materne and Reddy (2007)
Ustica, Pantelleria	Proline, sugar, amylase	Sidari et al. (2007)
Çağıl, Altın Toprak	Germination percentage, shoot and root length, shoot and root dry weight, and salt tolerance percentage	Kokten et al. (2010)
Nipper, PBA Flash, ILL2024	Biomass and grain yield	Siddique et al. (2013)
Siliana, Local oueslatia Nefza	Seed germination and seedling growth	Ouji et al. (2015)
Flash (CIPAL0411), Bounty CIPAL0415), Nipper (CIPAL0203)	Plant growth and yield traits	GRDC (2013)
Jordan 1	Seed germination, accumulation of reactive oxygen species, γ-aminobutyric acid (GABA) level	Al-Quraan and Al-Omari (2017)

(continued)

Table 4.3 (continued)

Accession	Selection criteria	References
Sapna, RLG258, RLG234	Dry matter yield, stress indices (TOL, SSI, STI, MP, GMP, YI, SSPI, and MSTI)	Kumawat et al. (2017)
Masoor2002, NL20-3-3, LN0188, M93, NL9775	Root and shoot length, root and shoot weight, total proteins contents, α-amylase, total soluble sugars, sodium ions (Na+), potassium ions (K+), sodium-to-potassium ratio (Na+/K+)	Aslam et al. (2017)
PDL1, PSL9, ILWL95	Seed germination, seedling growth, biomass accumulation, seedling survivability, salinity scores, root and shoot anatomy, sodium ion (Na+), chloride ion (Cl−), potassium ion (K+) concentrations, proline, antioxidant activities	Singh et al. (2017a)

4.2.8 Disease Resistance

It is anticipated that climate change is likely to exert a substantial effect on various insect pest management programs including host-plant resistance, natural plant products, bio-pesticides, natural enemies, and efficacy of synthetic chemicals. Lentil crop is often affected by several diseases and economically important diseases include Ascochyta blight (*Ascochyta lentis*), botrytis gray mold (*Botrytis cinereal* and *Botrytis fabae*), rust (*Uromyces viciae-fabae*), anthracnose (*Colletotrichum lentis*), Stemphylium blight (*Stemphylium botryosum*), powdery mildew (*Erysiphe pisi* and *Erysiphe polygoni*), and Fusarium wilt (*Fusarium oxysporum*). In general, foliar diseases including ascochyta blight, rust, anthracnose, botrytis gray mold, Stemphylium blight, and powdery mildew cause premature leaf drop, stem girdling, and produce shriveled seeds that are unmarketable. While major losses by soil-borne disease Fusarium wilt are due to leaf curling, reduced root development, discoloration of vascular tissue and stunted growth. Moderate to heavy yield losses have been reported for major diseases while some diseases have less economic impact based on the conducive environment for disease infection and spread and its duration during the cropping season (Chen et al. 2009). Ascochyta blight in Australia alone has been reported to cause an estimated loss of $16.2 million AUD in the conducive years (Murray 2012). Hence, proper management of diseases is suggested to ensure the sustainable productivity of lentil. Climatic change will have huge implications on our food production system and impact will also be seen on aggressiveness of pathogen through its development and survival rates (optimal conditions for infection), simultaneously on host reaction to pathogen attack (host specificity and mechanisms of

plant infection), which will significantly affect the impact of various diseases on crop growth and production (Elad and Pertot 2014). Among many, host-plant resistance is the most acceptable, environment–friendly, and economical control strategy to avert yield losses (Rubiales and Fondevilla 2012). In future also, to develop climate-resilient cultivars, reliance on durable, diverse, and novel host resistance will be the key to sustain crop production under various climatic pressures. Accordingly, partial to complete resistance sources have been identified within the cultivated species of lentil to various diseases and cultivars with improved resistance have been released.

Resistance sources to Ascochyta blight within the cultivated germplasm have been reported from several countries including India (Gurdip et al. 1982; Sugha et al. 1991), New Zealand (Cromey et al. 1987), Pakistan (Iqbal et al. 1990, 2010), Lebanon (Abi-Antoun et al. 1990), Syria (Erskine et al. 1996), Canada (Andrahennadi 1994), Australia (Nasir and Bretag 1998), and Ethiopia (Ahmed and Beniwal 1991). Several of these prominent sources are still being employed in the current breeding programs as a source of resistance to Ascochyta blight. Indianhead is still the major source of resistance in Australian and Canadian breeding programs (Tullu et al. 2010). Resistance for anthracnose disease was screened with 1771 accessions of which only 4 accessions from United States collection and 12 accessions from the German collection had resistance to race Ct1 (Buchwaldt et al. 2004). However, none of the accessions had resistant against most aggressive race Ct0 (Buchwaldt et al. 2004). Later, Shaikh et al. (2012) reported 23 genotypes were resistant to anthracnose in Canada. Of which, 15 genotypes were identified with Ct1 resistance, while 7 genotypes expressed Ct0 resistance and 1 genotype VIR 2633 from Georgia was found symptomless to both races. Significant yield losses associated with lentil rust disease led to evaluation of cultivated lentil germplasm for rust resistance and release of rust-resistant cultivars in countries where rust is prevalent including India (Singh et al. 1994), Bangladesh (Sarker et al. 1999a, b), Ethiopia (Negussie et al. 1998; Fikru et al. 2007), Morocco (Sakr et al. 2004), Chile (Peñaloza et al. 2007) and Pakistan (Sadiq et al. 2008). Likewise, several genotypes resistant to fusarium wilt have been identified across lentil growing countries such as India, Iraq, Ethiopia, Lebanon, Iran, Pakistan, Turkey, Syria, and Nepal as reviewed by Choudhary et al. (2013). Evaluation of lentil germplasm against botrytis gray mold resulted in moderate to high-resistant sources across botrytis gray mold predominant countries (Karki et al. 1993; Bretag and Materne 1999; Kuchuran et al. 2003; Lindbeck et al. 2008). Consequently, several cultivars were released with resistance to botrytis gray mold, such as Nipper, a selection from a cross between Indianhead (resistant) and Northfield (susceptible) was released in 2006 for cultivation in Australia by Pulse Breeding Australia (PBA) (Lindbeck et al. 2008). Efforts have been made by ICARDA in association with Bangladesh Agricultural Research Institute (BARI) to develop Stemphylium blight-resistant cultivars to boost the disease resistance and subsequent yields (Sarker et al. 1999a, b; Sarker et al. 2004). Recently, Kant et al. (2017) screened Australian lentil germplasm and found significant variation for Stemphylium blight resistance.

Nonetheless, several of the released lentil cultivars have been reported to have changed their respective reaction within a short period of commercial release. This

may be explained by the possible selective adaptation of the pathogen population and hence selection of highly aggressive isolates that can overcome the resistance with changing climate. Loss of resistance in Australian cultivars Northfield and Nipper to *A. lentis* has been speculated as a case of selective adaptation of pathogen since several aggressive isolates of the pathogen have been recovered within these cultivars (Davidson et al. 2016). Additionally, the narrow pedigree of these cultivars with paralleled pathogen evolution, threaten the sustainability of several cultivars. Subsequently, accessions from exotic germplasm particularly wild species have been tested to various diseases for resistance. This revealed some great variations for resistance within the wild species that may be transferred to the cultigen as reviewed by Singh et al. (2018). A novel primary gene pool accession ILWL 180 has been found highly resistant to recently recovered highly aggressive *A. lentis* isolates from Australia (Dadu et al. 2017). Successful introgression of resistance to anthracnose from wild lentil to the cultivar has been reported from Canada (Fiala et al. 2009; Vail et al. 2012).

Viruses are known to affect lentils and at least 30 different species of the virus have been reported to naturally infect lentil. Among them, the most important viruses that can cause significant yield losses includes bean leafroll virus, bean yellow mosaic virus, beet western yellow virus, cucumber mosaic virus, faba bean necrotic yellow virus, pea enation mosaic virus-1, pea seed-borne mosaic virus, and pea streak virus (Kumari et al. 2009). They cause none or a minimum of 3% to a maximum of 61% yield losses in lentil depending on the conditions available during the cropping season (Kumari et al. 2009). Several sources of resistance and cultivars with resistance to different viruses have been identified and released (Makkouk and Kumari 1990; Kumari and Makkouk 1995; Makkouk et al. 2001; Latham and Jones 2001; Rana et al. 2016).

4.2.9 Insect Resistance

Effects of climate change on insect pests is of greater importance as the insects are involved in many biotic interactions such as plants, natural enemies, pollinators, and other organisms, which are the key players of the ecological functions (Boullis et al. 2015). Environmental effect will trigger diversified insect populations, changed geographical distribution, insect–plant interactions, activities and abundance of natural enemies, emergence of new biotypes, and crop losses associated with insect pests. Changes in geographical distribution, diversity, and abundance of insect pests will also be influenced by changes in the cropping pattern influenced by climate change. Major insect pests may move to temperate regions, leading to greater damage in crops. Geographical distribution of many tropical and subtropical insect pests will extend, along with shifts in production areas of their host plants (Gonzalez and Bell 2013; Sharma 2014). Among nearly 36 insect pests infecting lentil crop, aphids (*Aphis craccivora* and *Acyrthosiphon pisum*), leaf weevils (*Sitona* spp.), lygus bugs, (*Lyguss* spp.) and cutworm (*Agrotis ipsilon*) are of economic significance, some

minor field pests such as thrips (*Thrips*, *Kakothrips*, and *Frankiniella*), bud weevils (*Apionarrogans*), pea moth, (*Cydia nigricana*), pod borers (*Helicoverpa armigera* and *Heliothis* spp.), lima bean pod borer (*Etiella zinckenella*), root aphids (*Smynthurodes betae*), and leaf miners (*Liriomyza* spp. and *Phytomyza* spp.) infest the crop (Stevenson et al. 2007). These minor pests may become a significance in future with changing climatic conditions. Stevenson et al. (2007) have summarized locations and regions around the world which specify the status of various insect pests, such as aphids and lima bean pod borer are major lentil pests in India, lima bean pod borer and leaf weevils in Turkey, whereas aphids, thrips, and leaf weevils are most prevalent in central Spain.

Aphids cause significant loss to the lentil as they feed directly on crop and act as a vector in transmitting plant viruses. Hossain et al. (2017) reported relative abundance of lentil aphids at different sowing dates during the winter season and its effect on lentil yield. Aphid population and infestation increased with the delayed sowing. The crop sown in November received less aphid infestation and consequently produced higher yield than the December-sown crop. Spotted aphid, and cowpea aphid population had negative impact of higher temperature. Sharma et al. (1995) also suggested that aphid population was sensitive to changing temperature and relative humidity. High humidity, moderate temperature, and low rainfall are conducive for growth and multiplication of aphids. In long run with changing patterns of weather and host–pest interactions, host resistance and effective biological control could be the best strategy instead of heavy reliance on chemical control. Few tolerant genotypes (2 and 23) have been reported based on 2 and 3 years of screening work, respectively, and were grouped as five distinctive groups for tolerance based on pedigree analysis (Kumari et al. 2007).

Leaf weevils could be another major threat with changing climate and can cause huge economic losses when abiotic stresses affect seedling growth along with weevil attack. As larvae feed on root nodules which leads to failure of atmospheric nitrogen fixation. However, climate change adaptation strategies like early sowing would be beneficial to escape terminal drought stress, studies have shown that nodule damage by larvae in early sown crops was higher than late sown lentil crop (Weigand et al. 1992; Stevenson et al. 2007). Future lentil cultivars with chemical defenses against adult weevil could be one of the important trait s to consider. So far, no genotypes have been found to be resistant to weevil infection in lentil germplasm (Erskine et al. 1994). Genetic engineering might help to transfer genes found in red clover which leads to expression of formononetin and related metabolites offering chemical defense against adult weevil. Pod borer is another serious pest on many crops, however, not a major threat to lentil. Pod borer incidence had significantly negative correlation with low temperature and rainfall. Though rising temperature might change the population dynamics, host resistance, and plant traits which act as physical barriers and transgenics for expression of defense chemicals are direct measures, and in general, resilient lentil cultivars for other biotic and abiotic stresses will indirectly equip lentil crop to sustain yields through adaption to changing insect pest infestations.

4.2.10 Nutrient and Water Use Efficiency (NUE and WUE)

World agricultural soils are deficient in one or more of the essential nutrients to support healthy and productive plant growth. Overall nutrient use efficiency in the plant is a function of capacity of the soil to supply adequate levels of nutrients, and the ability of the plant to acquire, transport in roots and shoot and to remobilize to other parts of the plant. Inter and intraspecific variation for plant growth and mineral nutrient use efficiency are known to be under genetic and physiological control and are modified by plant interactions with environmental variables. Identification of plant traits for nutrient absorption, transport, utilization, and mobilization in plant cultivars should greatly enhance nutrient use efficiency. Overall nutrient usage in the plants is governed by the flux of ions from the soil to the root surface and by the influx of ions into roots followed by their transport to the shoots and remobilization to plant organs. The root morphological traits such as length, thickness, surface area, and volume have profound effect on the plant's ability to acquire and absorb nutrients from the soil (Barber, 1995). Plant environment interaction (solar radiation, rainfall, and temperature) and their response to diseases, insects, and root microbes have a great influence on nutrient use efficiency of plants and their subsequent yields (Arkin and Taylor 1981; Fageria 1992; Barber 1995; Marschner 1995; Baligar 1997; Fageria and Baligar 1997).

Winter legumes require a neutral to alkaline soil pH for their optimum growth and yield. Root growth of legumes is particularly severely restricted in acid soils. Lentil is most sensitive to acidic pH followed by chickpea and field pea. Minor variations in soil pH drastically affect the availability of nutrients for crop growth and productivity. Sutaria et al. (2010) found that the extensive root system with balanced fertilization and organic matter in adequate amount assisted in the efficient absorption and utilization of other nutrients thereby optimizing nutrient use efficiency in lentil. Organic nutrients enhance macro and micronutrients availability in the root zone which improved nutrient use efficiency by creating microenvironment for root growth and number of nodules (Singh et al. 2001).

Water use efficiency (WUE) measures the water quality used by the crop during its growth period to produce a unit quantity of the crop yield. Therefore, the lower the water requirement per unit of crop yield, the higher the WUE. With climate change temperatures will rise and an increase in extremes of rainfall or drought will be evident in many areas where lentil is grown. Water availability and day length influence vital physiological processes and determine the input use efficiency of plants. Light and temperature affecting transpiration and dry matter production will further have implications on WUE according to weather changes. In short-season Mediterranean environments, species with early flowering, podding, and seed set have higher yields and WUE than those with later flowering, podding, and seed set (Siddique et al. 2001). When the yields and water use of chickpea and lentil were compared over 12 growing seasons at Tel Hadya in Syria, the WUE for grain yield varied from 1.9 to 5.5 (kg/ha/mm in chickpea and from 2.1 to 5.2 kg/ha/mm, respectively, depending on growing season.

Another important trait that increases WUE is partial stomatal closure, which generally reduces water loss more than it reduces CO_2 uptake, thus increasing dry matter accumulation per unit of water transpired. However, the factors that alter transpiration will have a direct impact on mass flow of water to the root surface, and with it, alter the mechanism of ion transport and possibly nutrient uptake also.

Farmers in Iran usually sow lentil in early spring (March) and harvest around July. Under these circumstances, the crop encounters low winter rainfall, low WUE, and often temperature stress and terminal drought during reproductive stages (Azimzadeh 2010). Recently, some farmers tried a dormant seeding management (DS) in lentil. In this management system, it is assumed that germination would take place once the initial soil moisture in the top-soil layer filled to the volumetric transpirable soil water. While the temperature of top-soil layer is above the base of 2 °C. Furthermore, the crop germination is stopped due to lower temperatures than base temperature of lentil. This method might increase grain yield, WUE, and duration of lentil growing season. The change in the management practice could be effective for saving water for the lentil and better exploiting from precipitations over growing season. The change in the sowing date management of lentil would be even more effective for higher grain yield and WUE when early maturing cultivar is selected.

4.3 Genetic Resources of CS Genes

Lentil is a self-pollinating true diploid ($2n = 2x = 14$) annual plant which belongs to tribe *Vicieae*, the genus *Lens* of family Fabaceae (Leguminosae) and has 4 Gbp genome size (Arumuganathan and Earle 1991). Based on seed size, lentil encompasses two groups—microsperma (small seeded of 2–6 mm size range) and macrosperma (large seeded of 6–9 mm size range). Cultivated lentil has been presumed to be originated from close wild species *L. orientalis* (Zohary 1972), cultivated and *L. orientalis* genotypes show high cross compatibility and fertile hybrids. Lentil is believed to be originated in the Near East around the Fertile Crescent which was further domesticated in Southern Turkey following Nile, Europe, Greece, and further Asia (Renfrew 1969; Ladizinsky 1979; Cubero 1984). Recent classification of genus *Lens* has classified it into four gene pools (primary, secondary, tertiary and quaternary) and have changed sub-species status of *orientalis*, *odomensis*, and *tomentosus* from earlier classification (Ferguson et al. 2000) to species level. Primary gene pool has one cultivated species (*L. culinaris*) and remaining six wild species belong to four genes pool such as *L. orientalis* and *L. tomentosus* (primary); secondary gene pool has *L. lamotte and L. odemensis; tertiary gene pool comprises L. ervoides* and quaternary gene pool has *L. nigricans* (Wong et al. 2015). Wild species from primary and secondary gene pools are easily crossable with cultivated lentil, unlike with the wild species from the remaining two gene pools (Gupta and Sharma 2007; Singh et al. 2013b).

For climate-resilient lentil cultivars combined resistance to major biotic stresses and/or abiotic stresses will help to sustain lentil yield in variable climate. Without

any doubt, wild crop relatives offer an opportunity to be utilized for untapped rich source of desirable genes such as resistance to biotic and abiotic stresses Table 4.4. Improved root traits for better tolerance of stresses especially water and availability of nutrient for healthy crop growth will be key traits to target and wild lentils could be most appropriate ones to be explored for such traits. The research so far has shown that wild lentil species possess huge variation for various agro-morphological traits along with biotic and abiotic stresses, which is quite understandable as these untapped sources are preserved in nature and have not lost these genes during the process of domestication which emphasized more on selection for few important genes for high yields. Traditional and molecular approaches for gene pyramiding might be able to bring such traits in common genetic backgrounds to have climate-resilient lentil cultivars with a broad genetic base. Among few attempts to evaluate wild lentil accessions for useful climate-smart agro-morphological traits, *L. orientalis* accessions has some desirable traits such as early flowering and maturity (Hamdi et al. 1991; Gupta and Sharma 2007), higher leaves/plant, peduncles/plant, pods/plant, seeds/plant and leaf area (Ferguson and Robertson 1999) when cultivated and few more wild species were evaluated for various morphological, phenological and yield related characters. Another study revealed useful traits after evaluation of 405 wild lentil accessions from 4 gene pools which were collected from ICARDA gene bank (Singh et al. 2014). Among various abiotic stresses, cold stress could be detrimental and can limit lentil production due to injury to vegetative tissues with further damage to floral parts leading to flower and pod abortion (Eujayl et al. 1999 and Singh et al. 2018). *L. orientalis* accessions originating from high elevation areas *revealed* greater tolerance to cold stress than in the cultivated lentil (Hamdi et al. 1996). Finding diseases resistance sources is one of the key to develop disease-resistant cultivars which will be able to withstand new disease pressures, as these sources of resistance could be new and can provide long-term resistance to lentil cultivars. Among many diseases, fusarium wild is quite devastating and few researchers (Bayaa et al. 1995; Nasir 1998), found seeding and/or adult stage vascular wilt resistance from *L. orientalis*, *L. nigricans*, and *L. ervoides* accessions. ICARDA researchers found a good level of resistance from *L. orientalis* and *L. ervoides* (year 2000–2007) for Fusarium wilt and further evaluated them for agronomic traits at various locations to improve breeding strategies to develop better and well-adapted breeding lines. The first report of Ascochyta blight-resistant accessions from wild sources was from Bayaa et al. (1994) who found a fairly large number of accessions to be resistant from *L. orientalis*, *L. odemensis*, *L. nigricans* and *L. ervoides.* Ahmad et al. (1997a) identified sources of resistance to the major diseases of lentil, viz., rust, vascular wilt and Ascochyta blight in the wild relatives of lentil.

Hybridization efforts to transfer these useful CS traits from wilds to cultivated background to generate a wide spectrum of variability has not seen groundbreaking efforts. Among few attempts of crossing cultivated x wild lentil species from primary and secondary gene pools have most successful reports which include to greater extent *L. orientalis* accessions followed by *L. odomensis* to be readily crossable with cultivated lentil (Ladizinsky 1979; Ladizinsky et al. 1984; Muehlbauer et al. 1989; Vandenberg and Slinkard 1989; Ladizinsky and Abbo 1993; Hamdi and

Table 4.4 Useful wild germplasm for introgression of CS traits in cultivated lentil

Trait	Wild resource	References
Anthracnose resistance	*L. ervoides*, *L. lamottei*, *L. nigricans*	Tullu et al. (2006)
Ascochyta blight resistance	*L. ervoides*, *L. orientalis*, *L. odemensis* *L. nigricans*, *L. montbretii*	Bayaa et al. (1994) Tullu et al. (2006, 2010) Dadu et al. (2016, 2017)
Fusarium wilt resistance	*L. orientalis*, *L. ervoides*	Bayaa et al. (1995), Gupta and Sharma (2007)
Powdery mildew resistance	*L. orientalis*, *L. nigricans*	Gupta and Sharma (2007)
Rust resistance	*L. orientalis*, *L. ervoides*, *L. nigricans*, *L. odemensis*	Gupta and Sharma (2007)
Drought tolerance	*L. odemensis*, *L. ervoides*, *L. nigricans*	Hamdi and Erskine (1996), Gupta and Sharma (2007)
Cold tolerance	*L. orientalis*	Hamdi et al. (1996)
Yield attributes	*L. orientalis*	Gupta and Sharma (2007)
Resistance to orobanche	*L. ervoides*, *L. odemensis*, *L. orientalis*	Ferna' Ndez-Aparicio et al. (2009)
Resistance to sitona weevils	*L. odemensis*, *L. ervoides*, *L. nigricans*, *L. orientalis*	El-Bouhssini et al. (2008)

Erskine 1994; Fratini et al. 2004; Gupta and Sharma 2007; Kumari et al. 2018). Wide hybridization between cultivated and wild lentils does not always lead to successful crosses due to species, and genotypic level differences within species. Genetically distant remaining species from secondary, tertiary, and quaternary gene pools are not easily crossable with cultivated lentil and harbor genes for many climate-resilient traits. The fertilization barriers exist due to asynchronous flowering and mainly due to hybrid embryo abortion (Abbo and Ladizinsky 1991, 1994; Ahmad et al. 1995; Gulati et al. 2001; Gupta and Sharma 2005; Fratini and Ruiz 2006; Fiala 2006). Even some species of primary/secondary gene pool such as *L. tomentosis* (Ladizinsky 1999) has shown crossability barriers due to embryo abortion and hybrid fertility. To break these barriers, few remediations are researched and have had successful results for the inclusion of genotypes of these wild species into cultivated lentil gene base. Some examples include application of GA_3 growth hormone and embryo/ovule rescue techniques and understanding similarity of species for pollen and pistil morphology to overcome postfertilization barrier (Cohen et al. 1984; Ladizinsky et al. 1988; Ladizinsky 1993; Ahmad et al. 1995; Gupta and Sharma 2005; Fratini et al. 2006). Dadu et al. (2016) reported the success of approximately 100 crosses with 100 ppm GA_3 application immediately after pollination from a cross between AB resistant accession from *L. orientalis* and cultivated lentil.

The crossability potential and techniques to overcome some existing pre–postfertilization barriers suggest that these wild accessions with CS traits can be exploited

for breeding climate-resilient cultivars to sustain lentil production under climatic variability.

Successful introgression through conventional or modified techniques does not reflect much for breeding programs unless filial generations are advanced and evaluated at field level. There are a handful of reports which evaluated fixed interspecific lines for various CS traits.

Among few attempts of interspecific hybridization, Gupta and Sharma (2007) developed interspecific hybrids and segregating generations (F_2, BC_1) from cultivated and *L. orientalis* and *L. odemensis* crosses and observed greater genetic variability with numerous transgressive segregants for various agro-morphological traits. Field evaluation of 76 advanced breeding lines (Gupta and Sharma 2007) and 20 intraspecific fixed lines for various agro-morphological traits revealed superiority of few lines for grain yield and related traits (Kumari et al. 2018). Anthracnose resistance genes identified from *L. ervoides* (Tullu et al. 2006) were introgressed into cultivated lentils using embryo rescue technique (Fiala et al. 2009). $F_{7:8}$ recombinant inbred lines exhibited resistance and validated successful introgression of anthracnose resistance genes from *L. ervoides* (Fiala et al. 2009).

Singh et al. (2013b) successfully crossed cultivated lentils with accessions from various gene pools *(L. orientalis*, *odemensis*, *lamottei*, and *ervoides*) and studied F_2 generations for yield and related traits indicating transgressive segregants with a potential for their inclusion in CS breeding program. Some progress has been made in introgression of alien genes for resistance to Ascochyta blight, anthracnose and cold in cultivated lentil (Hamdi et al. 1996; Ye et al. 2002; Fiala 2006; Dadu et al. 2017, 2018). In Canada, anthracnose resistance was transferred between different gene pools from *L. ervoides* to cultivated lentil and 150 recombinant inbred lines were developed. The same technique can be used to develop hybrids between cultivated lentil and *L. lamottei* (Fiala 2006). Gorim and Vandenberg (2017a) studies root and shoot traits of wild and cultivated lentils for drought tolerance and revealed their genetic diversity for drought tolerance. Segregation generations (F_3, F_4, and F_5) from two cultivated lentil and *L. orientalis* and *L. ervoides* crosses revealed substantial variation for most of the agronomic traits, whereas, F_5 recombinant inbred lines of one cross had resistance to wilt (Singh et al. 2017b).

4.4 Classical Mapping and Traditional Breeding for CS Traits

For the association of markers with different traits of interest, we need to develop biparental or multiparental mapping populations for classical mapping. The biparental mapping populations may be F_2, backcross, double haploid (DH), and recombinant inbred lines (RIL). In lentil, some efforts have been made by various labs around (USA, Australia, India, and Morocco) in the development of biparental mapping populations for desired traits and are used in marker trait association studies

Table 4.5 Recombinant inbred lines mapping populations developed for different traits

Trait	Cross	Population size	Organization
Drought	ILL7946 × ILL7979	174	ICARDA
Cold	ILL4605 × ILL10657	153	ICARDA
Earliness	ILL7115 × ILL8009	150	ICARDA
Rust	ILL5888 × ILL6002	152	ICARDA
Fusarium wilt	ILL213 × ILL5883, Precoz × Idlib 2	150	ICARDA
Zinc Content	ILL5722 × ILL9888	177	ICARDA
	ILL9888 × ILL5480	149	ICARDA
Iron content	ILL9932 × ILL9951	193	ICARDA
Early growth vigor	DPL15 × ILL7663	160	IIPR, India
Root traits	IPL98/193 × EC208362	160	IIPR, India
Earliness	Precoz × L4603	160	IIPR, India
Earliness	ILL10829 × ILWL30	180	NBPGR, India
Pod number and earliness	ILL8006 × ILWL62	185	NBPGR, India

Source Adapted from Kumar et al. (2015); *ICARDA* International Center for Agricultural Research in the Dry Areas, Morocco; *NBPGR* National Bureau of Plant Genetic Resources, New Delhi, India

(Table 4.5). RIL populations were developed from the crosses developed between contrasting parents through single seed descent (SSD) method. The Indian Institute of Pulses Research (IIPR) has recently developed a RIL population from a cross between ILL6002 and ILL7663 to identify and map early growth vigor genes. Further, the identification of markers linked to the genes or quantitative trait loci (QTLs) governing these traits will help in the development of genotype having high biomass at an early stage. Furthermore, the National Bureau of Plant Genetic Resources has also developed wide cross populations against pod number and earliness and validated these traits under multilocation testing under varied ecological conditions (Singh et al. 2017b). The first genetic map in lentil (linkage analysis) began during 1984 (Zamir and Ladizinsky 1984), the first map comprising DNA based markers was developed by Havey and Muehlbauer (1989). Subsequent maps were developed by several other workers in lentils (Table 4.6).

The classical manipulations refer to the transfer of genes through conventional hybridization. Most of the cultivars developed worldwide are only through intraspecific hybridization followed by pure line selection (Kumar et al. 2004b). The genetic manipulation of lentil is primarily based on the exploitation of two broad categories of cultivated lentils, i.e., macrosperma and microsperma through hybridization of desirable genes from one another (Chahota et al. 1996, 1997; Lal et al. 2000). The hybridization criteria are to introgress elite traits from macrosperma (erect growth habit and tolerance against prevailing biotic and abiotic stresses) and from microsperma (higher number of branches/plant, higher number of seeds/plant and higher seed yield/plant), which are considered important CS traits to address one or the

Table 4.6 List of various maps developed in lentil populations

Cross	Type and size (in parenthesis) of population	Type of marker mapped	Mapped length (cM) and no. of loci (in parenthesis)	References
L. culinaris × *L. orientalis*	RIL (14–180)	Isozyme and four morphological markers	– (20)	Tahir and Muehlbauer (1994)
L. culinaris × *L. orientalis*	F_2	Isozymes	– (10)	Zamir and Ladizinsky (1984)
L. culinaris × *L. ervoides*	F_3 (107) F_3 (22–56)	Isozymes 258(18)	258 (18)	Tadmor et al. (1987)
L. culinaris × *L. orientalis*	F_2 (113)	RAPD, ISSR, AFLP, SSR, CAPS, SRAPS, and morphological markers	2234 (200)	Duran et al. (2004), Fratini et al. (2004), de la Puente et al. (2013)
ILL5588 × L692-16-1 (s)	RIL (86)	SSR, AFLP	751 (283)	Hamwieh et al. (2005)
ILL5588 × ILL7537	F_2 (150)	RAPD, ISSR, and RGA	784 (114)	Rubeena et al. (2003a)
Eston × PI320937	RIL (94)	AFLP, RAPD, and SSR	1868 (207)	Tullu et al. (2008)
Precoz × WA8649041	RIL (94)	AFLP, ISSR, RAPD, and morphological markers	1396 (166)	Tanyolac et al. (2010)
ILL6002 × ILL5888	RIL (206)	SSR, RAPD, SRAP, and morphological markers	1565 (139)	Saha et al. (2013)
ILL5722 × ILL5588	RIL (94)	RAPD, ISSR, ITAP, and SSR	1392 (211)	Gupta et al. (2012a)
L830 × ILWL77	F_2 (114)	SSR, ISSR, and RAPD	3843 (199)	Gupta et al. (2012b)
CDC Robin × 964a-46	RIL (139)	SNP, SSR, and seed color genes	697 (561)	Sharpe et al. (2013a), Fedoruk et al. (2013)
Cassab × ILL2024	RIL (126)	SSR and SNP	1178 (318)	Kaur et al. (2014)
PI320937 × Eston	RIL (96)	AFLP, SSR, and SNP	840 (194)	Sever et al. (2014)
Precoz × WA8649041	RIL (101)	SNP	540 (519)	Temel et al. (2014)
ILL8006 × CDC Milestone	–	AFLP, SSR, and SNP	497 (149)	Aldemir et al. (2014)

(continued)

Table 4.6 (continued)

Cross	Type and size (in parenthesis) of population	Type of marker mapped	Mapped length (cM) and no. of loci (in parenthesis)	References
Precoz × L830	RIL (126)	SSR	1184 (219)	Verma et al. (2015)
Indianhead × Northfield; Indianhead × Digger; Northfield × Digger	RILs (117, 112, 114)	SNP	2429.6 (689)	Sudheesh et al. (2016)
L01-827A (*L. ervoides*) × IG 72815 (*L. ervoides*)	RIL (94)	SNP	740.9 (543)	Bhadauria et al. (2017)
ILL8006 × CDC Milestone	RIL (118)	SNP	497.1 (4177)	Aldemir et al. (2017)

Source Adapted from Kumar et al. (2015); Markers: *AFLP* Amplified fragment length polymorphism, *RAPD* Random amplified polymorphic DNA, *ISSR* Inter simple sequence repeat, *SSR* Simple sequence repeat, *CAPS* Cleaved amplified polymorphic sequences, *SRAPS* Sequence-related amplified polymorphism, *RGA* Resistance gene analog, *ITAP* Intron targeted amplified polymorphism, *SNP* Single nucleotide polymorphism

other stress. In lentil genetic improvement program, much has been reported about the creation of large amount of variation following hybridization of the microsperma and macrosperma lentils primarily for higher yields. Chahota et al. (2007) reported transgressive segregants for seed yield and other important agro-morphological traits from 77% of microsperma × macrosperma crosses. The prime advantage of such hybridization is that two classes are easily crossable, but this hybridization provides limited variability for further improvement (Muench et al. 1991; Ferguson 2000; Duran et al. 2004). In many crops, the wild relatives still possess useful variation and source of the desirable trait that no longer exist in these cultivated counterparts.

4.5 Diversity Analysis

Since the middle of twentieth century, breeders have been successful in improving the performance of the germplasm with the higher yield potential, adaptation to mechanization, and new agricultural practices (Perez-de-Castro et al. 2012). However, breeding cultivars for higher yield potential gradually prompted replacement of traits useful to future climates in the cultivated crop community (Grassini et al. 2013). Hence, continuous development of new CS cultivars that can withstand and perform against the environmental changes without compromising on the genetic gain is needed. However, the genetic gain within a progeny is always dependent on the amount of variation existing between the parents that are selected for hybridization (Roy et al. 2013). Therefore, an estimate of genetic diversity for a given trait is sought to allow selection of better parents from the existing plant genetic resources.

4.5.1 Phenotype-Based Diversity Analysis

Visually accessible morphological traits are used to estimate the phenotypic frequencies within and between the populations of lentil (Singh et al. 2014). Traits that were routinely phenotyped may be classified into three major categories such as qualitative, phenological, and yield related. Qualitative traits included growth habit, leaf pubescence, leaflet size, stem pigmentation, flower petal color, tendrils, pod indehiscence, cotyledon color, seed coat color, seed coat pattern, and seed shape. Traits such as time to emergence, days to flowering, days to 50% flowering, and days to maturity were recorded to understand the variation for phenology within the lentil germplasm. While yield-related traits such as plant height, number of branches/plant, number of flowers/peduncle, number of nodes/plant, number of pods/plant, number of seeds/plant, 100 seed weight, biomass/plant, and yield/plant were used to estimate the genetic divergence for yield potential of the lentil germplasm. The first noted assessment of genetic variability for lentil was made by Barulina (1930), who reported variations between accessions for various morphological characters. Since then, several authors made useful contributions to unravel the genetic diversity through agro-morphological traits (Hoffman et al. 1988; Lázaro et al. 2001; Roy et al. 2013; Choudhary et al. 2017). Variations are evident for almost all the morphological traits within the species and among different species of lentil and thus allow for an effective selection. Diversity assessments of 405 accessions collected from 7 lentil species revealed remarkable variations for traits such as leaf pubescence, leaflet size, tendril length, and seed coat pattern both within and between the species (Singh et al. 2014).

Lentil germplasm also exhibited quite a variation for various phenological traits. Considerable variation was demonstrated within a global collection of 1370 accessions for days to flower and maturity (Erskine et al. 1989). It was also observed that the accessions varied with the changes in temperature and photoperiod for the time taken to flower (Erskine et al. 1990; Erskine et al. 1994; Bicer and Sakar 2008). Understandably, maximum number of studies were undertaken to decipher the genetic divergence for yield and yield contributing traits (Erskine and Choudhary 1986; Tullu et al. 2001; Zaccardelli et al. 2012; GAAD et al. 2018). Significant variation has been reported for seed yield and traits such as number of pods/plant, number of seeds/plant, and biomass/plant that are said to have a positive relationship with yield. Alternatively, significant and positive correlations between seed yield and traits including biological yield/plant, plant height, number of pods/plant, and number of seeds/pod have been reported (Bicer and Sakar, 2008; Zaccardelli et al. 2012). This implies that a greater potential still exists within lentil germplasm to mine and select for yield and yield contributing traits.

Lentil is confounded with several production constraints including biotic and abiotic stresses. Diseases that cause substantial yield lose. Interestingly, several sources of resistance to each disease have been detected within the cultivated, landraces, and wild species of lentil as reviewed by Chen et al. (2009). Similarly, significant differences within the germplasm were reported for boron toxicity, a problem in arid areas

of West Asia (Yau and Erskine 2000; Hobson et al. 2006). In addition, the evidence of ample genetic diversity within the germplasm for various minerals, mainly, iron (Fe) and Zinc (Zn) concentrations demonstrated a likely strategy to address the problem of micronutrient deficiencies usually associated with cultivars of lentil (Karaköy et al. 2012; Kumar et al. 2014a, 2018c; Shrestha et al. 2018).

4.5.2 Genotype-Based Diversity Analysis, Molecular Markers Applied

Although morphological characterization made useful contributions to the genetic diversity of lentil, these traits are often influenced by environment and display phenotypic plasticity (Bicer and Sakar 2008; Mondini et al. 2009; Govindaraj et al. 2015). Alternatively, biochemical and molecular markers offer numerous advantages over traditional morphological traits (Govindaraj et al. 2015). Biochemical markers involve analysis of seed storage proteins and isozymes (allele variants of an enzyme), and provide genotypic frequencies within and among the populations at functional gene level. Polymorphisms within number and molecular weight of polypeptides revealed through SDS-PAGE of seed storage proteins showed evidence for a greater genetic variation within the lentil germplasm (de la Rosa and Jouve 1992; Echeverrigaray et al. 1998; Piergiovanni and Taranto 2005; Zaccardelli et al. 2012). Additionally, proteomic technology using two-dimensional electrophoresis aided to analyze substantially higher number of proteins and demonstrated useful variations within lentil landraces of Italy (Scippa et al. 2008, 2010; Ialicicco et al. 2012). Isozyme and allozyme markers highlighted the differences within the functions of an enzyme between individuals and are routinely used to detect the differences within the lentil germplasm prior to the introduction of molecular markers (Zamir and Ladizinsky 1984; Hoffman et al. 1986; Erskine and Muehlbauer 1991; Ferguson et al. 1998b; Sultana and Ghafoor 2008).

The introduction and gradual evolution of molecular markers along with the shortcomings associated with morphological and biochemical markers observed the integration of various molecular markers to analyze and characterize the lentil germplasm. Molecular markers differentiate individuals by highlighting the differences within the genome caused due to either by an insertion/deletion/translocation/duplication/point mutation, etc. In addition, they are highly stable and detectable in all the plant tissues regardless of growth and development. Significant amount of variation has been reported within lentil germplasm by using various types of molecular markers such as restriction-hybridization-based restriction fragment length polymorphisms (RFLPs) (Havey and Muehlbauer 1989; Muench et al. 1991) PCR-based random amplified polymorphic DNAs (RAPDs) (Abo-Elwafa et al. 1995; Ford et al. 1997; Ferguson et al. 1998a; Sonnante and Pignone 2001; Sultana and Ghafoor 2008), and amplified fragment polymorphisms (AFLPs) (Sharma et al. 1996; Alghamdi et al. 2013; Idrissi et al. 2015b), microsatel-

lite variable number tandem repeats (VNTRs) (Závodná et al. 2000) and inter-simple sequence repeats (ISSRs) (Sonnante and Pignone 2001; de la Vega and Durán 2004; Sonnante and Pignone 2007; Scippa et al. 2008; Fikiru et al. 2007; Toklu et al. 2009; El-Nahas et al. 2011; Seyedimoradi and Talebi 2014; Datta et al. 2016), genomic SSRs (Jin et al. 2008; Hamwieh et al. 2009; Babayeva et al. 2009; Zaccardelli et al. 2012; Kumar et al. 2014b; Verma et al. 2014; Idrissi et al. 2015a; Roy et al. 2015; Koul et al. 2017) and expressed sequence tag (EST)-derived simple sequence repeats (SSRs) (Dikshit et al. 2015a; Kumar et al. 2018a). Utilizing comparative genomics, cross-genera SSR markers derived from ESTs sequences of *Medicago truncatula*, *Pisum sativum* and *Triolium pratense* have been used to characterize lentil germplasm (Reddy et al. 2010; Alo et al. 2011). More recently, the highly abundant genome-wide and gene-based single-nucleotide polymorphisms (SNPs) have been used to assess the genetic diversity of lentil (Lombardi et al. 2014; Basheer-Salimia et al. 2015). Additionally, an exome capture array targeting the protein-coding genes was developed and applied in lentil to evaluate the variation within and among the lentil species (Ogutcen et al. 2018).

4.5.3 Relationship with Wild Relatives

An understanding of the intra- and interspecies relationships in the genus and multiplicity of the taxa is needed for the improvement and climate-resilient lentil cultivars. This may be because all taxa are morphologically similar and differ only for a few (Galasso 2003). Thereafter, several studies attempted to revise the classification and thereby relationships among the species by using biochemical and molecular methods. These included isozymes (Hoffman et al. 1986; de la Rosa and Jouve 1992; Ferguson and Robertson 1996), SDS-PAGE (Ahmad and McNeil 1996; Ahmad et al. 1997b; Zimniak-Przybylska et al. 2001), chloroplast DNA (Muench et al. 1991; Mayer and Soltis 1994), RFLP (Havey and Muehlbauer 1989), RAPD (Abo-Elwafa et al. 1995; Sharma et al. 1995; Ahmad and McNeil 1996; de la Vega and Durán 2004), AFLP (Sharma et al. 1996), FISH karyotype (Galasso, 2003), ISSR (de la Vega and Durán 2004) and ITS (Mayer and Bagga 2002; Sonnante et al. 2003) and genomic and EST-SSRs (Alo et al. 2011; Dikshit et al. 2015b) and genome-wide SNPs (Wong et al. 2015). While the outcomes of all the studies did not agree with each other, the most agreed facts of all these studies has been that (i) *L. orientalis* is the progenitor of the cultivated lentil; (ii) *L. nigricans* is the distant relative as supported by the crossability experiments (Ladizinsky et al. 1984; Fiala et al. 2009); (iii) the relationships among the remaining taxa need reassessment. Recently, classification and four gene pool categories (Wong et al. 2015) were validated through an exome capture array method, which represents the coding fraction of the genome (Ogutcen et al. 2018). The results also supported that *Lens nigricans* as a distant relative to the cultivated species as it showed only a 70% alignment similarity with the exome of the cultivated species.

4.5.4 Relationship with Geographical Distribution

Lentil is one of the oldest domesticated crops (Ladizinsky 1979). The oldest remains of lentil found in Greece and Syria dated back to 11,000 BC and 8500–7500 BC, respectively (Erskine 1997). Ferguson et al. (1998a) mapped the highest genetic diversity for wild progenitor *L orientalis* within southeast Turkey and northwest Syria using the PCR-based markers such as RAPDs. Similarly, southern Syria, coastal border region between Syria and Turkey and west Turkey are suggested to be the centers for maximum variation and unique diversity for taxa *Lens odemensis*, *L ervoides*, and *L nigricans*, respectively.

Interestingly, lentil adapted well to the conditions in South Asia region and subsequently emerged as a major contributor to world's lentil production (Erskine et al. 1998). While lentil cultivation in countries like Canada and Australia has been relatively new but took over Indian subcontinent as major producers of lentil with the help of high-yielding cultivars supplemented by mechanization and advanced agricultural management practices. Genetic distinctness between the South Asian landraces and other region landraces were made evident through morphological, phenological, biochemical, and molecular markers. Based on the morphological variation, lentil landrace collection was divided into three major regional groups such as levantine group (Egypt, Jordon, Lebanon, and Syria), northern group (Greece, Iran, Turkey, and USSR), and Indian group, which included Indian subcontinent and Ethiopian collections (Erskine et al. 1989). However, there was a clear differentiation between Indian and Ethiopian collections at gene level as diagnosed by RAPD marker analysis (Ferguson et al. 1998b). Additionally, accessions from Afghanistan were clustered along with South Asian group and thus conclude that lentil was introduced into Indian subcontinent from West Asia through Afghanistan. A similar observation of germplasm relatedness between Afghanistan and South Asian was also made by Khazaei et al. (2016) at gene level using SNP markers. Nevertheless, the diversity within the South Asian group was predicted as low and is affected by limited introductions (Erskine et al. 1998; Lombardi et al. 2014).

While the landraces collected from the Mediterranean region, especially from countries Turkey and Greece demonstrated higher diversity and suggest the presence of substantial level of genetic variation within the germplasm (Lombardi et al. 2014). Several other authors also reported higher genetic diversity nature of Mediterranean region compared to Asia and USA (Erskine et al. 1989; Piergiovanni and Taranto 2003; Toklu et al. 2009). Alternatively, similarities were found among the collections from Mediterranean, North Africa, and Chile (Ferguson et al. 1998b; Lombardi et al. 2014; Khazaei et al. 2016). Northern temperate group was recently proposed based on the differences in agro-ecological regions around the world where lentil is grown (Khazaei et al. 2016). Assessment of the variation within the northern temperate region, especially of Canada, currently top producer of lentil, showed a narrow genetic variability among the breeding lines (Khazaei et al. 2016). A similar trend was observed within the Australian lentil germplasm and is attributable to

the limited introductions and also selection pressure for higher yield and specific adaptations such as disease resistance (Ford et al. 1997; Lombardi et al. 2014).

4.5.5 Extent of Genetic Diversity

In the process of domestication, lentil has been understood to have lost approximately 40% of genetic diversity (Alo et al. 2011). Evidently, breeding programs around the world possess a limited diversity within the cultivated lentil (Ferguson et al. 1998b; Lombardi et al. 2014; Khazaei et al. 2016). Especially, the diversity of South Asian, Canadian, and Australian germplasm is low as estimated by several authors using different methods. An assessment of a historic collection of Indian lentil accessions including cultivars released since 1975, advanced breeding lines, ready for release and a collection of germplasm lines using 260 SSR markers could reveal a mean polymorphic information content of 0.30 (Kumar et al. 2018b). This again resulted in 48–74% of genetic similarity between the genotypes and thus indicated a narrow genetic base. Contrary to this, the germplasm within the Mediterranean region demonstrated higher genetic diversity. The landraces from Turkey and Greece within the Mediterranean region showed greater divergence to that of other region landraces including America, Africa, Northern Europe, and Middle-East at gene level (Lombardi et al. 2014). Similarly, two ancient landraces (Capracotta and Conca casale) collected from South Central Italy showed greater variation between themselves and commercial cultivars at morphological, protein and DNA level (Scippa et al. 2008). While genetic variation within the wild species of lentil was found to be high compared to that of cultivated species at morphological, quantitative, protein, and DNA level (Havey and Muehlbauer 1989; de la Rosa and Jouve 1992; Singh et al. 2014). These evidence suggest the presence of substantial variation within the cultivated and wild species that could be mined for widening the genetic base, particularly of South Asia, Australia, and Canada regions (Dikshit et al. 2015a).

Estimation of the extent of genetic diversity also depends on the method used for analyzing the diversity as significant differences were claimed between different methods for their ability to detect the polymorphism. Assessment of lentil diversity observed an evolution of type of method used from morphological characters to SNP markers and with each upgradation, the polymorphism detectability power increased. Morphological evaluation of 405 wild accessions revealed only a variation of 18.97% but 98.26% of genetic dissimilarity was estimated using quantitative traits (Singh et al. 2014). A comparison of SDS-PAGE and ISSR marker techniques revealed greater differences between the two methods as seed proteins showed only a low level of genetic diversity as compared to that of ISSR markers (El-Nahas et al. 2011). Likewise, ISSR markers revealed a higher degree of variation within a collection of Italian landraces compared to RAPDs (Sonnante and Pignone, 2001). Interestingly, genome-derived SSRs revealed a higher average number of alleles and genetic diversity compared to EST derived SSRs within a collection of accessions from three species of lentil (Dikshit et al. 2015b). Sequence-based, and genome-wide

SNP markers have become preferred alternatives to the other markers because of their abundance throughout the genome, highly polymorphic status, and suitability for use in high-throughput genotyping and automated analysis (Rafalski 2002).

4.6 Molecular Mapping of CS Genes and QTLs

During the past several years, tremendous progress has been made for the development of molecular markers in lentil. These markers associated and tightly linked to gene/QTL controlling a trait of interest can be used to introgress that gene/QTL in the background of improved lines through marker-assisted selection (MAS) and breeding. Genetic linkage map construction has become a necessary tool for molecular genetics and plant breeding programs (Tanyolac et al. 2010). The availability of large numbers of molecular markers and large mapping populations is the first step for the construction of genetic linkage maps. These maps have served many purposes in basic and applied research. They have become a key tool for physical mapping of genomes and high-density linkage maps are directly used in breeding researches (Tanksley et al. 1989; Hamwieh et al. 2005). In lentil, most genome maps have been created with anonymous and dominant RAPD, AFLP, and ISSR markers. Eujayl et al. (1998b) first identified markers suitable for the selection of a simply inherited resistance trait loci for Fusarium wilt resistance (Fw). Subsequently, Ford et al. (1999) identified RAPD markers that were close and flanking the major dominant locus for Ascochyta blight resistance in the ILL5588 accession (Ral1/AbR1). Chowdhury et al. (2001) also developed RAPD markers that flanked the recessive Ascochyta blight resistance locus in the cultivar Indianhead (*ral2*). Rubeena et al. (2006) identified markers that flank the codominant Ascochyta blight resistance loci in ILL7537. Tullu et al. (2003) identified markers linked to the anthracnose resistance locus in accession PI320937 (*LCt-2*) (Eujayl et al. 1997, 1998a; Rubeena et al. 2003b). Nevertheless, these first-generation maps served as foundations upon which more detailed maps have been and will be generated. To maximize polymorphism for map construction in lentil, interspecific hybrid populations have been used (Paterson et al. 1991; Eujayl et al. 1997; Durán et al. 2004). Such populations have also been used to map quantitative traits related to plant structure, growth habit, and yield in lentil (Fratini et al. 2007). Though the use of F_2 populations in the 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.

In lentil, although molecular markers linked to desirable genes/QTLs have been reported, only those with tight association (<1.0 cM) and positive effect can be used in MAS. Among CS traits, other than biotic and abiotic stresses, agro-morphological traits also play an important role being directly or indirectly related to complex

trait like yield. Duran et al. (2004) detected five QTLs each for the height of the first ramification and flowering time, three for plant height, seven for pod dehiscence, and one each for shoot number and seed diameter. Other studies identified several QTLs using biparental mapping populations that control flowering time in lentil (Tahir et al. 1994; Fratini et al. 2007; Tullu et al. 2008; Kahraman et al. 2015). One QTL each for the seed weight (*qSW*) and seed size (*qSS)* traits explaining 48.4% and 27.5% of phenotypic variance, respectively, were identified. These QTLs were located on an average at 5.48 cM from markers indicating close marker-trait association and hence can be useful in marker-assisted breeding for improving the seed size and weight (Verma et al. 2015). Morphological markers, viz., cotyledon (Yc), anthocyanin in stem (Gs), pod indehiscence (Pi), seed coat pattern (Scp), flower color (W), radiation frost tolerance locus (Rf), early flowering (Sn), and ground color of the seed (Gc) were mapped as qualitative markers (Eujayl et al. 1998a; Duran et al. 2004; Hamwieh et al. 2005; Tullu et al. 2008).

QTLs for biotic and abiotic stress tolerances will play a key role for tagging genes of interest to develop CS cultivars which can harbor more than one key traits. For Ascochyta blight disease, three QTLs each were detected for resistance at seedling and maturity stages (Gupta et al. 2012a). These accounted for 34 and 61% of the total assessed phenotypic variation and demonstrated that resistance at different stages is potentially conditioned by different genomic regions. The flanking markers identified may be useful for MAS and pyramiding of potentially resistance genes into elite genetic backgrounds that are resistant throughout the cropping period. Tullu et al. (2003) mapped for anthracnose disease resistance (Lct-2). Whereas, Taran et al. (2003) identified lines with combined resistance to Ascochyta blight resistance (AbR1 and ral1) and Anthracnose (OPO61250) using gene pyramiding approach for developing cultivars resistance to both Ascochyta blight and anthracnose in lentil. Recently, QTLs conferring resistance to Stemphylium blight and rust using RIL populations were identified (Saha et al. 2010a, b).

Among abiotic stresses, Kahraman et al. (2004b) identified the QTLs for winter survival and winter injury, using a RIL population of 106 lines and showed that tolerance to low temperature is a multigenic trait. QTLs related to frost response were also related to yield under winter-sown conditions as reported by Barrios et al. (2007). In continuation with this finding, Barrios et al. (2017) also found that QTLs with a major effect for winter hardiness and yield seem to be closely located within a single linkage group, and they are tracked by using some molecular markers. Super-SAGE (serial analysis of gene expression) genomic analysis was used to analyze the allele-specific differential expression of transcripts potentially involved in frost tolerance by bulk segregant analysis among 90 F_9 RILs derived from the Precoz × WA8649041 lentil cross (Barrios et al. 2010). QTLs (qHt ss and qHt_ps, with 12.1 and 9.23% phenotypic variance) and its molecular mapping for heat tolerance in lentil based on seedling survival and pod set per plant under hydroponic assay were reported by Singh et al. (2017c). These QTLs would provide further opportunities to dissect the candidate genes and the development of molecular markers for improving lentil with heat tolerance. Kaur et al. (2014) identified QTLs for boron tolerance in Cassab × ILL2024 mapping population. The flanking markers identified may

be useful for MAS and pyramiding of potentially different resistance genes into elite backgrounds that are resistant throughout the cropping season. Recently, some considerable progress has been made in identifying QTLs related to drought tolerance in lentil. Genetic control and linkage of SSR markers for drought tolerance in lentil were first reported by Singh et al. (2016a, b). They identified a molecular marker associated with *Sdt* locus controlling seedling survival drought tolerance in lentil. These linked markers could be used in molecular breeding programs for introgression of seedling survival drought tolerance gene in high-yielding genotypes. A linkage map, fortified with 291 SSR markers and 75 QTLs for drought tolerance and yield-related traits were established in lentil using intraspecific RIL mapping population (L830 × Precoz) (Rana et al. 2016).

Subsequently, 18 QTLs for root and shoot traits (dry root biomass, number of lateral roots, RS ratio, and specific root length) associated with drought tolerance in a lentil recombinant inbred line population (RIL), ILL 6002 × ILL 5888, was identified by Idrissi et al. (2016) as a promising step toward a MAS approach. The authors also confirmed the stability of detected QTLs by performing the analysis on two consecutive seasons. They also identified a QTL-hotspot genomic region related to a number of root and shoot characteristics associated with drought tolerance such as dry root biomass, root surface area, lateral root number, dry shoot biomass, and shoot length was identified. Results from various studies could be used for marker-assisted selection in lentil breeding programs targeting CS traits for further genetic enhancement of this crop species (Tables 4.5 and 4.6). Further, the application of the next-generation sequencing (NGS) and genotyping by sequencing (GBS) technologies have facilitated speeding up the lentil genome or transcriptome sequencing projects and large discovery of genome-wide SNP markers for genetic and association mapping.

4.7 Marker-Assisted Breeding for CS Traits

The use of cost-effective DNA markers derived from the fine mapped position of the genes for important agronomic traits, biotic and abiotic stress tolerance regions, and MAS strategies will provide opportunities for breeders to develop high-yielding, climate smart, and better-quality genotypes. Marker-assisted backcross breeding (MABCB) will be more effective to integrate major genes or QTLs with large effect into widely grown genotypes.

4.7.1 Germplasm Characterization and Distinctiveness, Uniformity, and Stability (DUS) Test

Characterization of germplasm plays a vital role in identifying desirable genotypes to enhance yield and crop improvement. A Distinctiveness, Uniformity, and Stability (DUD) test is a descriptive assessment that establishes the identity of the new cultivar, by using morphological traits, as well as its uniformity and stability. The new cultivar is compared with the existing cultivars to establish its distinctness (Kwon et al. 2005). Remarkable variations among the traits for use in breeding and selection programs have been reported (Ramgiry et al. 1989; Tullu et al. 2001). Barulina (1930) first reported the detailed morphological descriptions of lentil landraces and species from Asia. Morphological markers like color of stem, flower and foliage color, plant habit, cotyledon and testa color, and testa pattern are important for testing hybridity and keeping genetic purity to be used in MAS. Different lentil cultivars were found to be distinct, uniform and stable for different seed, seedling, and flowering traits (Dixit et al. 2009; ul Hussan et al. 2018). Conventionally, morphological descriptors are routinely used for establishing the identity of cultivars. But these morphological descriptors have many drawbacks, such as influence of environment on trait expression, epistatic interactions, pleiotropic effects, etc. Recently, molecular marker techniques are used for varietal identification, differentiation between species, and in resolving many breeding problems in lentil (Lombardi et al. 2014). The most commonly used methods for DNA profiling and genotype characterization by determining their distance and uniformity are the RFLP, PCR-based techniques (RAPD, AFLP, and SSR). They are used selectively depending on the crop species and genetic constitution of the genotype. Several types of molecular markers including RAPD, RFLP, STS, SCAR, SNP, CAPS, AFLP, ISSR, and resistance gene analogue (RGA) markers have been identified and effectively used in lentil genotyping (Eujayl et al. 1998a; Rubeena et al. 2003a; Hamwieh et al. 2005; Saha et al. 2010a; Sharpe et al. 2013a). The transcriptome sequencing approach has generated EST databases, delivering large numbers of EST-derived SSR and SNP markers (Kaur et al. 2011; Sharpe et al. 2013b). Diverse promising interspecific and intraspecific lentil genotypes have also been studied for useful genetic variability and genetic diversity using morphological and molecular markers (Kumari et al. 2018; Tsanakas et al. 2018). Genetic linkage maps are essential tools for genomic and genetic studies, especially in mapping phenotypic traits. Several genetic linkage maps of lentil have been constructed using a range of molecular marker systems and mapping populations (Eujayl et al. 1998a; Gupta et al. 2012b; Rubeena et al. 2003a), including SSR (Hamwieh et al. 2005; Phan et al. 2007) and SNP markers (Fedoruk et al. 2013; Kaur et al. 2014; Sharpe et al. 2013b; Rodda et al. 2017).

4.7.2 Scope of Marker-Assisted Breeding (MAB) and Marker-Assisted Backcrossing (MABC)

As conventional breeding system requires more number of breeding cycles to combine many target traits in a genotype. Molecular-assisted breeding programs have reported twice the rate of genetic gain over phenotypic selection for various traits such as yield, biotic and abiotic stress resistance and quality attributes (Oliveira et al. 2008). A high correlation must exist between the desirable gene and molecular markers for practicability and success of MAS and the markers must be stable, reproducible and easy to assay (Yu et al. 2004). MAS has been effectively used for detecting, tracking, retaining, combining, and pyramiding different desirable genes for biotic and abiotic stresses (O'Boyle et al. 2007). However, MAS has not been employed successfully in lentil breeding program due to the absence of tightly linked markers. Inspite of huge potential as described earlier in the chapter, various CS traits have been mapped and tagged on linkage map which potentially through fine mapping can be used in MAS for breeding climate-resilient cultivars. Expression QTL (eQTL) can be identified for desirable traits by using suitable genetic materials and global genome expression profiling. The markers linked to this eQTLs will have huge potential in MAS compared to the markers identified by traditional QTL analysis since eQTL affect the expression of the genes for the desirable traits (Ford et al. 2018).

Simultaneous expression of more than one genes in a cultivar to develop durable resistance against biotic and abiotic stresses in crops will require stacking of multiple genes from multiple parents also known as gene pyramiding (Shi et al. 2009). In this technique, genetic markers are employed to identify and select specific genes or combine multiple resistance genes (Brahm and Friedt 2000; Richardson et al. 2006). The concept of gene pyramiding was proposed by Nelson (1978) to develop crop cultivars with few to several different oligo genes for durable disease resistance. This technique has been named as multitrait introgression, since genes governing two or more traits are often introgressed into a single recurrent parent (Rana et al. 2019). Gene pyramiding involves different methods such as multiple parent crossing, backcrossing, and recurrent section (Ribaut et al. 2010). Gene pyramiding using molecular markers depends upon several factors such as the number of genes/QTLs, the number of parents containing the target genes/QTLs, the heritability of target genes/QTLs, marker-target gene associations, duration needed to complete the gene assembly, and relative cost. It is a realistic approach that can be exploited in lentil breeding programs for the development of genetic stocks and precise development of CS traits. The possible breeding schemes that can be used for gene pyramiding involving MAS and the required population size in each segregating population have been discussed in lentil (Gupta et al. 2010). Pyramiding genes for resistance to Ascochyta blight and anthracnose in lentil were done by Taran et al. (2003) and Sari et al. (2018). Marker-assisted gene pyramiding has been used in other cereals and legumes for combining multiple genes/QTLs controlling both qualitative and quantitative stress resistance (Concibido et al. 2004; Richardson et al. 2006; Shi et al.

2009; Li et al. 2010; Wang et al. 2007; Luo et al. 2016). To date, no information is available on pyramiding genes for resistance to abiotic stresses in lentil crops. There is a great opportunity to take advantage of gene pyramiding in lentil, to develop elite lines, combining traits from multiple parents, particularly for resistance to biotic and abiotic stresses. MABC using trait-linked markers may also be used to develop superior lines once a major gene or QTL is identified and validated in the donor, as it will facilitate retaining the whole genome of the recurrent parent. MABC is a good choice when phenotyping of a trait of interest is expensive or difficult, the heritability of desirable trait is low, the expression of trait is in late stages of plant development, or traits controlled by a recessive gene or multiple genes need to combine for one or more traits. In chickpea, root traits, drought tolerance score, canopy temperature differential, and seed size in chickpea are governed by many QTLs (Varshney et al. 2013). The same QTLs hold for yield and yield-contributing characters such as seed number and seed weight. These traits will get more attention in the final selection of genotypes for abiotic stress tolerance. Under such situations, Marker-assisted recurrent selection (MARS), which involves intercrossing among selected individuals in each cycle of selection, may be used to avoid the limitations of MABC. The initial cost of using markers in MABC would be more expensive compared to conventional breeding in the short term, however, time savings could lead to an accelerated cultivar release which could translate into much profits in the long term.

4.8 Map-Based Cloning of CS Genes

Ideally, the genes controlling a trait of interest are the perfect marker for MAS. However, this is often made difficult because cloning of a gene is labor intensive and time consuming. Alternatively, marker(s) that are tightly linked to and flanking a gene locus that conditions a sizable genetic variation for the trait may be selected for with the premise that the associated chromosomal region contains the functional gene(s). Often, genetically linked markers to traits of interest are identified by coarse mapping and these have limited use in MAS because of the distance and hence chance of recombination between the marker and actual gene locus. Therefore, genomic regions where the trait is mapped should be fine mapped at high resolution and be validated across genetic backgrounds to determine their utility in MAS. Also, physical characterization of genomic regions of interest will facilitate cloning of the gene to develop direct markers (candidate genes) and/or physically closer markers to the gene, increasing the reliability for MAS. The most useful marker system for MAS should be locus specific, highly reproducible and easy to discern. These include sequence tagged site (STS), sequence characterized amplified region (SCAR) or allele specific amplified primer (ASAP), specific polymorphic locus amplification test (SPLAT), and PCR-based RFLP markers. When locus-specific markers are not polymorphic among the parental lines used in the breeding programs, sequence discriminative methods are required. These include SNP, cleaved amplified polymorphic site (CAPS), and derived CAPS (dCAPS) markers. More recently, a cleaved

amplified polymorphic sequences marker was developed to facilitate breeding and establishes a basis for map-based cloning of Ruv2 and breeding for rust resistance in cowpea and other legume crops (Wu et al. 2018).

In the last decade, few transcriptome sequencing works (Kaur et al. 2011; Verma et al. 2013) aid in the marker discovery and SNP-based linkage maps (Sharpe et al. 2013b, Temel et al. 2014). However, a comprehensive genome-wide physical map, and its integration with genetic maps possessing QTLs for important targeted traits and draft genome of lentil, is the need of the hour for facilitating cloning of candidate genes and enhancing molecular breeding programs. Most recently, a high-density consensus map was constructed using three different RIL populations based on DArT markers (Ates et al. 2018). The consensus map could provide insight into the lentil genome, also help to construct a physical map using a Bacterial Artificial Chromosome library and map-based cloning studies. To identify the genes responsible for the target QTL, fine mapping and map-based cloning strategies are necessary (Salvi and Tuberosa 2005).

4.9 Genome Libraries

Large-insert genomic DNA libraries are essential genomic resources for physical mapping, positional cloning, and genome sequencing of higher eukaryotes (Tanksley et al. 1995; Zhang et al. 1996). The BAC cloning system has become an invaluable tool in genomic studies because of its ability to stably maintain large DNA fragments and its ease of manipulation (Wang et al. 1995; Zhang et al. 1996). BAC libraries are an important resource for the development of molecular markers that can be used for MAS for desirable agronomic traits. The development of SSR markers from BAC-end sequences is very cost-effective (Temnykh et al. 2001) and offers genome-wide coverage as all repeat types are systematically sampled in the randomly selected BACs (Cho et al. 2004). Since the development of the BAC vector (O'Connor et al. 1989), many BAC libraries have been developed for the major crop species, such as wheat, rice, corn, and soybean. In recent years, however, BAC libraries have also been developed for several pulse crops including mungbean (*Vigna radiata* L.), cowpea (*V. unguiculata* L.), lupin (*Lupinus angustifolius* L.), chickpea (*Cicer arietinum* L.), pigeonpea (*Cajanus cajan* L.), field pea (*Pisum sativum* L.), lima bean (*Phaseolus lunatus* L.), and common bean (*P. vulgaris* L.).

Integrated physical, genetic and genome map should provide a foundation for cloning and isolation of QTLs/genes for molecular dissection of traits as well as markers for molecular breeding for lentil improvement. A physical map of chickpea was developed for the reference chickpea genotype (ICC 4958) using BAC libraries targeting 71,094 clones (~12 × coverage). Comprehensive analysis of markers in abiotic and biotic stress tolerance QTL regions led to identification of 654, 306, and 23 genes in drought tolerance 'QTL-hotspot' region, Ascochyta blight resistance QTL region and Fusarium wilt resistance QTL region, respectively (Varshney et al. 2017). In addition, several large-insert BAC and binary bacterial artificial chromosome

(BIBAC) based libraries were also constructed earlier for chickpea (Lichtenzveig et al. 2005; Zhang et al. 2010).

Most of the BAC applications in pulse crops to date are of structural genomics nature; however, the application of BACs in functional genomics analysis of pulses also has great potential. Since large-insert clones in BAC vectors are more likely to contain the necessary promoter, enhancer, and silencer combination, mimicking the natural expression of the gene of interest, the advantages of the BAC transgenic approach are significant compared to the conventional transgenic approach (Yang and Gong 2005). However, this has not been applied yet on lentil due to non-availability of BAC or YAC libraries. The need of the hour is to develop BAC/BIBAC or YAC libraries to facilitate map-based cloning of genes in lentil. Alternatively, the genome libraries developed in the closely related model legumes chickpeas and *Medicago*, will help lentil breeders to speedup the understanding of lentil genomes and assist map-based cloning of genes.

4.10 Genetic Transformations

Transgenic approach uses functional genes which are not available within the crossable gene pool. Thus, cloned genes are important genomic resources for making genetic manipulation through transformation. Commonly, the particle bombardment and the *Agrobacterium tumefaciens* infection methods have been used to introduce genes with novel functions. With the explosion of sequence information available in the databases, transformation systems have also become useful tools to study gene function via RNA interference 'knockout,' T-DNA insertion or transforming a genotype lacking a particular gene. Thus, a robust, reproducible, and efficient transformation system combined with a protocol to regenerate complete fertile plants from transformed cells is essential to fully study the plant gene functions. To date, the transformation of lentil has been reported through *A. tumefaciens*-mediated gene transfer (Lurquin et al. 1998) and biolistic transformation including electroporation (Chowrira et al. 1996) and particle bombardment (Gulati et al. 2002; Mahmoudian et al. 2002). Warkentin and McHughen (1992) reported the susceptibility of lentil to *A. tumefaciens*. All explants showed transient b-glucuronidase (GUS) expression at the wound sites except cotyledonary nodes, which were subsequently transformed by Sarker et al. (2003). Oktem et al. (1999) reported the first transient and stable chimeric transgene expression on cotyledonary lentil nodes using particle bombardment. Gulati et al. (2002) reported regeneration of the first fertile transgenic lentil plants on MS medium with 4.4 μM benzyladenine (BA), 5.2 μM gibberellic acid (GA3), and chlorsulfuron (5 nM for 28 days and 2.5 nM for the rest of the culture period), followed by micrografting and transplantation in soil. The first successful work was reported by Barton et al. (1997), using pCGP1258 plasmid construct on four lentil genotypes. Khatib et al. (2007) have developed herbicide-resistant lentil through *A. tumefaciens* mediated transformation. This was achieved with the same plasmid construct pCGP1258, harboring the gene conferring resistance to the

herbicide glufosinate ammonium that was transformed using *A. tumefaciens* strain AgL0. Akcay et al. (2009) reported the production of transgenic lentil plants via *Agrobacterium*-mediated transformation and the stable transmission of the *npt*II and *gus*A genes in the subsequent generations. However, these studies were mostly confined to establish transformation techniques rather than the introduction of genes into improved cultivars. Khatib et al. (2011) reported for the first time the introduction of the *DREB1A* gene into lentil for enhancing drought and salinity tolerance. The results showed that mRNA was accumulated and thus, the DREB1A gene was expressed in the transgenic plants.

Advanced molecular technology has enabled plant modifications at the genomic level. Several horizontal gene transfer approaches have addressed the issues related to challenges and limitations of genome boundary in transferring the alien gene of interest through vertical gene transfer methods. Techniques such as genetic transformation (*Agrobacterium*-mediated transformation and direct gene delivery system) have opened new pathways to transfer functional genes precisely from any organism into plant genome.

Trans-mitochondrial gene expression can be studied using reverse genetics when transformation strategy targets mitochondria instead of nucleus (Havey et al. 2002), which can target mitochondrial genes for transgenic crops. Kemble et al. (1988) put an effort to transform *Brassica napus* hybrid mitochondria through polyethylene glycol (PEG) or electroporation mediated protoplast fusion using recombinant vectors. Among other organelles, plastids with small genome size are used to construct suitable vectors by targeting their specific sequences for genetic transformation. Boynton et al. (1988) were the first to report the transformation of Chlamydomonas chloroplast. Since then there are many reports of transformation of new genes from chloroplast genomes via organogenesis in several plant species (Skarjinskaia, et al. 2003; Khan and Maliga 1999; Hou et al. 2003; Kumar et al. 2004a).

Plastid genetic engineering has seen success in crops of economic importance. Complete legume genome sequences will be essential for comparing intergenic spacer regions to develop transformation vectors for plastid genetic engineering as plastid genome information is not fully understood (Sabir et al. 2014). Fabaceae (legumes) in Papilionoids have certain level of variation for cell structural features and inverted repeat lacking clade (IRLC) offers opportunity to enhance understanding of genomic evolution mechanisms and its feasibility for genetic improvement (Sabir et al. 2014), which is mainly due to comprehensive knowledge of the genomes for vector construct followed by stable intergenic integration site selection in transplastomic crop legume species (Dufourmantel et al. 2004, 2006; Wei et al. 2011). Six new IRLC plastomes have complete sequences and lentil is among few which has most repetitive sequences, these findings highlight plastome evolution, transfer of functional genes over time, losses of introns indicative of new genomic rearrangements (Sabir et al. 2014).

To fast track gene discoveries plant metabolomics offers huge potential to identify novel genes relate to biosynthetic pathway mechanisms of plant-based natural products. Metabolomics aided with transcriptomics has paved the way to identify various genes functions and their characterization (Saito and Matsuda 2010). Among

legumes, most of the studies have concentrated in model legumes only. The traits described below are important for climate-resilient crops and shows the potential of this technology to be implemented in lentil crop. A decrease in oxylipins in Medicago was due to the effect of rhizobial node factor (Nod) (Zhang et al. 2012). Survival of salt-tolerant Lotus species involved successive changes for metabolic adjustments of shoot components (Sanchez et al. 2011), whereas, large number of mitochondria associated metabolites were identified for flooding stress in soybean which suggests requirement of higher levels of metabolites (amino acids, NAD, and NADH along with depleted free ATPs) for respiration and glycolysis (Komatsu et al. 2011). Specific metabolite markers (threonate, asparagine/ornithine and alanine/homoserine) for stresses like drought and salinity were developed through metabolite phenotyping of four Mediterranean lentil genotypes under drought and salinity stress (Muscolo et al. 2015). Metabolomics has huge potential though various challenges including metabolite identification at a large scale, limits its application.

Gene silencing which limits the mRNA availability for translation and eventually reduces the protein amount is another powerful technology for desired trait development. Different RNA silencing strategies as tools are available for selectively knocking down of specific genes/functions. MicroRNAs (miRNAs) are involved in the plant development process as well as in various stress responses, affecting the gene expression at the posttranscriptional level (Zhang et al. 2006). Therefore, under stress, increased gene expression of tolerant genotypes can be correlated to changes in miRNAs, which makes them good candidates for enhancing crop stress tolerance through transgenic breeding. Drought tolerance related miRNAs are discovered for various crops, 11 of them are identified in cowpea (Barrera-Figueroa et al. 2011) and heat stress response related eight miRNAs are being identified in common bean (Jyothi et al. 2015). RNA silencing has evolved as a natural defense to protect plants against viruses. Virus-induced gene silencing (VIGS) is promising to suppress plant gene expression using virus vectors with host gene's target region (Baulcombe 2004; Britt and May, 2003), though not used extensively in legumes. Vertical and horizontal approaches including RNAi and VIGS can be explored to understand the molecular mechanisms of host resistance in lentil. Cisgenesis offers the opportunity to modify genetic constitution of host plant via gene present naturally in a crossable and sexually compatible donor plant. Many genes from crop wild relatives and distant landraces of various crops have been identified which code for abiotic and biotic stress tolerance and resistance, various agronomical and quality traits, and been introgressed into the desired genotypes of crops. Such genes are known as cisgenes to separate them from the transgenes (Sprink et al. 2016) and cisgenesis take care of undesirable issues of linkage drag (Podevin et al. 2012), and introgression of desired genes into the host genotypes without affecting their other desirable traits. Abiotic stress tolerance is controlled by many genes and is complex, therefore, one gene or QTL introgression will not be enough for the introduction of stress tolerant (Hartung and Schiemann, 2014). Cisgenesis still need to emerge and can off-set concerns of genetically modified crops and technology at least for those traits which are still present in distant relatives of the crops.

4.11 Role of Bioinformatics

4.11.1 Gene and Genome Databases

With the advent of molecular approaches for plant breeding, based on genetic markers and genes, a need emerged for comprehensive sequence databases that will enable the annotation of these genomic features into functional proteins or transcription regulators such as transcription factors, methylation sites, or ncRNAs. This need was particularly crucial for non-model crops such as lentil, which lack the genomic resources available for well-studied model organisms. One of the first publicly accessible sequence databases, emerged in the early 1990s with the development of the internet, is the American National Center for Biotechnology Information (NCBI) GenBank collection. Three decades after its development it is still considered the most comprehensive and updated database, thanks to the International Nucleotide Sequence Database Collaboration, along with the DNA DataBank of Japan and the European Nucleotide Archive of The European Bioinformatics Institute in the European Molecular Biology Laboratory (EMBL-EBI). The NCBI databases now hold hundreds of trillions of existing cDNA, RNA, DNA, and protein sequences from collections spanning all available phyla groups (Cochrane et al. 2016). Since its foundation, the GenBank collection offered web-based platform equipped with a suite of bioinformatics tools for querying of genes of interest and performing homology-based searches, most notably the BLAST suite of tools, to find and retrieve the closest available sequences and provide certain functional and taxonomic annotation of the results (Camacho et al. 2009). The era of next-generation-sequencing (NGS), which introduced massively parallel high-throughput sequencing in 2005 and led to an explosion of sequencing projects that were submitted to NCBI's databases, also introduced reduced accuracy in the annotation of the submitted sequences, which were mostly annotated using high-throughput computational methods (Bidartondo 2008; Schnoes et al. 2009). Despite its reduced annotation accuracy, NCBI's databases are still widely used for annotation of sequences from non-model species, thanks to their unmatched coverage of sequences and taxonomy groups.

In the early 2000s, as sequencing technologies evolved and became more accessible and affordable, a new type of databases was developed and deployed, ones that were dedicated to specific species or narrow taxonomic groups and covered the entire (or close to) gene repertoire. These databases, however, were initially developed for just a handful of model plant species, which benefitted from fully sequenced, annotated, and curated genomes, such as Arabidopsis, rice, poplar, corn and in the legume family, the wild *Lotus japonicus* and cultivated alfalfa and soy (Yon Rhee et al. 2003; Retzel et al. 2007; Yamazaki et al. 2008; Sjödin et al. 2009; Grant et al. 2010; Andorf et al. 2016; Mun et al. 2016). As it was for GenBank, utilizing these databases for nonmodel crop research was still useful, by means of comparative genomics, or using homology-based searches to annotate an unknown gene and infer its function based on its closest annotated relatives.

4.11.2 Comparative Genome Databases

The shortcoming of using species-specific databases for comparative genomics is that it relies on prior knowledge of the evolutionary relationship between the crop and model species to select the most suitable database. In addition, this approach requires multiple comparisons against different databases, each using a potentially different interface and producing results in a different format, making the entire procedure extremely complicated, cumbersome and labor intensive. To overcome this, 'themed' databases were developed, combining information from multiple genomes, often focusing on a taxonomic group of interest. These databases provide advanced bioinformatic tools for comparing gene sequences and functions between species, as well as genome browsers, genetic maps and known genetic variants, markers, and even QTLs. This allows for a more targeted approach for annotating and comparing unknown genes and markers across crop plants. Notable comparative genome databases include the Phytozome Plant Comparative Genomics portal (https://phytozome.jgi.doe.gov/pz/portal.html, USA Department of Energy's Joint Genome Institute), which currently encompasses genomes of 64 plant species (including 8 legume species) (Goodstein et al. 2012). Another example of plant-specific database is Plaza (https://bioinformatics.psb.ugent.be/plaza, Ghent University), which covers 55 species of dicots (including 7 legume species) and 29 monocots (Van Bel et al. 2017). The Gramene database (http://www.gramene.org/, Gramene project), a resource for plant and crop comparative genomics, is based on Ensembl technology with collaboration with EMBL-EBI and offers access to curated genomic data both via its web portal and through data mining and programmatic access tools (Tello-Ruiz et al. 2018). More relevant to lentil are the Cool-Season Food Legume Crop Database (https://www.coolseasonfoodlegume.org/, Washington State University), which provides comparative genomics and genetics tools for chickpea, pea, lentil, and faba bean, though it only includes the full genome of chickpea; and KnowPulse (http://knowpulse.usask.ca/portal/, University of Saskatchewan Pulse Crop Research Group) which currently hosts the only publicly available annotated draft genome of lentil (Sanderson et al. 2011).

4.11.3 Protein and Pathway Databases

Relying on nucleotide sequences alone for homology-based functional annotation of unknown genes is limited to well-conserved genes which were previously identified and characterized in closely related species. When these requirements are not met, a more general approach is needed, based on the conservation of the protein amino acid sequence, which generally diverges in a slower pace than the nucleotide sequence, due to selection pressure to preserve the protein's function.

In addition to its nucleotide collections, NCBI hosts a broad protein database, named RefSeq, with over 121 million annotated proteins from 84,276 species

(Release 90, September 17, 2018), which can be searched against a query sequence. The European-based Universal Protein Resource (https://www.uniprot.org/), a collaboration between EMBL-EBI, the Swiss Institute of Bioinformatics and the Protein Information Resource, offers a similar computationally-annotated protein database (TrEMBL), but in addition, a smaller manually curated and reviewed protein collection (Swiss-Prot), which can be used with high confidence for functional annotations (The UniProt Consortium 2008). A plant-specific protein annotation project in underway at UniProt, to identify protein families unique to plants, which so far includes 39,669 entries from 1,998 species of Viridiplantae.

When a whole-protein approach is still unable to identify a candidate homologous gene, it is possible to perform homology searches against databases of protein subdomains to identify at least some elements of the gene that can be annotated and associated with a known function. Such search is performed using a profile hidden Markov model (profile HMM) algorithm and the available databases include the Protein Family database (http://pfam.xfam.org/) and the all-inclusive InterPro (http://www.ebi.ac.uk/interpro/, EMBL-EBI) database, which integrates protein families, domains and functional sites from a diverse range of source databases.

Once a protein or its domains are annotated, its functional role in molecular pathways can be depicted from pathway databases such as the Gene Ontologies (http://www.geneontology.org/), EggNOG (http://eggnogdb.embl.de), the Kyoto Encyclopedia of Genes and Genomes (https://www.genome.jp/kegg/) and Reactome (https://reactome.org/) databases (GO Consortium 2013; Huerta-Cepas et al. 2016; Kanehisa et al. 2016; Fabregat et al. 2018). The Plant Reactome (http://plantreactome.gramene.org/, Gramene project) enables a focused pathway search within the plants kingdom (Naithani et al. 2017), however, given the generalized nature of the protein-based approach, and the relatively modest computational resources required compared to nucleotide-based homology searches, it might be useful not to restrict the search to a particular phyla.

4.11.4 Gene Expression Databases

The actual function of genes of interest cannot always be inferred based on their nucleotide and protein sequences and domains, especially if they share little similarity to known annotated genes. In these cases, it is helpful to observe the gene's expression profiles under different environmental and biotic conditions and relate it to well-described molecular pathways by clustering with other genes who share similar expression patterns and their role had been previously established. For this purpose, gene expression databases were developed to collate and combine expression information from multiple species, under multiple experimental design. As it is for genomic data, the NCBI's Gene Expression Omnibus (GEO) database (https://www.ncbi.nlm.nih.gov/gds) is leading in terms of sheer breadth of stored data, originating from high-throughput microarray and RNA-Sequencing experiments (Clough and Barrett 2016). Following closely behind is the Expression

Atlas (https://www.ebi.ac.uk/gxa/plant/experiments, EMBL-EBI), which allows focusing on plant species and offers expression sets of 'baseline' and 'differential' experiments (Papatheodorou et al. 2018). Additional plant-only gene expression databases include Plexdb (http://www.plexdb.org), which in addition to plant species includes expression profiles of common plant pathogens, but unfortunately it was last updated in 2011 and is now outdated (Dash et al. 2012); and PLANEX (http://planex.plantbioinformatics.org/), a server offering analysis of co-expressed genes across plant species, based on the GEO database (Yim et al. 2013). Other useful resources for species-specific gene expression are the aforementioned model species genomic portals such as the Arabidopsis Information Resource (https://www.arabidopsis.org/), the Maize Genetics and Genomics Database (https://www.maizegdb.org/), SoyBase (https://soybase.org/soyseq/), and others.

As is the case for genomic resources, the vast majority of expression datasets in all of these databases focus on several model species, while only a single experiment, containing just 10 lentil samples, was found in NCBI's GEO (accession GSE11374, Mustafa et al. 2009). The same challenges exist therefore, when attempting to use gene expression databases for annotation of lentil genes and they require reliance on less than ideal datasets of closely related model species such as alfalfa and soybean.

4.11.5 Integration of Different Data

The genomic databases detailed in the previous sections offer different data types and strategies to query it, but their overarching aim is similar: to annotate and characterize genomic features. The abundance of distributed databases which often compete, however, complicates the annotation efforts. Several web portals were developed to streamline this process, by bringing together multiple databases and using a common system to query them, identify genes and smoothly transition results from one analysis to another.

The Gramene project (http://www.gramene.org/) brings together genome sequences, gene expression data and pathway databases for a range of crop and model plant species. In addition to a suite of data accessing and querying tools, the portal provides a tool to predict the functional consequences of known and unknown variants uploaded by the user (Tello-Ruiz et al. 2018).

Another web portal, the Legume Information System (LIS; https://legumeinfo.org/, National Center for Genome Resources), integrates legume genomes, gene families, protein domains, gene expression data, QTL, and genetic maps; and phenotyping data as a one-stop shop for legume researchers. LIS advocates use of common data templates, formats, schemas, and interfaces to facilitate data acquisition and analysis across all users and data types (Dash et al. 2016). A continued collaboration effort toward building genomic resources and capacity for crop legumes, as being done by KnowPulse, LIS and to a lesser extent the Cool-Season Food Legume Crop Database, is vital to fill in the gap and equip legume and lentil researchers with tools for molecular-based breeding methods.

4.12 Conclusion

Lentil gene pools consist of many wild relatives offering resistance to abiotic and biotic stresses as well as other important agronomic traits. Further, continuous efforts have been made in the past in cultivated x wild lentil genotype hybridization and few successful examples are there in which promising efforts were made to transfer CS targeted traits into cultivated lentils. However, so far, conventional breeding approaches have helped to utilize the available genetic variability of target traits within cultivated genepool, resulting in the development of several cultivars of lentil with tolerance or resistance to biotic and abiotic stresses. Recently, the linkage maps have provided the basis for development and increase the availability of genetic markers for genome studies such as the construction of physical mapping and map-based gene cloning. Limited population size, low heritability, lack of lentil-specific candidate genes, and nonavailability of genome libraries (BAC/YAC) are the main limiting factors in lentil genomics and thus reducing the pace of the genome-aided cultivar development. The access to high-throughput phenotyping and genotyping, construction of high-density maps with desirable markers and sequencing technologies are expected to speedup cultivar development with improved CS traits.

References

Abbo S, Ladizinsky G (1991) Anatomical aspects of hybrid embryo abortion in the genus *Lens* L. Bot Gaz 152(3):316–320

Abbo S, Ladizinsky G (1994) Genetical aspects of hybrid embryo abortion in the genus *Lens* L. Heredity 72(2):193

Abi-Antoun M, Kiwan P, Erskine W (1990) Talia 2-a lentil cultivar for Lebanon. Lens 17:3–4

Abo-Elwafa A, Murai K, Shimada T (1995) Intra-and inter-specific variations in *Lens* revealed by RAPD markers. Theor Appl Genet 90:335–340

Ahmad M, Mcneil DL (1996) Comparison of crossability, RAPD, SDS-PAGE and morphological markers for revealing genetic relationships within and among *Lens* species. Theor Appl Genet 93:788–793

Ahmad MAGF, Fautrier AG, McNeil DL, Burritt DJ, Hill GD (1995) Attempts to overcome post-fertilization barrier in interspecific crosses of the genus *Lens*. Plant Breed 114(6):558–560

Ahmad M, Fautrier A, Burritt D, Mcneil D (1997a) Genetic diversity and relationships in *Lens* species and their F_1 interspecific hybrids as determined by SDS-PAGE. NZ J Crop Hort 25:99–108

Ahmad M, Mcneil DL, Sedcole JR (1997b) Phylogenetic relationships in *Lens* species and their interspecific hybrids as measured by morphological characters. Euphytica 94:101–111

Ahmed S, Beniwal S (1991) Ascochyta blight of lentil and its control in Ethiopia. Intl J Pest Manage 37:368–373

Ahmed FE, Hall AE, DeMason DA (1992) Heat injury during floral development in cowpea (*Vigna unguiculata*, Fabaceae). Am J Bot 9(7):784–791

Akcay UC, Mahmoudian M, Kamci H, Yucel M, Oktem H (2009) *Agrobacterium tumefaciens*-mediated genetic transformation of a recalcitrant grain legume, lentil (*Lens culinaris* Medik). Plant Cell Rep 28:407–417. https://doi.org/10.1007/s00299-008-0652-4

Aksoy EM (2008) Effect of drought and salt stresses on the gene expression levels of antioxidant enzymes in lentil (*Lens culinaris* M.) seedlings. Yüksek Lisans Tezi, Orta Doğu Teknik Üniversitesi Fen Bilimleri Enstitüsü, Ankara

Aldemir, S, Ateş D, Temel HY, Yağmur B, Alsaleh A, Kahriman A, Özkan H, Vandenberg A, Tanyolaç MB (2017) QTLs for iron concentration in seeds of the cultivated lentil (*Lens culinaris* Medic.) via genotyping by sequencing. Turk J Agric For 41(4):243–255

Aldemir SB, Sever T, Ates D, Yagmur B, Kaya HB, Temel HY (2014) QTL mapping of genes controlling Fe uptake in lentil (*Lens culinaris* L.) seed using recombinant inbred lines. In: Plant and animal geonme conference XXII, 3360 pp. https://pag.confex.com/pag/xxii/webprogram/Paper9689.html

Alghamdi SS, Khan AM, Ammar MH (2013) Phenological, nutritional and molecular diversity assessment among 35 introduced lentil (*Lens culinaris* Medik.) genotypes grown in Saudi Arabia. Intl J Mol Sci 15:277–295

Ali A, Johnson DL, Stushnoff C (1999) Screening lentil (*Lens culinaris*) for cold hardiness under controlled conditions. J Agric Sci 133(3):313–319

Allahmoradi P, Mansourifar C, Saiedi M, Jalali Honarmand S (2013) Effect of different water deficiency levels on some antioxidants at different growth stages of lentil (*Lens culinaris* L.). Adv Environ Biol 7(4):535–543

Alo F, Furman BJ, Akhunov E, Dvorak J, Gepts P (2011) Leveraging genomic resources of model species for the assessment of diversity and phylogeny in wild and domesticated lentil. J Hered 102:315–329

Al-Quraan NA, Al-Omari HA (2017) GABA accumulation and oxidative damage responses to salt, osmotic and H_2O_2 treatments in two lentil (*Lens culinaris* Medik) accessions. Plant Biosyst 151(1):148–157

Al-Quraan NA, Al-Sharbati M, Dababneh Y, Al-Olabi M (2014) Effect of temperature, salt and osmotic stresses on seed germination and chlorophyll contents in lentil (*Lens culinaris* Medik). Acta Hort 1054:47–54

Amin MR, Karim MA, Islam MR, Aktar S, Hossain MA (2016) Effect of flooding on growth and yield of mungbean genotypes. Bang J Agric Res 41(1):151–162

Andorf CM, Cannon EK, Portwood JL (2016) MaizeGDB update: new tools, data and interface for the maize model organism database. Nucl Acids Res 44:D1195–D1201. https://doi.org/10.1093/nar/gkv1007

Andrahennadi C (1994) Genetics and linkage of isozyme markers and resistance to seedborne Ascochyta infection in lentil. MSc thesis, Department of Crop Science and Plant Physiology, University of Saskatchewan, Canada

Arkin GF, Taylor HM (eds) (1981) Modifying the root environment to reduce crop stress. ASAE Monograph No. 4. American Society of Agricultural Engineers, St. Joseph, MI

Arumuganathan K, Earle ED (1991) Nuclear DNA content of some important plant species. Plant Mol Bio Report 9(3):208–218

Asghar MJ, Abbas G, Shah TM (2010) Study of genetic diversity in some local and exotic lentil (*Lens culinaris* Medik) genotypes. Pak J Bot 42:2681–2690

Ashraf M, Chishti SN (1993) Waterlogging tolerance of some accessions of lentil (*Lens culinaris* Medic.). Trop Agric 70(1):60–67

Ashraf M, Waheed A (1990) Screening of local/exotic accessions of lentil (*Lens culinaris* Medic.) for salt tolerance at two growth stages. Plant Soil 128(2):167–76

Ashraf M, Waheed A (1993) Responses of some local/exotic accessions of lentil (*Lens culinaris* Medic.) to salt stress. J Agron Crop Sci 170(2):103–112

Ashraf M, Bokhari H, Cristiti SN (1992) Variation in osmotic adjustment of lentil (*Lens culinaris* Medic) in response to drought. Acta Bot Neerlandica 41:51–62

Asraf M, Zafar ZU (1997) Effect of potassium deficiency on growth and some biochemical characteristics in two lines of lentil (*Lens culinaris* Medic.). Acta Physiol Plant 19(1):9–15

Aslam M, Maqbool MA, Zaman QU, Shahid M, Akhtar MA, Rana AS (2017) Comparison of different tolerance indices and PCA biplot analysis for assessment of salinity tolerance in lentil (*Lens culinaris*) genotypes. Intl J Agric Biol 19(3):1

Aswaf A, Blair M (2012) Quantitative trait loci for rooting pattern traits of common beans grown under drought stress versus non-stress conditions. Mol Breed 30:681–695. https://doi.org/10.1007/s11032-011-9654-y

Ates D, Aldemir S, Alsaleh A, Erdogmus S, Nemli S, Kahriman A, Ozkan H, Vandenberg A, Tanyolac B (2018) A consensus linkage map of lentil based on DArT markers from three RIL mapping populations. PLoS ONE 3(1):e0191375

Ayoub AT (1977) Salt tolerance of lentil (*Lens esculenta*). J Hort Sci 52(1):163–168

Azimzadeh S (2010) Effect of planting dates, seed rates and row spacing on grain yield and yield components of a lentil (*Lens culinaris*) genotype in northern khorasan dry land condition. J Res Crop Sci 3(9):121–135

Babayeva S, Akparov Z, Abbasov M, Mammadov A, Zaifizadeh M, Street K (2009) Diversity analysis of Central Asia and Caucasian lentil (*Lens culinaris* Medik.) germplasm using SSR fingerprinting. Genet Resour Crop Evol 56:293

Babayeva S, Akparov Z, Damania A, Izzatullayeva V, Aslanova G, Abbasov M (2014) Genetic diversity for drought tolerance in lentils from Central Asia and the Caucasus: CACLentil. Alb J Agric Sci 13(2):1–8

Baligar VC (1997) Nutrient use efficiency in acid soils: nutrient management and plant use efficiency. In: Monitz AC, Furlani AMC, Fageria NK, Rosolem CA, Cantarells H (eds) Plant-soil interactions at low ph: sustainable agriculture and forestry production. Brazilian Soil Science Society Compinas, Brazil, pp 75–93

Bandeoğlu E, Eyidoğan F, Yücel M, Öktem HA (2004) Antioxidant responses of shoots and roots of lentil to NaCl-salinity stress. J Plant Growth Regul 42(1):69–77

Barber SA (1995) Soil nutrient bioavailability: a mechanistic approach, 2nd edn. Wiley, New York, NY

Barghi SS, Mostafaii H, Peighami F, Zakaria RA, Nejhad RF (2013) Response of in vitro pollen germination and cell membrane thermostabilty of lentil genotypes to high temperature. Intl J Agric 3(1):13

Barrera-Figueroa BE, Gao L, Diop NN, Wu Z, Ehler JD, Roberts PA (2011) Identification and comparative analysis of drought-associated microRNAs i two cowpea genotypes. BMC Plant Biol 11:127. https://doi.org/10.1186/1471-2229-11-127

Barrios A, Kahraman A, Aparicio T, Rodríguez M, Mosquera P, García P, McPhee K, Pérez de la Vega M, Caminero C (2007) Preliminary identification of QTLS for winter hardiness, frost tolerance and other agronomic characters in lentil (*Lens culinaris* Medik.) for Castilla y León (SPAIN) region. In: Proceedings of the 6th European conference on grain legumes, Lisbon, pp 12–16

Barrios A, Martin-Sanz A, Ramos S, Rotter B, Horres R, Plotner A, Kretzdorn N, Constantino Saldaña C, Perez de la Vega M, Winter P (2010) Allele-specific differential expression of transcripts potentially involved in cold tolerance QTL in lentil revealed by bulked extremes SuperTag digital gene expression (BE-STDGE) profiling and qRT-PCR. In: Proceedings of the 5th international food legumes research conference and 7th European conference on grain legumes, Antalya, pp 26–30

Barrios A, Aparicio T, Rodríguez MJ, de la Vega MP, Caminero C (2016) Winter sowing of adapted lines as a potential yield increase strategy in lentil (*Lens culinaris* Medik.). Span J Agric Res 14(2):0702

Barrios A, Caminero C, García P, Krezdorn N, Hoffmeier K, Winter P, de la Vega MP (2017) Deep super-SAGE transcriptomic analysis of cold acclimation in lentil (*Lens culinaris* Medik.). BMC Plant Biol 17(1):111

Barton J, Klyne A, Tennakon D, Francis C, Hamblin J (1997) Development of a system for gene transfer to lentils. In: Proceedings of international food legume research conference III, Adelaide, SA

Barulina O (1930) Lentil of USSR and of other countries. Bull Appl Bot Genet Plant Breed 40:1–319

Basheer-Salimia R, Camilli B, Scacchi S, Noli E, Awad M (2015) Assessment of genetic diversity in lentils (*Lens culinaris* Medik.) based on SNPs. Genet Mol Res 14(2):5870–5878

Baulcombe (2004) DNA silencing in plants. Nature 431(7006):356–363

Bayaa B, Erskine W, Hamdi A (1994) Response of wild lentil to *Ascochyta fabae* f. sp. *lentis* from Syria. Genet Resour Crop Evol 41(2):61–65
Bayaa B, Erskine W, Hamdi A (1995) Evaluation of a wild lentil collection for resistance to vascular wilt. Genet Resour Crop Evol 42(3):231–235
Bejiga G, Degago Y (2000) Region 4: Sub-Sahara Africa. In: Knight R (ed) Linking research and marketing opportunities for pulses in the 21st century. Springer, Dordrecht, pp 99–105
Belko N, Zaman-Allah M, Cisse N, Diop ND, Zombre G. Ehler JD (2012). Low soil moisture threshold for transpiration decline under water deficit correlates with lower canopy conductance and higher transpiration efficiency in drought tolerant cowpea. Funct Plant Biol 39:306–322. https://doi.org/10.1071/fp11282
Bhadauria V, Ramsay L, Bett KE, Banniza S (2017) QTL mapping reveals genetic determinants of fungal disease resistance in the wild lentil species *Lens ervoides*. Sci Rep. https://doi.org/10.1038/s41598-017-03463-9
Bhandari K, Siddique KH, Turner NC, Kaur J, Singh S, Agrawal SK, Nayyar H (2016) Heat stress at reproductive stage disrupts leaf carbohydrate metabolism, impairs reproductive function, and severely reduces seed yield in lentil. J Crop Improv 30(2):118–151
Bicer BT, Sakar D (2008) Studies on variability of lentil genotypes in South eastern Anatolia of Turkey. Notulae Bot Hort Agrobot Cluj-Napoca 36:20–24
Bidartondo MI (2008) Preserving accuracy in GenBank. Science 319:1616. https://doi.org/10.1126/science.319.5870.1616a
Biju S, Fuentes S, Gupta D (2017) Silicon improves seed germination and alleviates drought stress in lentil crops by regulating osmolytes, hydrolytic enzymes and antioxidant defense system. Plant Physiol Biochem 119:250–264
Biju S, Fuentes S, Gupta D (2018) The use of infrared thermal imaging as a non-destructive screening tool for identifying drought-tolerant lentil genotypes. Plant Physiol Biochem 127:11–24
Bluemel M, Dally N, Jung C (2015) Flowering time regulation in crops—what did we learn from Arabidopsis? Curr Opin Biotechnol 32:121–129
Boote KJ, Allen LH, Prasad PVV, Baker JT, Gesch RW, Snyder AM (2005) Elevated temperature and CO_2 impacts on pollination, reproductive growth and yield of several globally important crops. J Agric Meteorol 60:469–474
Boullis A, Francis F, Verheggen FJJ (2015) Climate change and tritrophic interactions: will modifications to greenhouse gas emissions increase the vulnerability of herbivorous insects to natural enemies? Environ Entomol 44(2):277–286
Boynton JE, Gillham NW, Harris EH, Hosler JP, Johnson AM, Jones AR et al (1988) Chloroplast transformation in Chlamydomonas with high velocity microprojectiles. Science 240:1534–1538
Brahm L, Friedt W (2000) PCR-based markers facilitating marker assisted selection in sunflower for resistance to downy mildew. Crop Sci 40(3):676–682
Bretag T, Materne M (1999) Evaluation of 36 lentil lines for resistance to ascochyta blight and botrytis grey mould. In: Summary of field research in the Wimmera, pp 38–40
Britt AB, May G (2003) Re-engineering plant gene targeting. Trends Plant Sci (in press)
Buchwaldt L, Anderson K, Morrall R, Gossen B, Bernier C (2004) Identification of lentil germ plasm resistant to *Colletotrichum truncatum* and characterization of two pathogen races. Phytopathology 94:236–243
Buddenhagen IW, Richards RA (1988) Breeding cool season food legumes for improved performance in stress environments. In: Summerfield RJ (ed) World crops: cool season food legumes. Springer, Dordrecht, pp 81–95
Camacho C, Coulouris G, Avagyan V (2009) BLAST+: architecture and applications. BMC Bioinform 10:421. https://doi.org/10.1186/1471-2105-10-421
Chahota RK, Gupta VP, Sharma SK (1996) Combining ability and genetic architecture of macrosperma × microsperma derived crosses. J Hill Res 9:341–346
Chahota RK, Sharma SK, Gupta VP (1997) Heterotic and inbreeding effects in lentil crosses involving macrosperma and microsperma. Crop Improv 24:74–77

Chahota RK, Kishore N, Dhiman KC, Sharma TR, Sharma SK (2007) Predicting transgressive segregants in early generation using single seed descent method-derived micro-macrosperma gene pool of lentil. Euphytica 156:305–310

Chakherchaman SA, Mostafaei H, Imanparast L, Eivazian MR (2009) Evaluation of drought tolerance in lentil advanced genotypes in Ardabil region, Iran. J Food Agric Environ 7(3/4):283–288

Chakraborty U, Pradhan D (2010) Biochemical responses of lentil (*Lens culinaris* Medik.) to elevated temperature stress. J Pharm Biol Chem Sci 1(3):575–585

Chen C, Miller P, Muehlbauer F, Neill K, Wichman D, McPhee K (2006) Winter pea and lentil response to seeding date and micro-and macro-environments. Agron J 98(6):1655–1663

Chen W, Basandrai AK, Basandrai D, Banniza S, Bayaa B, Buchwaldt L, Davidson J, Larsen R, Rubiales D, Taylor PWJ (2009) Diseases and their management. In: Erskine W, Muehlbauer FJ, Sarker A, Sharma B (eds) The lentil: botany, production and uses. CABI, Wallingford, pp 269–270

Cho S, Chen W, Muehlbauer FJ (2004) Pathotype-specific genetic factors in chickpea (*Cicer arietinum* L.) for quantitative resistance to ascochyta blight. Theor Appl Genet 109(4):733–739

Choudhary A, Kumar S, Patil B (2013) Narrowing yield gaps through genetic improvement for fusarium wilt resistance in three pulse crops of the semi-arid tropics. SABRAO J Breed Genet 45:341–370

Choudhary R, Verma S, Panwar R, Chourasiya V, Pandey D (2017) Morphological characterization of lentil (*Lens culinaris* Medikus.) varieties based on six qualitative traits. J Pharmacogn Phytochem 6:1611–1615

Choudhury DR, Tarafdar S, Das M, Kundagrami S (2012) Screening lentil (*Lens culinaris* Medik.) germplasms for heat tolerance. Trends Biosci 5(2):143–146

Chowdhury MA, Andrahennadi CP, Slinkard AE, Vandenberg A (2001) RAPD and SCAR markers for resistance to acochyta blight in lentil. Euphytica 118(3):331–337

Chowrira GM, Akella V, Fuerst PE, Lurquin PF (1996) Transgenic grain legumes obtained by in planta electroporation-mediated gene transfer. Mol Biotechnol 5:85–96. https://doi.org/10.1007/bf02789058

Cicerali IN (2004) Effect of salt stress on antioxidant defense systems of sensitive and resistant cultivars of lentil (*Lens culinaris* M.). Doctoral dissertation, MSc thesis, Middle East Technical University, Ankara, Turkey

Clements JC, Haqqani AM, Siddique KH, French RJ (1997) Drought tolerance in lentil (*Lens culinaris*). Intl Food Legume Res Conf 3:22–26

Clough E, Barrett T (2016) The gene expression omnibus database. Methods Mol Biol 1418:93–110. https://doi.org/10.1007/978-1-4939-3578-9_5

Cochrane G, Karsch-Mizrachi I, Takagi T (2016) The international nucleotide sequence database collaboration. Nucl Acids Res 44:48–50. https://doi.org/10.1093/nar/gkv1323

Cohen D, Ladizinsky G, Ziv M, Muehlbauer FJ (1984) Rescue of interspecific Lens hybrids by means of embryo culture. Plant Cell Tissue Organ Cult 3(4): 343–347

Concibido VC, Diers BW, Arelli PR (2004) A decade of QTL mapping for cyst nematode resistance in soybean. Crop Sci 44(4):1121–1131

Covell S, Ellis RH, Roberts EH, Summerfield RJ (1986) The influence of temperature on seed germination rate in grain legumes: I. A comparison of chickpea, lentil, soyabean and cowpea at constant temperatures. J Exp Bot 37(5):705–715

Cromey MG, Mulholland RI, Russell AC, Jermyn WA (1987) *Ascochyta fabae* f. sp. *lentis* on lentil in New Zealand. NZ J Exp Agric 15:235–238

Croser JS, Clarke HJ, Siddique KH, Khan TN (2003) Low-temperature stress: implications for chickpea (*Cicer arietinum* L.) improvement. Crit Rev Plant Sci 22(2):185–219

Cubero JI (1984) Taxonomy, distribution and evolution of the lentil and its wild relatives. In: Genetic resources and their exploitation—chickpeas, faba beans and lentils. Springer, Dordrecht, pp 187–203

Dadu RHR, Ford R, Sambasivam P, Gupta D (2016) Screening of wild lentil germplasm to identify novel Ascochyta lentis resistance sources. Second international legume society conference, legumes for a sustainable world, pp 11–14 Toria, Portugal

Dadu RHR, Ford R, Sambasivam P, Gupta D (2017) A novel *Lens orientalis* resistance source to the recently evolved highly aggressive Australian *Ascochyta lentis* Isolates. Front Plant Sci 8:1038. https://doi.org/10.3389/fpls.2017.01038

Dai A (2011) Drought under global warming: a review. WIREs Clim Change 2:45–65. https://doi.org/10.1002/wcc.81

Dash S, Van Hemert J, Hong L, Wise RP, Dickerson JA (2012) PLEXdb: gene expression resources for plants and plant pathogens. Nucl Acids Res 40:D1194–D1201. https://doi.org/10.1093/nar/gkr938

Dash S, Campbell JD, Cannon EKS (2016) Legume information system (LegumeInfo.org): a key component of a set of federated data resources for the legume family. Nucl Acids Res 44:D1181–D1188. https://doi.org/10.1093/nar/gkv1159

Dash AP, De Kumar D, Mohanty S, Lenka D (2017) Screening of Lentil (*Lens culinaris* Medik.) genotypes and correlation analysis under PEG imposed water stress condition. Int J Bio-Res Stress Manage 8(4):539–547

Datta S, Prasoonpal G, Mayank K, Kumar S (2016) Genetic diversity analysis of lentil (*Lens culinaris* Medik) cultivars using inter simple sequence repeats markers. Mol Plant Breed 7(23):1–9

Davidson J, Smetham G, Russ MH (2016) Changes in aggressiveness of the Ascochyta lentis population in Southern Australia. Front Plant Sci 7:393

de la Puente R, Garcia P, Polanco C, Perez de la Vega M (2013) An improved intersubspecific genetic map in *Lens* including functional markers. Span J Agric Res 11:132–136

De La Rosa L, Jouve N (1992) Genetic variation for isozyme genes and proteins in Spanish primitive cultivars and wild subspecies of *Lens*. Euphytica 59:181–187

De La Vega MP, Durán Y (2004) Assessment of genetic variation and species relationships in a collection of "Lens" using RAPD and ISSR. Span J Agric Res 538–544

Delahunty A, Nuttall J, Nicolas M, Brand J (2015) Genotypic heat tolerance in lentil. In: Proceedings of the 17th ASA conference, 20–24 Sept 2015, Hobart, Australia, pp 20–24

Devi JM, Sinclair TR, Vadez V (2010) Genotypic variation in peanut for transpiration response to vapor pressure deficit. Crop Sci 50:191–196

Dhankher OP, Foyer CH (2018) Climate resilient crops for improving global food security and safety. Plant Cell Environ 41:877–884. https://doi.org/10.1111/pce

Dikshit HK, Singh A, Singh D (2015a) Genetic diversity in *Lens* species revealed by EST and genomic simple sequence repeat analysis. PLoS ONE 10:e0138101

Dikshit HK, Singh A, Singh D, Aski MS, Prakash P, Jain N, Meena S, Kumar S, Sarker A (2015a) Genetic diversity in *Lens* species revealed by EST and genomic simple sequence repeat analysis. PLoS ONE e0138101

Dixit G, Katiyar P, Singh B, Kumar S (2009) Lentil varieties in India. All India Coordinated Research Project on MULLaRP, IIPR, Kanpur, India

Dufourmantel N, Pelissier B, Garcon F, Peltier G, Ferullo JM, Tissot G (2004) Generation of fertile transplastomic soybean. Plant Mol Biol 55:479–489

Dufourmantel N, Tissot G, Garcon F, Pelissier B, Dubald M (2006) Stability of soybean recombinant plastome over six generations. Transgen Res 15:305–311

Duran Y, Fratini R, Garcia P, De la Vega MP (2004) An intersubspecific genetic map of Lens. Theor Appl Genet 108:1265–1273

Echeverrigaray S, Oliveira A, Carvalho M, Derbyshire E (1998) Evaluation of the relationship between lentil accessions using comparative electrophoresis of seed proteins [*Lens culinaris* Medik.]. J Genet Plant Breed 52(1):89–94

Elad Y, Pertot I (2014) Climate change impacts on plant pathogens and plant diseases. J Crop Improv 28(1):99–139

El-Bouhssini M, Sarker A, Erskine W, Joubi A (2008) First sources of resistance to Sitona weevil (*Sitona crinitus Herbst*) in wild Lens species. Genet Resour Crop Evol 55(1):1–4

El-Enany AE, AL-Anazi AD, Dief N, Wafa'a A (2013) Role of antioxidant enzymes in amelioration of water deficit and waterlogging stresses on *Vigna sinensis* plants. J Biol Earth Sci 3(1):144–153

Ellis RH, Barrett S (1994) Alternating temperatures and rate of seed germination in lentil. Ann Bot 74:519–524
El-Nahas A, El-Shazly H, Ahmed SM, Omran A (2011) Molecular and biochemical markers in some lentil (*Lens culinaris* Medik.) genotypes. Ann Agric Sci 56:105–112
Erskine W (1997) Lessons for breeders from land races of lentil. Euphytica 93:107–112
Erskine W, Choudhary M (1986) Variation between and within lentil landraces from Yemen Arab Republic. Euphytica 35:695–700
Erskine W, Muehlbauer F (1991) Allozyme and morphological variability, outcrossing rate and core collection formation in lentil germplasm. Theor Appl Genet 83:119–125
Erskine W, Saxena MC (1993) Problems and prospects of stress resistance breeding in lentil. In: Singh KB, Saxena MC (eds) Breeding for stress tolerance in cool-season food legumes. Wiley, New York, pp 51–62
Erskine W, Myveci K, Izgin N (1981) Screening a world lentil collection for cold tolerance. Lens Newsl 8:5–8
Erskine W, Adham Y, Holly L (1989) Geographic distribution of variation in quantitative traits in a world lentil collection. Euphytica 43:97–103
Erskine W, Ellis R, Summerfield R, Roberts E, Hussain A (1990) Characterization of responses to temperature and photoperiod for time to flowering in a world lentil collection. Theor Appl Genet 80:193–199
Erskine W, Hussain A, Tahir M, Bahksh A, Ellis RH, Summerfield RJ, Roberts EH (1994) Field evaluation of a model of photothermal flowering responses in a world lentil collection. Theor Appl Genet 88(3–4):423–428
Erskine W, Bayaa B, Saxena M (1996) Registration of ILL 5588 lentil germplasm resistant to vascular wilt and ascochyta blight. Crop Sci 36
Erskine W, Chandra S, Chaudhry M, Malik IA, Sarker A, Sharma B, Tufail M, Tyagi MC (1998) A bottleneck in lentil: widening its genetic base in South Asia. Euphytica 101(2):207–211
Erskine W, Sarker A, Kumari S (2016) Lentil breeding. In: Wrigley CW, Corke H, Seetharaman K, Faubion JM (eds) Encyclopedia of food grains, 2nd edn. Elsevier, Oxford, pp 317–324
Eujayl I, Baum M, Erskine W, Pehu E, Muehlbauer FJ (1997) The use of RAPD markers for lentil genetic mapping and the evaluation of distorted F2 segregation. Euphytica 96(3):405–412
Eujayl I, Baum M, Powell W, Erskine W, Pehu E (1998a) A genetic linkage map of lentil (*Lens* sp.) based on RAPD and AFLP markers using recombinant inbred lines. Theor Appl Genet 97(1/2):83–89
Eujayl I, Erskine W, Bayaa B, Baum M, Pehu E (1998b) Fusarium vascular wilt in lentil: inheritance and identification of DNA markers for resistance. Plant Breed 117:497–499. https://doi.org/10.1111/j.1439-0523.1998.tb01982.x
Eujayl I, Erskine W, Baum M, Pehu E (1999) Inheritance and linkage analysis of frost injury in lentil. Crop Sci 39(3):639–642
Fabregat A, Jupe S, Matthews L (2018) The reactome pathway knowledgebase. Nucl Acids Res 46:D649–D655. https://doi.org/10.1093/nar/gkx1132
Fageria NK (1992) Maximizing crop yields. Marcel Dekker, New York, NY
Fageria NK, Baligar VC (1997) Phosphorous—use efficiency by corn genotypes. J Plant Nutr 20:1267–1277
FAO (2016) The state of world fisheries and aquaculture. Contributing to food security and nutrition for all. Rome, Italy, 200 pp.
Faris ME, Takruri HR, Issa AY (2013) Role of lentils (*Lens culinaris* L.) in human health and nutrition: a review. Medit J Nutr Met 6(1):3–16
Farooq M, Gogoi N, Hussain M, Barthakur S, Paul S, Bharadwaj N, Migdadi HM, Alghamdi SS, Siddique KH (2017) Effects, tolerance mechanisms and management of salt stress in grain legumes. Plant Physiol Biochem 118:199–217
Fedoruk MJ, Vandenberg A, Bett KE (2013) Quantitative trait loci analysis of seed quality characteristics in lentil using single nucleotide polymorphism markers. Plant Genome 1(6):3

Ferguson M (2000) Conserved resources, priorities for collection and future prospects. In: Knight R (ed) Lining research and marketing opportunities for pulses in 21st century. Current plant science and biotechnology in agriculture, vol 34, pp 613–620

Ferguson ME, Robertson LD (1996) Genetic diversity and taxonomic relationships within the genus *Lens* as revealed by allozyme polymorphism. Euphytica 91:163–172

Ferguson M, Ford-Lloyd B, Robertson L, Maxted N, Newbury H (1998a) Mapping the geographical distribution of genetic variation in the genus *Lens* for the enhanced conservation of plant genetic diversity. Mol Ecol 7:1743–1755

Ferguson ME, Robertson LD, Ford-Lloyd BV, Newbury HJ, Maxted N (1998b) Contrasting genetic variation amongst lentil landraces from different geographical origins. Euphytica 102:265–273

Ferguson ME, Robertson LD (1999) Morphological and phenological variation in the wild relatives of lentil. Genet Resour Crop Evol 46(1):3–12

Ferguson ME, Maxted N, Van Slageren M, Robertson LD (2000) A re-assessment of the taxonomy of *Lens* Mill. (Leguminosae, Papilionoideae, Vicieae). Bot J Linn Soc 133:41–59

Fernández-Aparicio MF, Rispail N, Prats E, Morandi D, Garcia-Garrido JM, Dumas-Gaudot E, Rubiales D (2009) Parasitic plant infection is partially controlled through symbiotic pathways. Weed Res 1–7

Fiala JV (2006) Transferring resistance to Colletotrichum truncatum from wild lentil species to cultivated lentil species (*Lens culinaris subsp culinaris*). Doctoral dissertation, MSc thesis, University of Saskatchewan, Saskatoon, Canada

Fiala JV, Tullu A, Banniza S, Séguin-Swartz G, Vandenberg A (2009) Interspecies transfer of resistance to anthracnose in lentil. Crop Sci 49:825–830

Fikiru E, Tesfaye K, Bekele E (2007) Genetic diversity and population structure of Ethiopian lentil (*Lens culinaris* Medikus) landraces as revealed by ISSR marker. Afr J Biotechnol 6(12):1460–1468

Fikru E, Sarker A, Fikre A, Ahmed S, Ali K, Erskine W (2007) Registration of 'Assano' lentil. J Plant Registrat 1:41

Ford R, Pang E, Taylor P (1997) Diversity analysis and species identification in *Lens* using PCR generated markers. Euphytica 96:247–255. https://doi.org/10.1023/a:1003097600701

Ford R, Pang E, Taylor P (1999) Genetics of resistance to ascochyta blight (*Ascochyta lentis*) of lentil and the identification of closely linked RAPD markers. Theor Appl Genet 98(1):93–98

Ford R, Mustafa B, Sambasivam P, Baum M, Rajesh P (2018) Biotechnology and gene mapping in lentil. In: Grain legumes, vol 57. European Association for Grain Legume Research, pp 37–38

Fratini R, Ruiz ML (2006) Interspecific hybridization in the genus *Lens* applying in vitro embryo rescue. Euphytica 150:271–280

Fratini R, Ruiz ML, de la Vega MP (2004) Intra-specific and inter-sub-specific crossing in lentil. Can J Plant Sci 84:981–986

Fratini R, García P, Ruiz ML (2006) Pollen and pistil morphology, in vitro pollen grain germination and crossing success of *Lens* cultivars and species. Plant Breed 125(5):501–505

Fratini R, Durán Y, García P, De La Vega MP (2007) Identification of quantitative trait loci (QTL) for plant structure, growth habit and yield in lentil. Spanish J Agri Res 5(3):348–356

Gaad D, Laouar M, Abdelguerfi A, Gaboun F (2018) Collection and agro morphological characterization of Algerian accessions of lentil (*Lens culinaris*). Biodivers J Biol Divers 19:183–193

Galasso I (2003) Distribution of highly repeated DNA sequences in species of the genus *Lens* Miller. Genome 46:1118–1124

Gao J, Zhang Y, Zhang C, Qi F, Li X, Mu S, Peng ZO (2014) Characterization of the floral transcriptome of Moso bamboo (*Phyllostachys edulis*) at different flowering developmental stages by transcriptome sequencing and RNA-seq analysis. PLoS ONE 9(6):e98910

Gaur PM, Krishnamurthy L, Kashiwagi J (2008) Improving drought avoidance root traits in chickpea (*Cicer arietinum*)—current status of research at ICRISAT. Plant Prod Sci 11:3–11. https://doi.org/10.1626/pps.11.3

Gaur P, Saminen S, Krishnamurthy L (2015) High temperature tolerance in grain legumes. Legume Persp 7:23–24

Ghanem ME, Kibbou F, Guiguitant J, Sinclair TR (2017) Opportunities to improve the seasonal dynamics of water use in lentil (*Lens culinaris* Medik.) to enhance yield increase in water-limited environments. Chem Biol Technol Agric 4:22

GO Consortium (2013) Gene ontology annotations and resources. Nucl Acids Res 41:D530–D535. https://doi.org/10.1093/nar/gks1050

Gokcay D (2012) Physiological and biochemical screening of different Turkish lentil (*Lens culinaris* M.) cultivars under drought stress condition. Doctoral dissertation, Middle East Technical University, Ankara, Turkey

Golezani KG, Yengabad FM (2012) Physiological responses of lentil (*Lens culinaris* Medik) to salinity. Int J Agric Crop Sci 20:1531–1535

Gonzalez A, Bell G (2013) Evolutionary rescue and adaptation to abrupt environmental change depends upon the history of stress. Philos Trans R Soc B 368:20120079

Goodstein DM, Shu S, Howson R (2012) Phytozome: a comparative platform for green plant genomics. Nucl Acids Res 40:D1178–D1186. https://doi.org/10.1093/nar/gkr944

Gorim LY, Vandenberg A (2017a) Evaluation of wild lentil species as genetic resources to improve drought tolerance in cultivated lentil. Front Plant Sci 8:1129

Gorim LY, Vandenberg A (2017b) Root traits, nodulation and root distribution in soil for five wild lentil species and *Lens culin*aris (Medik.) grown under well-watered conditions. Front Plant Sci 8:1632

Govindaraj M, Vetriventhan M, Srinivasan M (2015) Importance of genetic diversity assessment in crop plants and its recent advances: an overview of its analytical perspectives. Genet Res Int 2015:431487

Grant D, Nelson RT, Cannon SB, Shoemaker RC (2010) SoyBase, the USDA-ARS soybean genetics and genomics database. Nucl Acids Res 38:D843–D846. https://doi.org/10.1093/nar/gkp798

Grassini P, Eskridge KM, Cassman KG (2013) Distinguishing between yield advances and yield plateaus in historical crop production trends. Nat Commun 4:2918

GRDC (2013) GRDC impact assessment report series: title: an economic analysis of GRDC investment in the lentil breeding program. http://www.grdc.com.au

Gulati A, Schryer P, McHughen A (2001) Regeneration and micrografting of lentil shoots. In Vitro Cell Dev Biol-Plant 37(6):798

Gulati A, Schryer P, McHughen A (2002) Production of fertile transgenic lentil (*Lens culinaris* Medik) plants using particle bombardment. Vitro Cell Dev Biol Plant 38:316–324. https://doi.org/10.1079/ivp2002303

Gupta D, Sharma SK (2005) Embryo-ovule rescue technique for overcoming post-fertilization barriers in interspecific crosses of Lens. J Lentil Res 2:27–30

Gupta D, Sharma SK (2007) Widening the gene pool of cultivated lentils through introgression of alien chromatin from wild *Lens* subspecies. Plant Breed 126:58–61

Gupta PK, Kumar J, Mir RR, Kumar A (2010) Marker-assisted selection as a component of conventional plant breeding. Plant Breed Rev 22:33–145

Gupta D, Taylor P, Inder P, Phan H, Ellwood S, Mathur P, Sarker A, Ford R (2012a) Integration of EST-SSR markers of *Medicago truncatula* into intraspecific linkage map of lentil and identification of QTL conferring resistance to ascochyta blight at seedling and pod stages. Mol Breed 1:429–439

Gupta D, Taylor PWJ, Inder P, Phan HTT, Ellwood SR, Mathur PN (2012b) Integration of EST-SSR markers of Medicago truncatula into intraspecific linkage map of lentil and identification of QTL conferring resistance to Ascochyta blight at seedling and pod stages. Mol Breed 30:429–439

Gupta M, Verma B, Kumar N, Chahota RK, Rathour R, Sharma SK, Bhatia S, Sharma TR (2012c) Construction of intersubspecific molecular genetic map of lentil based on ISSR, RAPD and SSR markers. J Genet 91(3):279–287

Gurdip S, Kuldip S, Gill A, Brar J (1982) Screening of lentil varieties/lines for blight resistance. Indian Phytopathol 35:678–679

Hamdi AH (1987) Variation in lentil (*Lens culinaris* Medik) in response to irrigation. Doctoral dissertation, Durham University, Durham, UK

Hamdi A, Erskine W (1994) Germplasm program legumes-annual report. ICARDA Aleppo, Syria
Hamdi A, Erskine W (1996) Reaction of wild species of the genus *Lens* to drought. Euphytica 91(2):173–179
Hamdi A, Erskine W, Gates P (1991) Relationships among economic characters in lentil. Euphytica 57:109–116
Hamdi A, Erskine W, Gates P (1992) Adaption of lentil seed yield to varying moisture supply. Crop Sci 32(4):987–990
Hamdi A, Küsmenoğlu I, Erskine W (1996) Sources of winter hardiness in wild lentil. Genet Resour Crop Evol 43(1):63–67
Hamdi A, Katerji N, Mastrorilli M, Ameen A (2000) Lentil (*Lens culinaris* Med.) sensitivity to salinity through the water use efficiency. International symposium on techniques to control salination for horticultural productivity 573:311–319
Hamwieh A, Udupa SM, Choumane W, Sarker A, Dreyer F, Jung C, Baum M (2005) A genetic linkage map of *Lens* sp. based on microsatellite and AFLP markers and the localization of fusarium vascular wilt resistance. Theor Appl Genet 110:669–677
Hamwieh A, Udupa SM, Sarker A, Jung C, Baum M (2009) Development of new microsatellite markers and their application in the analysis of genetic diversity in lentils. Breed Sci 59(1):77–86
Hartung F, Schiemann J (2014) Precise plant breeding using new genome editing techniques: opportunities, safety and regulation in the EU. Plant J 78(5):742–752. https://doi.org/10.1111/tpj.12413
Havey M, Muehlbauer F (1989) Variability for restriction fragment lengths and phylogenies in lentil. Theor Appl Genet 77:839–843
Havey MJ, Lilly JW, Bohanec B, Bartoszewski G, Malepszy S (2002) Cucumber: a model angiosperm for mitochondrial transformation? J Appl Genet 43:1–17
Hobson K, Armstrong R, Nicolas M, Connor D, Materne M (2006) Response of lentil (*Lens culinaris*) germplasm to high concentrations of soil boron. Euphytica 151:371–382
Hoffman DL, Soltis DE, Muehlbauer F, Ladizinsky G (1986) Isozyme polymorphism in *Lens* (Leguminosae). Syst Bot 392–402
Hoffman DL, Muehlbauer F, Ladizinsky G (1988) Morphological variation in *Lens* (Leguminosae). Syst Bot 87–96
Hossain MS, Alam MU, Rahman A, Hasanuzzaman M, Nahar K, Al Mahmud J, Fujita M (2017) Use of iso-osmotic solution to understand salt stress responses in lentil (*Lens culinaris* Medik.). South Afr J Bot 113:346–354
Hou BK, Zhou YH, Wan LH, Zhang ZL, Shen GF, Chen ZH, Hu ZM (2003) Chloroplast transformation in oilseed rape. Transgen Res 12:111–114
Huerta-Cepas J, Szklarczyk D, Forslund K, Cook H, Heller D, Walter MC, Rattei T, Mende DR, Sunagawa S, Kuhn M, Jensen LJ (2016) eggNOG 4.5: a hierarchical orthology framework with improved functional annotations for eukaryotic, prokaryotic and viral sequences. Nucl Acids Res 44:D286–D293. https://doi.org/10.1093/nar/gkv1248
Ialicicco M, Viscosi V, Arena S (2012) *Lens culinaris* Medik. seed proteome: analysis to identify landrace markers. Plant Sci 197:1–9
Idrissi O, Houasli C, Nsarellah N (2013) Comparaison de lignées avancées de lentille sous stress hydrique durant la phase de floraison et formation des gousses. Nat Technol 8:53–61
Idrissi O, Houasli C, Udupa SM, De Keyser E, Van Damme P, De Riek J (2015a) Genetic variability for root and shoot traits in a lentil (*Lens culinaris* Medik.) recombinant inbred line population and their association with drought tolerance. Euphytica 204(3):693–709
Idrissi O, Udupa SM, Houasli C, De Keyser E, Van Damme P, De Riek J (2015b) Genetic diversity analysis of Moroccan lentil (*Lens culinaris* Medik.) landraces using simple sequence repeat and amplified fragment length polymorphisms reveals functional adaptation towards agro-environmental origins. Plant Breed 134:322–332
Idrissi O, Udupa SM, De Keyser E, McGee RJ, Coyne CJ, Saha GC, De Riek J (2016) Identification of quantitative trait loci controlling root and shoot traits associated with drought tolerance in a lentil (*Lens culinaris* Medik.) Recombinant inbred line population. Front Plant Sci (7):1174

Iqbal S, Bakhsh A, Malik R (1990) Identification of resistant sources to ascochyta blight in lentil. Lens 17:26–27
Iqbal SM, Ghafoor A, Ali S, Ahmad I (2010) Identification of resistant source of ascochyta blight from local lentil germplasm. Pak J Phytopathol 22:29–33
Jayasundara HP, Thomson BD, Tang C (1997) Responses of cool season grain legumes to soil abiotic stresses. In: Advances in agronomy, vol 63. Academic Press, pp 77–151
Jin L, Jian-Ping G, Dong-Xu X, Zhang X-Y, Jing G, Xu-Xiao Z (2008) Genetic diversity and population structure in lentil (*Lens culinaris* Medik.) germplasm detected by SSR markers. Acta Agron Sin 34:1901–1909
Johansen C, Baldev B, Brouwer JB, Erskine W, Jermyn WA, Li-Juan L, Malik BA, Miah AA, Silim SN (1994) Biotic and abiotic stresses constraining productivity of cool season food legumes in Asia, Africa and Oceania. In: Muehlbauer FJ, Kaiser WJ (eds) Expanding the production and use of cool season food legumes. Kluwer Academic Publishers, Dordrecht, Netherlands, pp 175–194
Johnson CR, Combs Jr GF, Thavarajah P (2013) Lentil (*Lens culinaris* L.): a prebiotic-rich whole food legume. Food Res Intl 51(1):107–113
Jyothi MN, Rai DV, Nagesh Babu R (2015) Identification and characterization of high temperature stress responsive novel miRNAs in French bean (*Phaseolus vulgaris*). Appl Biochem Biotechnol 176:835. https://doi.org/10.1007/s12010-015-1614-2
Kahraman A, Kusmenoglu I, Aydin N, Aydogan A, Erskine W, Muehlbauer FJ (2004a) Genetics of winter hardiness in 10 lentil recombinant inbred line populations. Crop Sci 44(1):5–12
Kahraman A, Kusmenoglu I, Aydin N, Aydogan A, Erskine W, Muehlbauer FJ (2004b) QTL mapping of winter hardiness genes in lentil. Crop Sci 44(1):13–22
Kahraman A, Temel HY, Aydoğan A, Tanyolac MB (2015) Major quantitative trait loci for flowering time in lentil. Turk J Agric For 39(4):588–595
Kanehisa M, Sato Y, Kawashima M (2016) KEGG as a reference resource for gene and protein annotation. Nucl Acids Res 44:D457–D462. https://doi.org/10.1093/nar/gkv1070
Kang UG, Choi JS, Kim JJ, Cho JS (2017) Yield potentials of rice and soybean as affected by cropping systems in mid-mountainous paddy soils of Korea. 한국토양비료학회지 Kor J Soil Sci Fert 50(4):259–274
Kant P, Materne M, Rodda MS, Slater AT (2017) Screening lentil germplasm for stemphylium blight resistance. Australas Plant Pathol 46(2):1–8
Karaköy T, Erdem H, Baloch FS (2012) Diversity of macro-and micronutrients in the seeds of lentil landraces. Sci World J. http://dx.doi.org/10.1100/2012/710412
Karki PB, Joshi S, Chaudhary G, Chaudhary RN (1993) Studies on botrytis gray mold of chickpea in Nepal. In: Haware MP, Gowda CLL, McDonald D (eds) Recent advances in research on botrytis gray mold of chickpea. ICRISAT, Patancheru, AP, India, pp 11–13
Katerji N, Van Hoorn JW, Hamdy A, Mastrorilli M, Oweis T, Erskine W (2001) Response of two varieties of lentil to soil salinity. Agric Water Manage 47(3):179–190
Katerji N, Van Hoorn JW, Hamdy A, Mastrorilli M (2003) Salinity effect on crop development and yield, analysis of salt tolerance according to several classification methods. Agric Water Manage 62(1):37–66
Kaur S, Cogan NO, Pembleton LW, Shinozuka M, Savin KW, Materne M, Forster JW (2011) Transcriptome sequencing of lentil based on second-generation technology permits large-scale unigene assembly and SSR marker discovery. BMC Genomics 12(1):265
Kaur S, Cogan NI, Stephens A, Noy D, Butsch M, Forster J (2014) EST-SNP discovery and dense genetic mapping in lentil (*Lens culinaris* Medik.) enable candidate gene selection for boron tolerance. Theor Appl Genet 127:703–713
Kemble RJ, Barsby TL, Yarrow SA (1988) Ectopic expression of mitochondrial gamma carbonic anhydrase 2 causes male sterility by anther indehiscence. Plant Mol Biol 70(471):485
Keshtiban RK, Carvani V, Imandar M (2015) Effects of salinity stress and drought due to different concentrations of sodium chloride and polyethylene glycol 6000 on germination and seedling growth characteristics of lentil (*Lens culinaris* Medik). Adv Environ Biol 15:445–451

Khan MS, Maliga P (1999) Fluorescent antibiotic resistance marker for tracking plastid transformation in higher plants. Nat Biotechnol 17:910–915

Khatib F, Koudsieh S, Ghazal B, Barton J, Tsujimoto H, Baum M (2007) Developing herbicide resistant lentil (*Lens culinaris* Medikus subsp. *culinaris*) through *Agrobacterium*-mediated transformation. Arab J Plant Protec 25:185–192

Khatib F, Makris A, Yamaguchi-Shinozaki K, Kumar S, Sarker A, Erskine W (2011) Expression of the DREB1A gene in lentil (*Lens culinaris* Medik. subsp *culinaris*) transformed with the Agrobacterium system. Crop Pasture Sci 62:488–495. https://doi.org/10.1071/cp10351

Khazaei H, Caron CT, Fedoruk M, Diapari M, Vandenberg A, Coyne CJ, McGee R, Bett KE (2016) Genetic diversity of cultivated lentil (*Lens culinaris* Medik.) and its relation to the world's agro-ecological zones. Front Plant Sci 7:1093

Kokten K, Karakoy T, Bakoglu A, Akcura M (2010) Determination of salinity tolerance of some lentil (*Lens culinaris* M.) varieties. J Food Agric Environ 8(1):140–143

Komatsu S, Yamamoto A, Nakamura T, Nouri MZ, Nanjo Y, Nishizawa K (2011) Comprehensive analysis of mitochondria in roots and hypocotyls of soybean under flooding stress using proteomics and metabolomics techniques. J Proteome Res 10:3993–4004. https://doi.org/10.1021/pr2001918

Koul PM, Sharma V, Rana M, Chahota RK, Kumar S, Sharma TR, (2017) Analysis of genetic structure and interrelationships in lentil species using morphological and SSR markers. 3 Biotechnology 7(1):83

Kuchuran M, Banniza S, Vandenberg B (2003) Evaluation of lentil varieties for resistance to botrytis gray mould. In: Meeting the challenge: opportunities and pressures within the pulse industry. In: Proceedings of pulse field days, Saskatoon, Jan 6, pp 6–7

Kumar J, Solanki RK (2014) Evaluation of lentil germplasm for agro-morphological traits. J Food Legume 27(4):302–306

Kumar J, Van Rheenen HA (2000) Brief communication. A major gene for time of flowering in chickpea. J Hered 91(1):67–68

Kumar S, Dhingra A, Daniell H (2004a) Stable transformation of the cotton plastid genome and maternal inheritance of transgenes. Plant Mol Biol 56:203–216

Kumar S, Gupta S, Chandra S, Singh BB (2004b) How wide is the genetic base of pulse crop? Pulses in new perspective. In: Ali M, Singh BB, Kumar S, Dhar V (eds) Indian Society of pulses research and development. Indian Institute of Pulses Resserch, Kanpur, India, pp 211–222

Kumar J, Basu PS, Srivastava E, Chaturvedi SK, Nadarajan N, Kumar S (2012) Phenotyping of traits imparting drought tolerance in lentil. Crop Past Sci 63(6):547–554

Kumar SK, Barpete S, Kumar J, Gupta P, Sarker A (2013) Global lentil production: constraints and strategies. SATSA Mukhapatra-Annu Tech 17:1–3

Kumar H, Dikshit HK, Singh A (2014a) Characterization of grain iron and zinc in lentil (*Lens culinaris* Medikus *culinaris*) and analysis of their genetic diversity using SSR markers. Aust J Crop Sci 8:1005

Kumar J, Srivastva E, Singh M, Kumar S, Nadarajan N, Sarker A (2014b) Diversification of indigenous gene-pool by using exotic germplasm in lentil (*Lens culinaris* Medikus subsp. *culinaris*). Physiol Mol Biol Plants 20:125–132

Kumar S, Rajendra K, Kumar J, Hamwieh A, Baum M (2015) Current knowledge in lentil genomics and its application for crop improvement. Front Plant Sci 6:78

Kumar J, Gupta S, Gupta P, Dubey S, Tomar RSS, Kumar S (2016a) Breeding strategies to improve lentil for diverse agro-ecological environments. Indian J Genet 76:530–549

Kumar J, Kant R, Kumar S, Basu PS, Sarker A, Singh NP (2016b) Heat tolerance in lentil under field conditions. Legume Genom Genet 23:7

Kumar J, Gupta S, Biradar RS, Gupta P, Dubey S, Singh NP (2018a) Association of functional markers with flowering time in lentil. J Appl Genet 59(1):9–21

Kumar J, Gupta S, Dubey S, Gupta P, Gupta DS, Singh N (2018b) Genetic diversity changes in Indian lentils over the times. J Plant Biochem Biotechnol 27:415–422

Kumar S, Choudhary AK, Rana KS, Sarker A, Singh M (2018c) Bio-fortification potential of global wild annual lentil core collection. PLoS ONE 13:e0191122

Kumar J, Kumar S, Gupta DS, Dubey S, Gupta S, Gupta P (2019) Molecular marker assisted gene pyramiding in lentils. In: Singh M (ed) Lentils. Academic Press, Elsevier, pp 125–139

Kumari S, Makkouk K (1995) Variability among twenty lentil genotypes in seed transmission rates and yield loss induced by pea seed-borne mosaic potyvirus infection. Phytopathol Mediter 34:129–132

Kumari J, Ahmad R, Chandra S (2007) Identification and pedigree analysis of lentil (*Lens culinaris*) genotypes tolerant to black aphids (*Aphis craccivora*). Indian J Agric Sci 77(8):544–545

Kumari SG, Larsen R, Makkouk KM, Bashir M (2009) 19 Virus diseases and their control. In: Erskine W, Muehlbauer FJ, Sarker A, Sharma B (eds) The lentil: botany, production and uses. CABI, Wallingford, pp 269–270

Kumari M, Mittal RK, Chahota RK, Thakur K, Lata S, Gupta D (2018) Assessing genetic potential of elite interspecific and intraspecific advanced lentil lines for agronomic traits and their reaction to rust (*Uromyces viciae-fabae*). Crop Pasture Sci 69(10):999–1008

Kumawat KR, Gothwal DK, Singh D (2017) Salinity tolerance of lentil genotypes based on stress tolerance indices. J Pharmacogn Phytochem 4:1368–1372

Kusmenoglu I, Aydin N (1995) The current status of lentil germplasm exploitation for adaptation to winter sowing in the Anatolian highlands. Autumn-sowing of lentil in the Highlands of West Asia and North Africa. In: Keatinge JDH, Kusmenoglu I (eds) Autumn Sowing of lentil in the highlands of West Asia and North Africa. Central Research Institute for Field Crops (CRIFC), Ankara, Turkey, pp 63–71

Kwon YS, Lee JM, Yi GB, Yi SI, Kim KM, Soh EH, Bae KM, Park E, Song IH, Kim BD (2005) Use of SSR markers to complement tests of distinctiveness, uniformity, and stability (DUS) of pepper (*Capsicum annuum* L.) varieties. Mol Cells 19:428–435

Ladizinsky G (1993) Lentil domestication: on the quality of evidence and arguments. Econ Bot 47(1):60–64

Lachaâl M, Grignon C, Hajji M (2002) Growth rate affects salt sensitivity in two lentil populations. J Plant Nutr 25(12):2613–2625

Ladizinsky G (1979) The origin of lentil and its wild genepool. Euphytica 28:179–187

Ladizinsky G (1999) Identification of the lentil's wild genetic stock. Genet Resour Crop Evol 46:115–118

Ladizinsky G, Abbo S (1993) Cryptic speciation in *Lens culinaris*. Genet Resour Crop Evol 40(1):1–5

Ladizinsky G, Braun D, Goshen D, Muehlbauer F (1984) The biological species of the genus *Lens* L. Bot Gaz 145:253–261

Ladizinsky G, Pickersgill B, Yamamoto K (1988) Exploitation of wild relatives of the food legumes. In: Summerfield RJ (ed) World crops, cool season food legumes. Kluwer Academic Publishers, Dordrecht, pp 967–987

Lal C, Sharma SK, Chahota RK (2000) Combining ability and heterosis for growth parameters in microsperma × macrosperma lentil. Crop Res 19:115–121

Latham L, Jones R (2001) Incidence of virus infection in experimental plots, commercial crops, and seed stocks of cool season crop legumes. Aust J Agric Res 52:397–413

Lázaro A, Ruiz M, De La Rosa L, Martín I (2001) Relationships between agro/morphological characters and climatic parameters in Spanish landraces of lentil (*Lens culinaris* Medik.). Genet Resour Crop Evol 48:239–249

Li X, Han Y, Teng W, Zhang S, Yu K, Poysa V, Anderson T, Ding J, Li W (2010) Pyramided QTL underlying tolerance to Phytophthora root rot in mega-environments from soybean cultivars 'Conrad' and 'Hefeng 25'. Theor Appl Genet 121(4):651–658

Lichtenzveig J, Scheuring C, Dodge J, Abbo S, Zhang HB (2005) Construction of BAC and BIBAC libraries and their applications for generation of SSR markers for genome analysis of chickpea, *Cicer arietinum* L. Theor Appl Genet 110(3):492–510

Lindbeck K, Bretag T, Materne M (2008) Field screening in Australia of lentil germplasm for resistance to botrytis grey mould. Aust Plant Pathol 37:373–378
Lombardi M, Materne M, Cogan NO, Rodda M, Daetwyler HD, Slater AT, Forster JW, Kaur S (2014) Assessment of genetic variation within a global collection of lentil (*Lens culinaris* Medik.) cultivars and landraces using SNP markers. BMC Genet 15(1):150
Luo Y, Ma T, Zhang A, Ong KH, Li Z, Yang J, Yin Z (2016) Marker-assisted breeding of the rice restorer line Wanhui 6725 for disease resistance, submergence tolerance and aromatic fragrance. Rice 9(1):66
Lurquin PF, Cai Z, Stiff CM, Fuerst EP (1998) Half-embryo cocultivation technique for estimating the susceptibility of pea (*Pisum sativum* L.) and lentil (*Lens culinaris* Medik.) cultivars to *Agrobacterium tumefaciens*. Mol Biotechnol 9:175–179
Maher L, Armstrong R, Connor D (2003) Salt tolerant lentils—a possibility for the future. In: Proceedings of the 11th Australian agronomy conference, Feb, The Australian Society of Agronomy, Geelong, Victoria, pp 2–6
Mahmoudian M, Yucel M, Oktem HA (2002) Transformation of lentil (*Lens culinaris* M.) cotyledonary nodes by vacuum infiltration of *Agrobacterium tumefaciens*. Plant Mol Biol Rep 20:251–257 https://doi.org/10.1007/bf02782460
Makkouk K, Kumari S (1990) Variability among 19 lentil genotypes in seed transmission rates and yield loss induced by broad bean stain virus infection. Lens Newsl 17:31–33
Makkouk K, Kumari S, Sarker A, Erskine W (2001) Registration of six lentil germplasm lines with combined resistance to viruses. Crop Sci 41:931
Malik AI, Ailewe TI, Erskine W (2015) Tolerance of three grain legume species to transient waterlogging. AoB Plants 1:7. https://doi.org/10.1093/aobpla/plv040
Mamo T, Richter C, Heiligtag B (1996) Salinity effects on the growth and ion contents of some chickpea (*Cicer arietinum* L.) and lentil (*Lens culinaris* Medic.) varieties. J Agron Crop Sci 176(4):235–247
Marschner H (1995) Mineral nutrition of higher plants. Academic Press, San Diego, CA
Materne M, Reddy AA (2007) Commercial cultivation and profitability. In: Yadav SS, McNeil D, Stevenson PC (eds) The lentil—an ancient crop for modern times. Springer, Dordrecht, Rotterdam, The Netherlands, pp 173–186
Materne M, Siddique KH (2009) Agroecology and crop adaptation. In: Erskine W, Muehlbauer F, Sarker F, Sharma F (eds) The lentil: botany, production and uses. CABI, Wallingford, UK, pp 47–63
Mayer M, Bagga S (2002) The phylogeny of *Lens* (Leguminosae): new insight from ITS sequence analysis. Plant Syst Evol 232:145–154
Mayer M, Soltis P (1994) Chloroplast DNA phylogeny of *Lens* (Leguminosae): origin and diversity of the cultivated lentil. Theor Appl Genet 87:773–781
Mia MW, Yamauchi A, Kono Y (1996) Root system structure of six food legume species: inter- and intraspecific variations. Jpn J Crop Sci 65(1):131–140
Mishra BK, Srivastava JP, Lal JP (2014) Drought stress resistance in two diverse genotypes of lentil imposed at different phenophases. J Food Legume 27(4):307–314
Mishra BK, Srivastava JP, Lal JP, Sheshshayee MS (2016) Physiological and biochemical adaptations in lentil genotypes under drought stress. Russ J Plant Physiol 63(5):695–708
Mishra BK, Srivastava JP, Lal JP (2018) Drought resistance in lentil (*Lens culinaris* Medik.) in relation to morphological, physiological parameters and phenological developments. Intl J Curr Microbiol Appl Sci 7(1):2288–2304
Mondini L, Noorani A, Pagnotta MA (2009) Assessing plant genetic diversity by molecular tools. Diversity 1:19–35
Muehlbauer FJ, Weeden NF, Hoffman DL (1989) Inheritance and linkage relationships of morphological and isozyme loci in lentil (*Lens Miller*). J Heredity 80(4):298–303
Muehlbauer FJ, Cho S, Sarker A, McPhee KE, Coyne CJ, Rajesh PN, Ford R (2006) Application of biotechnology in breeding lentil for resistance to biotic and abiotic stress. Euphytica 147(1–2):149–165

Muench D, Slinkard A, Scoles G (1991) Determination of genetic variation and taxonomy in lentil (*Lens Miller*) species by chloroplast DNA polymorphism. Euphytica 56:213–218
Mun T, Bachmann A, Gupta V (2016) Lotus base: an integrated information portal for the model legume *Lotus japonicus*. Sci Rep 6:39447. https://doi.org/10.1038/srep39447
Murray GM (2012) diseases. Grains Research and Development Corporation, Victoria, Australia
Murray GA, Eser D, Gusta LV, Eteve G (1988) Winterhardiness in pea, lentil, faba bean and chickpea. In: Summerfield RJ (ed) World crops: cool season food legumes. Kluwer Academic Publishers, Dordrecht, Netherlands, pp 831–843
Muscolo A, Sidari M, Anastasi U, Santonoceto C, Maggio A (2014) Effect of PEG-induced drought stress on seed germination of four lentil genotypes. J Plant Interact 9(1):354–363
Muscolo A, Junker A, Klukas C, Weigelt-Fischer K, Riewe D, Altmann T (2015) Phenotypic and metabolic responses to drought and salinity of four contrasting lentil accessions. J Exp Bot 66:5467–5480. https://doi.org/10.1093/jxb/erv208
Mustafa BM, Coram TE, Pang ECK (2009) A cDNA microarray approach to decipher lentil (*Lens culinaris*) responses to Ascochyta lentis. Australas Plant Pathol 38:617–631. https://doi.org/10.1071/AP09048
Naithani S, Preece J, D'Eustachio P (2017) Plant reactome: a resource for plant pathways and comparative analysis. Nucl Acids Res 45:D1029–D1039. https://doi.org/10.1093/nar/gkw932
Nasir M (1998) Improvement of drought and disease resistance in lentil in Nepal, Pakistan and Australia. Mid-term Report 1995–1998. Victorian Institute for Dryland Agriculture, Agriculture Victoria, Horsham
Nasir M, Bretag T (1998) Reactions of lentil accessions from 25 different countries to Australian isolates of *Ascochyta lentis*. Genet Resour Crop Evol 45:297–299
Negussie T, Bejiga G, Million E (1998) Lentil rust outbreak in Gimbichu district. Ethiopia, AgriTopia
Nelson RR (1978) Genetics of horizontal resistance to plant diseases. Annu Rev Phytopathol 16(1):359–378
Nessa B, Islam MR, Haque MM, Ahmed JU (2007) Soil flooding tolerance in lentil at vegetative stage. Prog Agri 18(2):17–24
Nuttall JG, Armstrong RD (2010) Impact of subsoil physicochemical constraints on crops grown in the Wimmera and Mallee is reduced during dry seasonal conditions. Soil Res 48(2):125–139
O'Boyle PD, Kelly JD, Kirk WW (2007a) Use of marker-assisted selection to breed for resistance to common bacterial blight in common bean. J Am Soc Hort Sci 132(3):381–386
O'Boyle PD, Kelly JD, Kirk WW (2007b) Use of marker-assisted selection to breed for resistance to common bacterial blight in common bean. J Am Hort Sci 132(3):381–386
O'Connor M, Peifer M, Bender W (1989) Construction of large DNA segments in *Escherichia coli*. Science 44(491):1307–1312
Ogutcen E, Ramsay L, Von Wettberg EB, Bett KE (2018) Capturing variation in *Lens* (Fabaceae): development and utility of an exome capture array for lentil. Appl Plant Sci 6:e01165
Oktem H, Mahmoudian M, Yucel M (1999) GUS gene delivery and expression in lentil cotyledonary nodes using particle bombardment. Lens Newsl 26:2–6
Öktem HA, Eyidoðan F, Demirba D, Bayraç AT, Öz MT, Özgür E, Selçuk F, Yücel M (2008) Antioxidant responses of lentil to cold and drought stress. J Plant Biochem Biotechnol 17(1):15–21
Oliveira L, Melo L, Brondani C, Peloso M, Brondani R (2008) Backcross assisted by microsatellite markers in common bean. Genet Mol Res 7(4):000–010
Ouji A, El-Bok S, Mouelhi M, Younes MB, Kharrat M (2015) Effect of salinity stress on germination of five Tunisian lentil (*Lens culinaris* L.) genotypes. Eur Sci J 11(21):30
Papatheodorou I, Fonseca NA, Keays M (2018) Expression Atlas: gene and protein expression across multiple studies and organisms. Nucl Acids Res 46:D246–D251. https://doi.org/10.1093/nar/gkx1158
Paterson AH, Tanksley SD, Sorrells ME (1991) DNA markers in plant improvement. Adv Agron 46:39–90

Peñaloza E, Tay JU, France AI (2007) Calpun-INIA, a large seed size and rust-resistant lentil (*Lens culinaris* Medik.) cultivar. Agric Técnica 67:68–71
Perez-De-Castro A, Vilanova S, Cañizares J (2012) Application of genomic tools in plant breeding. Curr Genom 13:179–195
Phan HT, Ellwood SR, Hane JK, Ford R, Materne M, Olive RP (2007) Extensive macrosynteny between *Medicago truncatula* and *Lens culinaris* ssp. *culinaris*. Theor Appl Genet 114(3):549–558
Piergiovanni A, Taranto G (2003) Geographic distribution of genetic variation in a lentil collection as revealed by SDS-PAGE fractionation of seed storage proteins [*Lens culinaris* Medik.]. J Genet Breed (Italy) 57(1):39–46
Piergiovanni AR, Taranto G (2005) Assessment of the genetic variation in Italian lentil populations by electrophoresis (SDS-PAGE) of seed storage proteins. Plant Genet Resour Newsl (IPGRI/FAO) 41:33–38
Podevin N, Devos Y, Davies HV, Nielsen KM (2012) Transgenic or not? No simple answer! EMBO Rep 13(12):1057–1061
Porch TG, Jahn M (2001) Effects of high-temperature stress on microsporogenesis in heat-sensitive and heat-tolerant genotypes of Phaseolus vulgaris. Plant Cell Environ 24(7):723–731
Rad MR, Ghasemi A, Arjmandinejad A (2010) Study of limit irrigation on yield of lentil (*Lens culinaris*) genotypes of national plant gene bank of Iran by drought resistance indices. Am Eurasian J Agric Environ Sci 7(2):238–241
Rafalski A (2002) Applications of single nucleotide polymorphisms in crop genetics. Curr Opin Plant Biol 5:94–100
Rahimi A, Norton R, McNeil D, Hoseini SM (2009) Effects of salinity and temperature on germination, seedling growth and ion relations of two lentil (*Lens culinaris*) cultivars. Seed Technol 1:76–86
Rahman MM, Sarker A, Kumar S, Ali A, Yadav NK, Rahman L (2009) Breeding for short season environments. In: Erskine W, Muehlbauer F, Sarker A, Sharma B (eds) The lentil: botany, production and uses. CAB International, Wallingford, UK, pp 121–136
Rai R, Singh RP (1999) Effect of salt stress on interaction between lentil (*Lens culinaris*) genotypes and *Rhizobium* spp. strains: symbiotic N_2 fixation in normal and sodic soils. Biol Fertil Soils 29(2):187–195
Rai R, Nasar SK, Singh SJ, Prasad V (1985) Interactions between Rhizobium strains and lentil (*Lens culinaris* Linn.) genotypes under salt stress. J Agric Sci 104(1):199–205
Ramgiry S, Paliwal K Tomar S (1989) Variability and correlations of grain yield and other quantitative characters in lentil. Lens Newsl 16(1):129–210
Rana M (2016) Molecular mapping of quantitative trait loci for drought tolerance and yield traits in lentil. CSKHPKV, Palampur, India
Rana J, Gautam N, Gayacharan MS (2016) Genetic resources of pulse crops in India: an overview. Indian J Genet Pl Br 76:420–436
Rana M, Sood A, Hussain W, Kaldate R, Sharma TR, Gill R, Kumar S, Singh S (2019) Gene pyramiding and multiple character breeding. In: Singh M (ed) Lentils. Academic Press, pp 83–124
Ray H, Bett K, Tar'an B, Vandenberg A, Thavarajah D, Warkentin T (2014) Mineral micronutrient content of cultivars of field pea, chickpea, common bean, and lentil grown in Saskatchewan, Canada. Crop Sci 54(4):1698–1708
Reda A (2015) Lentil (*Lens culinaris* Medikus) current status and future prospect of production in Ethiopia. Adv Plants Agric Res https://doi.org/10.15406/apar.2015.02.00040
Reddy M, Rathour R, Kumar N, Katoch P, Sharma T (2010) Cross-genera legume SSR markers for analysis of genetic diversity in *Lens* species. Plant Breed 129:514–518
Renfrew JM (1969) The archaeological evidence for the domestication of plants: methods and problems. In: The domestication and exploitation of plants and animals, pp 149–172
Retzel EF, Johnson JE, Lamblin AF, Paule CE (2007) Legume resources: MtDB and Medicago.Org. In: Edwards D (ed) Plant bioinformatics: methods and protocols. Humana Press, Totowa, NJ, pp 261–274

Rhee SY, Beavis W, Berardini TZ, Chen G, Dixon D, Doyle A, Garcia-Hernandez M, Huala E, Lander G, Montoya M, Miller N (2003) The Arabidopsis Information Resource (TAIR): a model organism database providing a centralized, curated gateway to Arabidopsis biology, research materials and community. Nucl Acids Res 31(1):224–228

Ribaut JM, Hoisington D (1998) Marker-assisted selection: new tools and strategies. Trends Plant Sci 3(6):236–239

Ribaut JM, De Vicente MC, Delannay X (2010) Molecular breeding in developing countries: challenges and perspectives. Curr Opin Plant Biol 13(2):213–218

Richardson K, Vales M, Kling J, Mundt C, Hayes P (2006) Pyramiding and dissecting disease resistance QTL to barley stripe rust. Theor Appl Genet 113(3):485–495

Roberts EH, Summerfield RJ, Muehlbauer FJ, Short RW (1986) Flowering in lentil (*Lens culinaris* Medic.): the duration of the photoperiodic inductive phase as a function of accumulated daylength above the critical photoperiod. Ann Bot 58(2):235–248

Rodda MS, Davidson J, Javid M, Sudheesh S, Blake S, Forster JW, Kaur S (2017) Molecular breeding for ascochyta blight resistance in lentil: Current progress and future directions. Front Plant Sci 8:1136

Roy S, Islam M, Sarker A, Malek M, Rafii M, Ismail M (2013) Determination of genetic diversity in lentil germplasm based on quantitative traits. Aust J Crop Sci 7:14

Roy S, Ray B, Sarker A, Das S (2015) DNA fingerprinting and genetic diversity in lentil germplasm using SSR markers. Asian J Conserv Biol 12:2

Rubeena, TP, Taylor P, Ades P, Ford R (2006) QTL mapping of resistance in lentil (*Lens culinaris* ssp. *culinaris*) to ascochyta blight (*Ascochyta lentis*). Plant Breed 125(5):506–512

Rubeena TP, Ford R, Taylor PWJ (2003a) Construction of an intraspecific linkage map of lentil. Theor Appl Genet 107:910–916

Rubeena TP, Ford R, Taylor PWJ (2003b) Molecular mapping the lentil (*Lens culinaris* ssp. culinaris) genome. Theor Appl Genet 107:910–916

Rubeena A, Taylor PWJ, Ades PK, Ford R (2006) QTL mapping of resistance in lentil (*Lens culinaris* ssp. *culinaris*) to ascochyta blight (*Ascochyta lentis*). Plant Breed 125:506–512. https://doi.org/10.1111/j.1439-0523.2006.01259.x

Rubiales D, Fondevilla S (2012) Future prospects for ascochyta blight resistance breeding in cool season food legumes. Front Plant Sci 3:27

Sabir J, Schwarz E, Ellison N, Zhang J, Baeshen NA, Mutwakil M, Jansen R, Ruhlman T (2014) Evolutionary and biotechnology implications of plastid genome variation in the inverted-repeat-lacking clade of legumes. Plant Biotechnol 12:743–754

Sadiq MS, Haidar S, Haq MA, Abbas G (2008) A high yielding and disease resistant mutant of lentil developed through seed irradiation of an exotic germplasm. Can J Pure Appl Sci 2(2):411–416

Saha GC, Sarker A, Chen W, Vandemark GJ, Muehlbauer FJ (2010a) Inheritance and linkage map positions of genes conferring resistance to stemphylium blight in lentil. Crop Sci 50:1831–1839

Saha GC, Sarker A, Chen WD, Vandemark GJ, Muehlbauer FJ (2010b) Identification of markers associated with genes for rust resistance in *Lens culinaris* Medik. Euphytica 175:261–265. https://doi.org/10.1007/s10681-010-0187-y

Saha GC, Sarker A, Chen W, Vandemark GJ, Muehlbauer FJ (2013) Inheritance and linkage map positions of genes conferring agromorphological traits in *Lens culinaris*. Int J Agron. https://doi.org/10.1155/2013/618926

Saito K, Matsuda F (2010) Metabolomics for functional genomics, systems biology, and biotechnology. Annu Rev Plant Biol 61:463–489

Sakr B, Sarker A, El Hassan H, Kadah N (2004) Registration of 'Hamria' lentil. Crop Sci 44:686

Salam MA, Islam MT (1994) Growth, yield and leaf-water attributes of some advanced mutant lentil lines under different soil moisture regimes [*Lens culinaris*]. Lens Newsl 21:32–35

Salehi M (2012) The study of drought tolerance of lentil (*Lens culinaris* Medik) in seedling growth stage. Int J Agron Plant Prod 3(1):38–41

Salehi M, Haghnazari A, Shekari F, Faramarzi A (2008) The study of seed yield and seed yield components of lentil (*Lens culinaris* Medik) under normal and drought stress conditions. Pak J Biol Sci 11(5):758–762

Salvi S, Tuberosa R (2005) To clone or not to clone plant QTLs: present and future challenges. Trends Plant Sci 10(6):297–304

Sanchez DH, Pieckenstain FL, Escaray F, Erban A, Kraemer U, Udvardi MK (2011) Comparative ionomics and metabolomics in extremophile and glycophytic *Lotus* species under salt stress challenge the metabolic preadaptation hypothesis. Plant, Cell Environ 34:605–617. https://doi.org/10.1111/j.1365-3040.2010.02266.x

Sanderson L, Barlow E, Vijayan P (2011) Know pulse: a breeder-focused web portal that integrates genetics and genomics of pulse crops with model genomes. Can J Plant Sci 91:395–395. https://doi.org/10.4141/CJPS11501

Saraf CS, Patil RR, Prashad M (1985) Correlation and regression studies in lentil cultivars. LENS 12:11–12

Sari E, Bhadauria V, Ramsay L, Borhan MH, Lichtenzveig J, Bett KE, Vandenberg A, Banniza S (2018) Defense responses of lentil (*Lens culinaris*) genotypes carrying non-allelic ascochyta blight resistance genes to *Ascochyta lentis* infection. PLoS ONE 13(9):e0204124

Sarker A, Erskine W, Hassan M, Afzal M, Murshed A (1999a) Registration of 'Barimasur-4' Lentil. Crop Sci 39:876

Sarker A, Erskine W, Sharma B, Tyagi MC (1999) Inheritance and linkage relationship of days to flower and morphological loci in lentil (*Lens culinaris* Medikus subsp. *culinaris*). J Hered 90(2):270–275

Sarker A, Aydin A, Aydogan SH, Sabaghpour H, Ketata I, Kusmenoglu Erskine W (2002) Winter lentils promise improved nutrition and income in west Asian highlands. ICARDA Caravan 16:14–16

Sarker R, Mustafa BM, Biswas A, Mahbub S, Nahar M, Hashem R (2003) In vitro regeneration in lentil (*Lens culinaris* Medik.). Plant Tiss Cult 13:155–163

Sarker A, Erskine W, Abu Bakr M, Matiur Rahman M, Ali Afzal M, Saxena MC (2004) Lentil improvement in Bangladesh. A success story of fruitful partnership between the Bangladesh Agricultural Research Institute and the International Center for Agricultural Research in the Dry Areas. APAARI Publication 1, pp 1–38

Sarker A, Erskine W, Singh M (2005) Variation in shoot and root characteristics and their association with drought tolerance in lentil landraces. Genet Res Crop Evol 52(1):89–97

Saxena MC (1993) The challenge of developing biotic and abiotic stress resistance in cool-season food legumes. In: Singh KB, Saxena MC (eds) Breeding for stress tolerance in cool-season food legumes. Wiley, Chichester, Oxford, UK, pp 3–14

Saxena MC (2009) Plant morphology, anatomy and growth habit. In: Erskine W, Muehlbauer FJ, Sarker BS (eds) The lentil: botany, production and uses. CAB International, Wallingford, UK, pp 34–46

Scheben A, Wolter F, Batley J, Puchta H, Edwards D (2017) Towards CRISPR/Cas crops—bringing together genomics and genome editing. New Phytol 216(3):682–698

Schnoes AM, Brown SD, Dodevski I, Babbitt PC (2009) Annotation error in public databases: Misannotation of molecular function in enzyme superfamilies. PLoS Comput Biol 5. https://doi.org/10.1371/journal.pcbi.1000605

Scippa G, Trupiano D, Rocco M, Viscosi V, Di Michele M, D'andrea A, Chiatante D (2008) An integrated approach to the characterization of two autochthonous lentil (*Lens culinaris*) landraces of Molise (south-central Italy). Heredity 101:136

Scippa GS, Rocco M, Ialicicco M (2010) The proteome of lentil (*Lens culinaris* Medik.) seeds: discriminating between landraces. Electrophoresis 31:497–506

Sehgal A, Sita K, Kumar J, Kumar S, Singh S, Siddique KH, Nayyar H (2017) Effects of drought, heat and their interaction on the growth, yield and photosynthetic function of lentil (*Lens culinaris* Medikus) genotypes varying in heat and drought sensitivity. Front Plant Sci 17(8):1776

Sever T, Ates D, Aldemir SB, Yagmur B, Kaya HB, Temel HY (2014) Identification QTLs controlling genes to Se uptake in lentil seeds. In: Proceedings of the plant and animal genome XXII conference, San Diego, CA, p 359

Seversike TM, Sermons SM. Sinclair TR, Carter TE, Rufry TW (2013) Temperature interactions with transpiration response to vapor pressure deficit among cultivated and wild soybean genotypes. Physiol Plant 148:62–73. https://doi.org/10.1111/j.1399-3054.2012.01693.x

Seyedimoradi H, Talebi R (2014) Detecting DNA polymorphism and genetic diversity in Lentil (*Lens culina*ris Medik.) germplasm: comparison of ISSR and DAMD marker. Physiol Mol Biol Plants 20:495–500

Shaikh R, Diederichsen A, Harrington M, Adam J, Conner RL, Buchwaldt L (2012) New sources of resistance to Colletotrichum truncatum race Ct0 and Ct1 in *Lens culinaris* Medikus subsp. culinaris obtained by single plant selection in germplasm accessions. Genet Resour Crop Evol 60:193–201

Sharma HC (2014) Climate change effects on insects: Implications for crop protection and food security. J Crop Improv 28:229–259

Sharma SK, Dawson IK, Waugh R (1995) Relationships among cultivated and wild lentils revealed by rapd analysis. Theor Appl Genet 91:647–654. https://doi.org/10.1007/BF00223292

Sharma SK, Knox MR, Ellis THN (1996) AFLP analysis of the diversity and phylogeny of Lens and its comparison with RAPD analysis. Theor Appl Genet 93:751–758. https://doi.org/10.1007/bf00224072

Sharpe AG, Ramsay L, Sanderson LA, Fedoruk MJ, Clarke WE, Li R, Kagale S, Vijayan P, Vandenberg A, Bett KE (2013a) Ancient orphan crop joins modern era: gene-based SNP discovery and mapping in lentil. BMC Genomics 14(1):192

Sharpe AG, Ramsay L, Sanderson LA, Fedoruk MJ, Clarke WE, Rong L (2013b) Ancient orphan crop joins modern era: gene-based SNP discovery and mapping in lentil. BMC Genomics 14:1–13

Shi A, Chen P, Li D, Zheng C, Zhang B, Hou A (2009) Pyramiding multiple genes for resistance to soybean mosaic virus in soybean using molecular markers. Mol Breed 23(1):113

Shizuya H, Birren B, Kim UJ (1992) Cloning and stable maintenance of 300-kilobase-pair fragments of human DNA in Escherichia coli using an F-factor-based vector. Proc Natl Acad Sci USA 89(18):8794–8797

Shrestha R, Siddique KH, Turner NC, Turner DW, Berger JD (2005) Growth and seed yield of lentil (*Lens culina*ris Medikus) genotypes of West Asian and South Asian origin and crossbreds between the two under rainfed conditions in Nepal. Aust J Agric Res 56(9):971–981

Shrestha R, Turner NC, Siddique KH, Turner DW, Speijers J (2006) A water deficit during pod development in lentils reduces flower and pod numbers but not seed size. Aust J Agric Res 57(4):427–438

Shrestha R, Rizvi AH, Sarker A, Darai R, Paneru RB, Vandenberg A, Singh M (2018) Genotypic variability and genotype × environment interaction for iron and zinc content in lentil under Nepalese environments. Crop Sci 58:1–8. https://doi.org/10.2135/cropsci2018.05.0321

Siahsar BA, Ganjali S, Allahdoo M (2010) Evaluation of drought tolerance indices and their relationship with grain yield of lentil lines in drought stressed and irrigated environments. Aust J Basic Appl Sci 4(9):4336–4346

Sidari M, Muscolo A, Anastasi U, Preiti G, Santonoceto C (2007) Response of four genotypes of lentil to salt stress conditions. Seed Sci Technol 35(2):497–503

Sidari M, Santonoceto C, Anastasi U, Preiti G, Muscolo A (2008) Variations in four genotypes of lentil under NaCl-salinity stress. Am J Agric Biol Sci 3(1):410–416

Siddique KHM (1999) Abiotic stresses of cool season pulses. In: Trials OF (ed) Birchip cropping. Birchip, Vicxtoria, Australia

Siddique KH, Loss SP, Pritchard DL, Regan KL, Tennant D, Jettner RL, Wilkinson D (1998) Adaptation of lentil (*Lens culinaris* Medik.) to Mediterranean-type environments: effect of time of sowing on growth, yield, and water use. Aust J Agric Res 49(4):613–626

Siddique KH, Regan KL, Tennant D, Thomson BD (2001) Water use and water use efficiency of cool season grain legumes in low rainfall Mediterranean-type environments. Eur J Agron 15(4):267–280

Siddique KH, Erskine W, Hobson K, Knights EJ, Leonforte A, Khan TN, Paull JG, Redden R, Materne M (2013) Cool-season grain legume improvement in Australia—use of genetic resources. Crop Pasture Sci 64(4):347–360

Silim SN, Saxena MC, Erskine W (1993a) Adaptation of lentil to the Mediterranean environment. I. Factors affecting yield under drought conditions. Exp Agric 29(1):9–19

Silim SN, Saxena MC, Erskine W (1993b) Adaptation of lentil to the Mediterranean environment. II. Response to moisture supply. Exp Agric 29(1):21–28

Singh KP (2001) Evaluation of osmoitic drought tolerance in lentil genotypes during seed germination. Ann Plant Physiol 15(1):31–33

Singh DP, Singh BB (1991) Evaluation of exotic germplasm in lentil. Narendra Deva J Agric Res 6:304–306

Singh BB, Tewari TN, Singh AK (1993) Stress studies in lentil (*Lens esculenta* Moench) III. Leaf growth, nitrate reductase activity, nitrogenase activity and nodulation of two lentil genotypes exposed to sodicity. J Agron Crop Sci 171(3):196–205

Singh I, Singh J, Singh A, Chauhan M (1994) Pant Lentil 4: a high yielding, rust-, wilt- and blight-resistant variety for the North-Western Plains of India. Lens Newsl 21:8–9

Singh RA, Roy NK, Haque MS, Pusa SI (2001) Changes in growth and metabolic activity in seedlings of lentil (*Lens culinaris* Medic) genotypes during salt stress. Indian J Plant Physiol 6(4):406–410

Singh D, Dikshit HK, Singh R (2013a) A new phenotyping technique for screening for drought tolerance in lentil (*Lens culinaris* Medik.). Plant Breed 132(2):185–90

Singh M, Rana MK, Kumar K, Bisht IS, Dutta M, Gautam NK, Bansal KC (2013b) Broadening the genetic base of lentil cultivars through inter sub-specific and interspecific crosses of Lens taxa. Plant Breed 132:667–675

Singh M, Bisht IS, Dutta M, Kumar K, Kumar S, Bansal KC (2014) Genetic studies on morpho-phenological traits in lentil (*Lens culinaris* Medikus) wide crosses. J Genet 93(2):561–566

Singh D, Singh CK, Tomar RS, Chaturvedi AK, Shah D, Kumar A, Pal M (2016) Exploring genetic diversity for heat tolerance among lentil (*Lens culinaris* Medik.) genotypes of variant habitats by simple sequence repeat markers. Plant Breed 135(2):215–223

Singh D, Singh CK, Tomar RSS, Taunk J, Singh R, Maurya S, Chaturvedi AK, Pal M, Singh R, Dubey SK (2016) Molecular assortment of *Lens* species with different adaptations to drought conditions using SSR markers. PLoS ONE 11(1):e0147213

Singh D, Singh CK, Taunk J, Tomar RS, Chaturvedi AK, Gaikwad K, Pal M (2017a) Transcriptome analysis of lentil (*Lens culinaris* Medikus) in response to seedling drought stress. BMC Genomics 18(1):206

Singh M, Rana JC, Saxena DC, Saxena A, Sarker A (2017b) Comparative agronomic performance and reaction to Fusarium wilt of *Lens culinaris* × *L. orientalis* and *L. culinaris* × *L. ervoides* derivatives. Front Plant Sci. https://doi.org/10.3389/fpls.2017.01162

Singh D, Singh CK, Singh Tomar RS, Pal M (2017c) Genetics and molecular mapping of heat tolerance for seedling survival and pod set in lentil. Crop Sci 57(6):3059–3067

Singh M, Sharma SK, Singh B, Malhotra N, Chandora R, Sarker A, Singh K, Gupta D (2018) Widening the genetic base of cultivated gene pool following introgression from wild Lens taxa. Plant Breed 137(4):470–485

Sita K, Sehgal A, Kumar J, Kumar S, Singh S, Siddique KH, Nayyar H (2017) Identification of high-temperature tolerant lentil (*Lens culinaris* Medik.) genotypes through leaf and pollen traits. Front Plant Sci 19(8):744

Sjödin A, Street NR, Sandberg G, Gustafsson P, Jansson S (2009) The Populus Genome Integrative Explorer (PopGenIE): a new resource for exploring the Populus genome. New Phytol 182(4):1013–1025

Skarjinskaia M, Svab Z, Maliga P (2003) Plastid transformation in *Lesquerella fe*ndleri, an oilseed Brassicacea. Transgen Res 12(1):115–122

Solaiman Z, Colmer TD, Loss SP, Thomson BD, Siddique KH (2007) Growth responses of cool-season grain legumes to transient waterlogging. Aust J Agric Res 58(5):406–412

Solanki R, Singh S, Kumar J (2010) Molecular marker assisted testing of hybridity of F1 plants in lentil. Food Legumes 23:21–24

Sonnante G, Pignone D (2001) Assessment of genetic variation in a collection of lentil using molecular tools. Euphytica 120:301–307

Sonnante G, Pignone D (2007) The major Italian landraces of lentil (*Lens culinaris* Medik.): their molecular diversity and possible origin. Genet Resour Crop Evol 54:1023–1031

Sonnante G, Galasso I, Pignone D (2003) ITS sequence analysis and phylogenetic inference in the genus *Lens* Mill. Ann Bot 91:49–54

Spaeth SC, Muehlbauer F (1991) Registration of three germplasms of winter hardy lentil. Crop Sci 31(5):1395

Sprink T, Eriksson D, Schiemann J, Hartung F (2016) Regulatory hurdles for genome editing: process vs. product-based approaches in different regulatory contexts. Plant Cell Rep 35(7):1493–1506. https://doi.org/10.1007/s00299-016-1990-2

Srivastava RP, Vasishtha H (2012) Saponins and lectins of Indian chickpeas (*Cicer arietinum)* and lentils (*Lens culinaris*). Indian J Agric Biochem 25(1):44–47

Stevenson PC, Dhillon MK, Sharma HC, Bouhssini ME (2007) Insect pests of lentil and their management. In: Yadav SS, McNeil DL, Stevenson PC (eds) Lentil. Springer, Dordrecht, pp 331–348

Stoddard FL, Balko C, Erskine W, Khan HR, Link W, Sarker A (2006) Screening techniques and sources of resistance to abiotic stresses in cool-season food legumes. Euphytica 147(1–2):167–186

Storer NP, Thompson GD, Head GP (2012) Application of pyramided traits against Lepidoptera in insect resistance management for Bt crops. GM Crops Food 3(3):154–162

Subbarao GV, Johansen C, Slinkard AE, Nageswara Rao RC, Saxena NP, Chauhan YS, Lawn RJ (1995) Strategies for improving drought resistance in grain legumes. Crit Rev Plant Sci 14(6):469–523

Sudheesh S, Rodda MS, Davidson J, Javid M, Stephens A, Slater AT, Cogan NO, Forster JW, Kaur S (2016) SNP-based linkage mapping for validation of QTLs for resistance to ascochyta blight in lentil. Front Plant Sci 7:1604

Sugha S, Singh B, Sharma S (1991) Performance of lentil varieties/germplasm lines against blight. Lens 18:34–35

Sultana T, Ghafoor A (2008) Genetic diversity in ex-situ conserved *Lens culinaris* for botanical descriptors, biochemical and molecular markers and identification of landraces from indigenous genetic resources of Pakistan. J Intl Plant Biol 5:484–490

Summerfield RJ, Roberts EH, Erskine W, Ellis RH (1985) Effects of temperature and photoperiod on flowering in lentils (*Lens culinaris* Medic.). Ann Bot 56(5):659–671

Sutaria GS, Akbari KN, Vora VD, Hirpara DS, Padmani, DR (2010) Response of legume crops to enriched compost and vermicompost on vertic ustochrept under rain fed agriculture. Legume Res: An Int J 33(2)

Tadmor Y, Zamir D, Ladizinsky G (1987) Genetic mapping of an ancient translocation in the genus *Lens*. Theor Appl Genet 73:883–892

Tahir M, Muehlbauer FJ (1994) Gene-mapping in lentil with recombinant inbred lines. J Hered 85:306–310

Tahir M, Muehlbauer FJ, Spaeth SC (1994) Association of isozyme markers with quantitative trait loci in random single seed descent derived lines of lentil (*Lens culinaris* Medik.). Euphytica 75(1–2):111–119

Tanksley SD, Young ND, Paterson AH, Bonierbale MW (1989) RFLP mapping in plant breeding: new tools for an old science. Biotechnology 7(3):257

Tanksley SD, Ganal MW, Martin GB (1995) Chromosome landing: a paradigm for map-based gene cloning in plants with large genomes. Trends Genet 11(2):63–68

Tanyolac B, Ozatay S, Kahraman A, Muehlbauer FJ (2010) Linkage mapping of lentil genome using recombinant inbred lines revealed by AFLP, ISSR, RAPD and some morphologic markers. J Agric Biotechnol Sustain Develop 2:1–6

Taran B, Buchwaldt L, Tullu A, Banniza S, Warkentin TD, Vandenberg A (2003) Using molecular markers to pyramid genes for resistance to ascochyta blight and anthracnose in lentil (*Lens culinaris* Medik). Euphytica 134(2):223–230

Taran B, Warkentin TD, Vandenberg A (2013) Fast track genetic improvement of ascochyta blight resistance and double podding in chickpea by marker-assisted backcrossing. Theor Appl Genet 126(6):1639–1647

Tello-Ruiz MK, Naithani S, Stein JC et al (2018) Gramene 2018: unifying comparative genomics and pathway resources for plant research. Nucl Acids Res 46:D1181–D1189. https://doi.org/10.1093/nar/gkx1111

Temel HY, Gol D, Kahriman A, Tanyolac MB (2014) Construction of linkage map trough genotyping by sequencing in lentil. In: Proceedings of plant and animal genome conference XXII, San Diego, CA, p 358

Temnykh SG, DeClerck A, Lukashova L, Lipovich S, Cartinhour, McCouch S (2001) Computational and experimental analysis of microsatellites in rice (*Oryza sativa* L.): frequency, length variation, transposon associations, and genetic marker potential. Genome Res 11(8):1441–1452

Tewari TN, Singh BB (1991) Stress studies in lentil (*Lens esculenta* Moench). Plant Soil 136(2):225–230

Thavarajah D (2017) Lentil *(Lens culinaris* Medikus): a whole food rich in prebiotic carbohydrates to combat global obesity. InTechOpen

The UniProt Consortium (2008) The universal protein resource (UniProt). Nucl Acids Res 36:D190–D195. https://doi.org/10.1093/nar/gkm895

Thiel T, Michalek W, Varshney R, Graner A (2003) Exploiting EST databases for the development and characterization of gene-derived SSR-markers in barley (*Hordeum vulgare* L.). Theor Appl Genet 106:411–422

Toker C, Mutlu N (2011) Breeding for abiotic stresses. In: Pratap A, Kumar J (ed) Biology and breeding of food legumes. CAB International, Wallingford, UK, pp 1:241–1:260

Toklu F, Karaköy T, Haklı E, Bicer T, Brandolini A, Kilian B, Özkan H (2009) Genetic variation among lentil (*Lens culinaris* Medik) landraces from Southeast Turkey. Plant Breed 128(2):178–186

Tsanakas GF, Mylona PV, Koura K, Gleridou A, Polidoros AN (2018) Genetic diversity analysis of the Greek lentil (*Lens culinaris*) landrace 'Eglouvis' using morphological and molecular markers. Plant Genet Resour 16(5):1–9

Tullu A, Kusmenoglu I, McPhee K, Muehlbauer F (2001) Characterization of core collection of lentil germplasm for phenology, morphology, seed and straw yields. Genet Resour Crop Evol 48(2):143–152

Tullu A, Buchwaldt L, Warkenti T, Taran B, Vandenberg A (2003) Genetics of resistance to anthracnose and identification of AFLP and RAPD markers linked to the resistance gene in PI 320937 germplasm of lentil (*Lens culinaris* Medikus). Theor Appl Genet 106(3):428–434

Tullu A, Tar'an B, Breitkreutz C, Banniza S, Warkentin TD, Vandenberg A, Buchwaldt L (2006) A quantitative-trait locus for resistance to ascochyta blight [*Ascochyta lentis*] maps close to a gene for resistance to anthracnose [*Colletotrichum truncatum*] in lentil. Can J Plant Pathol 28(4):588–595

Tullu A, Taran B, Warkentin T, Vandenberg A (2008) Construction of an intraspecific linkage map and QTL analysis for earliness and plant height in lentil. Crop Sci 48:2254–2264

Tullu A, Banniza S, Tar'an B, Warkentin T, Vandenberg A (2010) Sources of resistance to ascochyta blight in wild species of lentil (*Lens culinaris* Medik.). Genet Resour Crop Evol 57:1053–1063

Turan MA, Turkmen N, Taban N (2007) Effect of NaCl on stomatal resistance and proline, chlorophyll, Na, Cl and K concentrations of lentil plants. J Agron 6:378–381

Udupa SM, Robertson LD, Weigand F, Baum M, Kahl G (1999) Allelic variation at (TAA)n microsatellite loci in a world collection of chickpea. Mol Gen Genet 261:354–363

ul Hussan S, Khuroo N, Lone A, Dar Z, Dar S, Dar M (2018) Study of variability and association analysis for various agromorphological traits in lentil (*Lens culinaris* M.). J Pharm Phytochem 7(2): 2172–2175

Vadez V, Rao S, Kholova J, Krishnamurthy L, Kashiwaji J, Ratnakumar P (2008) Root research for drought tolerance in legumes: quo-vadis? J Food Legumes 21:77–85

Vail S, Strelioff J, Tullu A, Vandenberg A (2012) Field evaluation of resistance to Colletotrichum truncatum in *Lens culinaris*, *Lens ervoides*, *and Lens ervoides* × *Lens culinaris* derivatives. Field Crops Res 126:145–151

Van Bel M, Diels T, Vancaester E, Kreft L, Botzki A, Van de Peer Y, Coppens F, Vandepoele K (2017) PLAZA 4.0: an integrative resource for functional, evolutionary and comparative plant genomics. Nucl Acids Res 46(D1):D1190–D1196

Van Hoorn JW, Katerji N, Hamdy A, Mastrorilli M (2001) Effect of salinity on yield and nitrogen uptake of four grain legumes and on biological nitrogen contribution from the soil. Agric Water Manage 51(2):87–98

Vandenberg A (2006) Sources of resistance to anthracnose *Colletotrichum truncatum* in wild *Lens* species. Genet Resour Crop Evol 53:111–119

Vandenberg A, Slinkard AE (1989) Inheritance of four new qualitative genes in lentil. J Heredity 80(4):320–322

Varshney NK, Singh NB (2017) Synthesis of choline and glycine betaine and alleviation of sodium chloride toxicity. Indian J Sci Res 7(2):173–176

Varshney RK, Song C, Saxena RK, Azam S, Yu S, Sharpe AG, Cannon S, Baek J, Rosen BD, Tar'an B, Millan T (2013) Draft genome sequence of chickpea (*Cicer arietinum*) provides a resource for trait improvement. Nat Biotechnol 31(3):240

Varshney RK, Saxena RK, Jackson SA (2017) Future prospects. In: Varshney RK, Saxena RK, Jackson SA (eds) The pigeonpea genome. Springer, Cham, Switzerland, pp 99–104

Verma P, Shah N, Bhatia S (2013) Development of an expressed gene catalogue and molecular markers from the de novo assembly of short sequence reads of the lentil (*Lens culinaris* Medik.) transcriptome. Plant Biotechnol J 11:894–905. https://doi.org/10.1111/pbi.12082

Verma P, Sharma TR, Srivastava PS, Abdin MZ, Bhatia S (2014) Exploring genetic variability within lentil (*Lens culinaris* Medik.) and across related legumes using a newly developed set of microsatellite markers. Mol Biol Rep 41:5607–5625. https://doi.org/10.1007/s11033-014-3431-z

Verma P, Goyal R, Chahota RK, Sharma TR, Abdin MZ, Bhatia S (2015) Construction of a genetic linkage map and identification of QTLs for seed weight and seed size traits in lentil. PLoS ONE e0139666

Verslues PE, Agarwal M, Katiyar-Agarwal S, Zhu J, Zhu JK (2006) Methods and concepts in quantifying resistance to drought, salt and freezing, abiotic stresses that affect plant water status. Plant J 45(4):523–539

Wang GL, Holsten TE, Song WY, Wang HP, Ronald PC (1995) Construction of a rice bacterial artificial chromosome library and identification of clones linked to the Xa21 disease resistance locus. Plant J 7(3):525–533

Wang J, Chapman SC, Bonnett DG, Rebetzke GJ, Crouch J (2007) Application of population genetic theory and simulation models to efficiently pyramid multiple genes via marker-assisted selection. Crop Sci 47(2):582–588

Warkentin TD, McHughen D (1992) *Agrobacterium tumefaciens*-mediated beta-glucuronidase (GUS) gene expression in lentil (*Lens culinaris* Medik.) tissues. Plant Cell Rep 11:274–278

Wei Z, Liu Y, Lin C, Wang Y, Cai QA, Dong Y, Xing (2011) Transformation of alfalfa chloroplasts and expression of green fluorescent protein in a forage crop. Biotechnol Lett 33(12):2487–2494

Weigand S, Pala M, Saxena MC (1992) Effect of sowing date, fertilizer and insecticide on nodule damage by *Sitona crinitus Herbst* (Coleoptera: Curculionidae) and yield of lentil (*Lens culinarie* Medik.) in northern Syria. J Plant Dis Prot 174–181

Williams DJ, McHughen A (1986) Plant regeneration of the legume *Lens culinaris* Medik. (lentil) in vitro. Plant Cell Tiss Organ Cult 7(2):149–153

Wiraguna E, Malik AI, Erskine W (2017) Waterlogging tolerance in lentil (*Lens culinaris* Medik. subsp. culinaris) germplasm associated with geographic origin. Genet Resour Crop Evol 64(3):579–586

Wong MM, Gujaria-Verma N, Ramsay L, Yuan HY, Caron C, Diapari M, Vandenberg A, Bett KE (2015) Classification and characterization of species within the genus *Lens* using genotyping-by-sequencing (GBS). PLoS ONE 10(3):e0122025

Wu W, Cheng S (2014) Root genetic research, an opportunity and challenge to rice improvement. Field Crop Res 165:111–124. https://doi.org/10.1016/j.fcr.2014.04.013

Wu X, Li G, Wang B, Hu Y, Wu X, Wang Y, Lu Z, Xu P (2018) Fine mapping Ruv2, a new rust resistance gene in cowpea (*Vigna unguiculata*), to a 193-kb region enriched with NBS-type genes. Theor Appl Genet 17:1

Yamazaki Y, Yoshimura A, Nagato Y, Kurata N (2008) Oryzabase: an integrated rice science database. In: Khush GS (ed) Advances in rice genetics. World Scientific Publishing Company, Toh Tuck Link, Singapore, pp 380–383

Yang XW, Gong S (2005) An overview on the generation of BAC transgenic mice for neuroscience research. Curr Protoc Neurosci 31(1):5–20

Yasin M, Zahid MA, Ghafoor A, Ahmad Z (2002) Genotypic behavior of lentil (*Lens culinaris* Medik) towards salinity. In: Ahmad R, Malik KA (eds) Prospects for saline agriculture. Springer, Dordrecht, Netherlands, pp 231–235

Yau SK, Erskine W (2000) Diversity of boron-toxicity tolerance in lentil growth and yield. Genet Resour Crop Evol 47:55–62

Ye G, McNeil DL, Hill GD (2002) Breeding for resistance to lentil ascochyta blight. Plant Breed 121(3):185–191

Yim WC, Yu Y, Song K, Jang CS, Lee BM (2013) PLANEX: the plant co-expression database. BMC Plant Biol 13(1):83

Yu JK, Dake TM, Singh S, Benscher D, Li W, Gill B, Sorrells ME (2004) Development and mapping of EST-derived simple sequence repeat markers for hexaploid wheat. Genome 47(5):805–818

Yuan HY, Saha S, Vandenberg A, Bett KE (2017) Flowering and growth responses of cultivated lentil and wild Lens germplasm toward the differences in red to far-red ratio and photosynthetically active radiation. Front Plant Sci 21(8):386

Zaccardelli M, Lupo F, Piergiovanni AR, Laghetti G, Sonnante G, Daminati MG, Sparvoli F, Lioi (2012) Characterization of Italian lentil (*Lens culinaris* Medik.) germplasm by agronomic traits, biochemical and molecular markers. Genet Resour Crop Evol 59(5):727–738

Zaman MW, Mian MAK, Rahman MM (1989) Variability and correlation studies in local germplasm of lentil in Bangladesh. Lens Newsl 16:17–19

Zaman-Allah M, Jenkinson DM, Vadez V (2011) A conservative pattern of water use, rather than deep or profuse rooting, is critical for the terminal drought tolerance of chickpeas. J Exp Bot 62:4239–4252. https://doi.org/10.1093/jxb/err139

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

Závodná M, Kraic J, Paglia G, Gregova E, Morgante M (2000) Differentiation between closely related lentil (*Lens culinaris* Medik.) cultivars using DNA markers. Seed Sci Technol 28:217–219

Zhang HB, Choi S, Woo SS, Li Z, Wing RA (1996) Construction and characterization of two rice bacterial artificial chromosome libraries from the parents of a permanent recombinant inbred mapping population. Mol Breed 2(1):11–24

Zhang X, Yuan YR, Pei Y, Lin SS, Tuschl T, Patel DJ, Chua NH (2006) Cucumber mosaic virus-encoded 2b suppressor inhibits Arabidopsis Argonaute1 cleavage activity to counter plant defense. Genes Dev 20(23):3255–3268

Zhang X, Scheuring CF, Zhang M, Dong JJ, Zhang Y, Huang JJ, Chen W (2010) A BAC/BIBAC-based physical map of chickpea, *Cicer arietinum* L. BMC Genomics 11(1):501

Zhang N, Venkateshwaran M, Boersma M, Harms A, Howes-Podoll M, den Os D, Ané JM, Sussman MR (2012) Metabolomic profiling reveals suppression of oxylipin biosynthesis during the early stages of legume–rhizobia symbiosis. FEBS Lett 586(19):3150–3158

Zimniak-Przybylska Z, Przybylska J, Krajewski P (2001) Electrophoretic seed globulin patterns and species relationships in the genus *Lens* Miller. J Appl Genet 42:435–447
Zohary D (1972) The wild progenitor and the place of origin of the cultivated lentil: *Lens culinaris*. Econ Bot 26:326–332