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CENTENARY REVIEW

Recent progress in the ancient lentil

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SUMMARY

Lentil (*Lens culinaris* Medikus subsp. *culinaris*) was among the first crops domesticated and has become an important food legume crop in the farming and food systems of many countries globally. Its seed is a rich source of protein, minerals, and vitamins for human nutrition, and the straw is a valued animal feed. Its ability in nitrogen and carbon sequestration improves soil nutrient status, which in turn provides sustainability in production systems. In the current paper, research progress achieved in lentil improvement at national and international levels is reviewed.

Since the late 1970s there have been significant national and international lentil improvement programmes, with the main objectives being to develop phenologically adapted, stress resistant and high-yielding cultivars with improved production packages.

Systematic research on lentil started recently, compared to other early-domesticated crops. During the last two and a half decades, research progress has been made in various aspects of the crop. Large numbers of germplasm have been collected, evaluated and preserved at national and international levels, with the International Center for Agricultural Research in the Dry Areas (ICARDA) holding the largest collection of cultivated and wild germplasm accessions. A major effort has been made to study the genetic variation in the world germplasm collection, in order to understand local adaptation and to develop specific research programmes. Genotypes with resistance to various biotic and abiotic stresses, particularly resistance to vascular wilt, rust and Ascochyta blight have been identified, and directly exploited or used in breeding programmes. New genotypes have been bred with good standing ability, suitable for mechanical harvest for West Asia and North Africa. Through introduction and hybridization, the genetic base of lentil has been broadened, most particularly in South Asia, by breaking an ancient genetic bottleneck.

Agronomic practices, including seeding time, seed rate, tillage requirements, soil type, and weed control, are optimized locally and improved production packages have been developed to realize higher yield. To date, a total of 91 improved cultivars have been released globally, emanating from genetic material supplied by ICARDA. Due to adoption of improved varieties combined with production technologies, the average global productivity has increased from 611 kg/ha to 966 kg/ha, and total production from 1·3 million tonnes to 3·8 million tonnes in the last three decades. Research at the molecular level, including construction of a lentil genetic linkage map, identification of molecular markers, and genetic transformation, has progressed considerably.

INTRODUCTION

Lentil (*Lens culinaris* Medikus subsp. *culinaris*), an annual diploid (2n = 2x = 14) plant, is a short, slender annual legume that was among the earliest of plants to be domesticated in the Fertile Crescent of the Near East. It plays an important role in human, animal, and soil health improvement. Its seed is a rich source of protein, other minerals (K, P, Fe, Zn) and vitamins for human nutrition (Bhatty 1988; Savage 1988), and the straw is a valued animal feed (Erskine *et al.* 1990*a*). Furthermore, because of its high lysine and tryptophan content, its consumption with wheat or

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rice provides a balance in essential amino acids for human nutrition. Its cultivation improves soil nitrogen, carbon and organic matter status, thus providing sustainable crop production systems. Lentil is one of the most important pulses for crop intensification in West Asia and diversification in South Asia (Sarker *et al*. 2004*b*).

Despite its importance, lentil remained an under-researched crop until the late 1970s. Under the Consultative Group of International Agricultural Research (CGIAR), the International Center for Agricultural Research in the Dry Areas (ICARDA) started systematic lentil research in 1977. The Center has worked closely with national agricultural research systems of the developing and developed world to address its mission. Some national programmes, such as that in India, started improvement activities earlier, focusing mainly on the collection of local germplasm and pureline selection (Tyagi & Sharma 1981). Although research is now being carried out in about 40 countries globally, substantive programmes are under way in the major producing countries of India, Canada, Turkey, Iran, Australia, Nepal, Bangladesh, Syria, Ethiopia, Morocco, Pakistan and the USA.

TRENDS IN LENTIL PRODUCTION AND TRADE

Lentil is an important dietary component in Afghanistan, Bangladesh, India, Nepal, Pakistan, Ethiopia, Morocco, Tunisia, Sudan, Iran, Syria, Turkey, Egypt and Iraq. Many of these countries are also major producers. Countries in Southern Europe, Central Asia and the Caucasus and in Latin America grow and consume lentil to a lesser extent. During the last two decades, the crop has been grown in developed countries such as Australia, Canada and the USA, and has become an important agricultural export commodity. Canada is now the second largest producer after India, with an area of about 700 000 ha (Tullu *et al*. 2005). However, world lentil production has tripled in the last three decades from 1·05 million MT in 1971 to 3·8 million MT in 2004, through a 124% increase in sown area and a 58% increase in average national yield from 611 to 966 kg/ha (FAO 2004).

Internationally, the trade in small-seeded, red cotyledon lentil is dominated by Australia, Canada and Turkey, whereas the market in the large-seeded, green lentil is held by Canada and USA. Countries in the Indian Subcontinent, West Asia and North Africa are the major importers of red lentil. Southern Europe and South America import large-seeded green lentils (Sarker & Erskine 2002).

PHYLOGENY

'Lens' is the Latin word for a disc-shaped object, and Tournefort was the first to use the word 'Culinaris' to reflect its culinary use and edibility. The genus *Lens* Miller belongs to the Family Leguminosae, Subfamily Papilionaceae and is in the tribe Vicieae. All species in the genus are diploid with $2n = 14$ chromosomes and have similar karyotypes. Lentil has different names in 10 languages (Robertson & Erskine 1997).

The taxonomy of *Lens* has undergone numerous changes. Early taxonomists classified lentil into the genus *Ervum* L., but later *Lens* was accepted as a separate genus. Since *Lens culinaris* was validly published by Medikus in 1787, this name has priority over *Lens esculenta*, used by Moench in 1794 (Westphal 1974). Initially five species were recognized in the genus: *L. culinaris*, *L. ervoides*, *L. montbretii*, *L. nigricans* and *L. orientalis*. Alefeld (1866) recognized eight sub-species (varieties) of lentil. Barulina (1930), however, did not accept this classification. Williams *et al*. (1974) suggested *L. culinaris* and *L. orientalis* as subspecies of *L. culinaris*, and with support from Ladizinsky's work (1979) it was concluded that *L. culinaris* subsp. *orientalis* is the progenitor of cultivated lentil, *L. culinaris* subsp. *culinaris*. In a recent re-classification, van Oss *et al*. (1997) suggested that the genus *Lens* consisted of seven taxa: the cultivated lentil *L. culinaris* Medikus subsp. *culinaris*, its wild progenitor *L. culinaris* subsp. *orientalis* (Boiss.) Ponert, *L. odemensis* (Ladz., *L. ervoides* (Brign.) Grande, *L. nigricans* (M. Bieb.) Godr. and two recently recognized species, *L. tomentosus* Ladiz. and *L. lamottei* Czefr.

Several authors have used biochemical and molecular methods to supplement traditional taxonomic methods of identification and also to study taxonomic relationships within the genus *Lens*. Analysing previous findings based on origin and spread, morphological, cytological, cytogenetics observations and more recently on the basis of isozyme and molecular studies (Ferguson & Robertson 1996), *Lens* was re-classified by Ferguson *et al*. (2000) into seven taxa split into four species:

Lens culinaris Medikus subsp. *culinaris*
subsp. *orientalis* (Boiss.) Ponert
subsp. *tomentosus* (Ladiz.) Ferguson *et al*. (2000)
subsp. *odemensis* (Ladiz.) Ferguson *et al*. (2000)
Lens ervoides (Brign.) Grande
Lens nigricans (M. Bieb.) Godr.
Lens lamottei Czefr.

Most lentil researchers now accept this latest classification.

STATUS OF GENETIC RESOURCES AND AVAILABLE VARIABILITY

The largest germplasm collection, globally, is maintained at ICARDA. Several expeditions were made jointly with national programmes to collect lentil

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germplasm from South, West and Central Asian and North African countries. ICARDA conserves 9935 cultivated accessions, of which 8789 accessions are landraces collected from 71 countries and 1146 are breeding lines bred at ICARDA, and 585 wild relatives collected from 12 countries. So far, 7624 accessions have been characterized for various morphological and phenological traits. To fill the gaps in the collection, ICARDA is still collecting from unexplored areas with National Agricultural Research Systems (NARS), particularly in Central Asia and the Caucasus.

The ICARDA Lentil Improvement Programme is built upon the foundation of the germplasm collection and its efficient use. Studies on genetic variability have been conducted at various institutions, and considerable variation among the characters for use in breeding and selection programmes have been reported for morphological traits (Erskine & Witcombe 1984; Shahi *et al.* 1986; Lakhani *et al.* 1986; Baidya *et al.* 1988; Sarwar *et al.* 1982; Erskine *et al.* 1985, 1989; Erskine & Choudhary 1986; Ramgiry *et al.* 1989; Sarker *et al.* 2005), responses in flowering to temperature and photoperiod (Erskine *et al.* 1990*b*, 1994), winter-hardiness (Erskine *et al.* 1981; Sarker *et al.* 2004*a*); iron deficiency chlorosis (Erskine *et al.* 1993) and boron imbalances (Yau & Erskine 2000; Srivastava *et al.* 2000), and drought tolerance (Hamdi *et al.* 1996; Sarker & Erskine 2002; Malhotra *et al.* 2004). Resistance to fungal diseases (Khare 1981; Agarwal *et al.* 1993; Bayaa *et al.* 1994, 1995; Nasir & Bretag 1998; Bayaa & Erskine 1998) Haddad *et al.* (1978) and viruses (Makkouk *et al.* 2001) have been reported.

Wild relatives have also shown marked variability for morphological traits (Robertson & Erskine 1997), winter-hardiness (Hamdi *et al.* 1996), drought tolerance (Hamdi & Erskine 1996) and disease resistance (Bayaa *et al.* 1994; Tullu *et al.* 2005).

LANDRACES AND PRODUCTION CONSTRAINTS

Average lentil yields are low because of the limited yield potential of landraces, which are also vulnerable to an array of stresses. The yield limiting factors are lack of seedling vigour, slow leaf area development, high rate of flower drop, low proportion of pod setting, poor dry matter accumulation, low harvest index, lack of lodging resistance, low or no response to inputs, and various biotic and abiotic stresses. The major abiotic limiting factors to lentil production are low moisture availability and high temperature stress in spring, and, at high elevations, cold temperatures in winter (Johansen *et al.* 1992). Mineral imbalances like boron, iron, and salinity and sodicity, though localized, do cause substantial yield loss. Among biotic stresses, the rust, vascular wilt and Ascochyta blight diseases caused by *Uromyces viciae-fabae* (Pers.) Schroet., *Fusarium oxysporum* f. sp. *lentis* Schlecht and *Ascochyta fabae* Speg. f. sp. *lentis*, respectively, are globally important fungal pathogens of lentil (Agarwal *et al.* 1993; Bayaa & Erskine 1998; Sarker *et al.* 2004*b*). Other diseases such as botrytis blight (*Botrytis cinerea* Pers.), stemphylium blight (*Stemphylium botryosum* Wallr.), collar rot (*Sclerotium rolfsii* Sacc.), root rot (*Rhizoctonia solani* Kuhn) and stem rot (*Sclerotinia sclerotiorum* (Lib.) de Bary) are local problems. Additional constraints to production include agronomic problems of pod dehiscence and lodging, and inattention to crop management by growers.

Adequate variability for many of lentil's important traits exist within the crop gene pool, allowing manipulation through plant breeding. However, several other important traits, such as biomass yield, pod shedding, nitrogen fixation, resistance to pea leaf weevil (*Sitona* sp.), aphids, and the parasitic weed broomrape (*Orobanche* sp.), cannot currently be addressed by breeding because of insufficient genetic variation.

MAJOR RESEARCH ACCOMPLISHMENTS

Improved agronomic practices developed

One of the key factors to achieve higher yield is the use of appropriate agronomic practices. Since the early 1980s, experimentation has been conducted in the main production zones to optimize land preparation, sowing date, seed rate, seeding depth, crop harvest time and other crop management options including weed control. Lentils are grown on a wide variety of soils from sandy loam to deep peaty soils. Land preparation varies according to the soil type, climate and previous crop in the field.

The lentil is sensitive to weed competition. Throughout its range, sowing is generally delayed to allow cultivation after early rains to improve weed control. So early sowing with adequate provision for weed control generally results in major yield gains. Lentil is normally planted at the beginning of the winter season except in cold-prone highland areas, where the crop is spring-sown. In South Asia, optimum lentil sowing starts from late October and continues up to early December, but the optimum seeding time is before 15 November (Ali *et al.* 1993; Ahad & Motior 1993; Neupane & Bharati 1993). In lowland Mediterranean areas, lentil planting time continues until the middle of December (Saxena 1981). Weed control is achieved by applying herbicide as well as hand-weeding.

Seed rate varies from region to region, and with seed size. In South Asia, seed rates of 30–40 kg/ha are recommended (Zaman & Miah 1989). In West Asia,

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100–120 kg/ha seed rate produces higher yield with an optimum plant stand of 275–300 plants/m² (Silim *et al*. 1990). In agriculturally mechanized countries, lentil is drilled, but elsewhere it is still hand-broadcast (Gowda & Kaul 1982). Planting depth is generally determined by the amount of soil moisture during seeding. In row sowings it exceeds 2·5 cm. In broadcasting, the depth varies considerably. Considering all these factors, improved production packages have been developed in each producing country.

Relay cropping is a system where the second crop is sown before the harvest of the first crop, and is commonly practiced in South Asia (Ali *et al*. 1993). Relay cropping provides the plants with more time for vegetative growth and reduces production costs compared to sole cropping, due to zero tillage. Research on relay cropping by the national programmes of Bangladesh, Nepal and India has led to yield increases by optimizing seed rate (40–45 kg/ha) and time of seeding in rice fields (15–20 days before rice harvest under saturated soil moisture) (Ali *et al*. 2003).

Seed priming is another technology through which substantial yield improvement can be achieved. In farmers' fields in South Asia, patchy plant stands resulting from poor and uneven germination are noticeable when lentil is sown after several tillage operations. During land preparation, soil moisture is depleted through evaporation and patches of uneven soil surface remain. When lentil seed is broadcast, some seeds remain in the soil without germinating. The technique of seed priming, where seed is soaked in water, usually overnight, before being surface dried and then sown, has been shown to improve plant stands, enhance early vigour and provide benefits in terms of earlier maturity, reduced disease infection and increased yield (Harris *et al*. 2001). Research on seed priming with improved varieties has shown that a yield increase of 29–38% can be achieved after seed priming for 8 h (Ali *et al*. 2003).

Identification and exploitation of resistance to abiotic stresses

Winter-hardiness

In the highlands of Central Anatolia of Turkey, Iran, Afghanistan, and the Baluchistan province of Pakistan, lentil production can be increased significantly by shifting sowing from spring to early spring or winter sowing. Winter cropping allows optimum vegetative growth and the development of higher yield potential (frequently >50% higher than spring sown yields) and provides higher water-use efficiency from winter precipitation, providing the cultivar is winter-hardy. There is the potential to replace about 400 000 ha of spring lentil with a winter crop in the highlands of West Asia (Sakar *et al*. 1988).

Spring-sown lentils in the highlands frequently suffer from terminal drought, which can be avoided by early sowing; this also allows taller canopy development suitable for mechanical harvest. Cultivars with winter-hardiness (such as '*Kafkas*', *Cifci*' and '*Uzbek*') are now being cultivated in Turkey. Several additional lines are identified for future release (LC 9978057, LC 9977006, LC 9977116, LC 9978013, ILL 759, ILL 1878, ILL 4400, ILL 7155, ILL 8146, ILL 8611 and ILL 9832). In Iran, lines with winter-hardiness, early growth vigour and rapid ground cover (ILL 662, ILL 857, ILL 975, ILL 1878) are under on-farm evaluation. Selection at the Arid Zone Research Center, Baluchistan, Pakistan resulted in the release of cultivar '*ShirAZ-96*', based on ICARDA germplasm for winter cultivation (Sarker *et al*. 2004*b*). The focus in winter/autumn sowing is to translate the research results into production gains on-farm; in this regard weed control is critical. Production increases from early sowing are only possible in combination with winter-hardiness.

Drought tolerance

Tolerance to moisture stress is a key trait in rainfed lentil production. Drought is the major abiotic stress in many countries of the world (Johansen *et al*. 1992). In the Mediterranean environment of West Asia and North Africa, lentil generally suffers from terminal drought. In South Asia the crop is grown on conserved soil moisture, and occasionally faces intermittent drought. Drought tolerance research, particularly the development of screening techniques and identification of drought-tolerant genotypes, became a key research issue in ICARDA's crop improvement strategy (Malhotra *et al*. 2004). Drought tolerance mechanisms, such as escape, dehydration avoidance and dehydration tolerance have been used to select drought-tolerant genotypes. Traits like early seedling establishment, early growth vigour and ground coverage, high biomass, early flowering and maturity were taken into consideration to select drought-tolerant genotypes. Selection in drought-prone sites is the key to success in identification of drought-tolerant genotypes. Seedling shoot and root traits such as taproot length and lateral root number are important traits for drought tolerance (Sarker *et al*. 2005). The resulting drought-tolerant lines are being tested by NARS (Malhotra *et al*. 2004). This will remain a key research thrust in lentil improvement programmes.

Salinity tolerance

Soil salinity is a major obstacle to crop production in arid and semi-arid regions of the world. Like other field crops, lentil often suffers from soil salinity, as it is very sensitive to this. Nevertheless, some genetic variation in response to salinity has been reported

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(Ashraf & Waheed 1990, 1998; Ameen 1999; Sarker & Erskine, unpublished).

Mineral imbalances

Soil mineral imbalances sometimes pose a serious threat to lentil production locally. Boron toxicity occurs primarily in some arid areas in alkaline soils and is reported from Australia, India, Pakistan, Iraq, Peru and Turkey. Screening has revealed significant variation in boron toxicity with tolerance reported in lentil (Yau & Erskine 2000). In contrast, boron deficiency is a problem in other regions, such as the eastern Terai plain of Nepal, eastern India and northern Bangladesh, where the soil is leached. Landraces from Nepal and Bangladesh have been shown to be tolerant to B-deficiency, and accessions of West Asian origin were highly inefficient in B-deficient soil (Srivastava *et al.* 2000). Among B-deficiency tolerant lines, ILL 2580, ILL 5888, ILL 8009 and ILL 8010 showed higher potential in the B-deficient Chitwan region of Nepal.

Identification and exploitation of resistance to biotic stresses

Diseases

Among biotic stresses, diseases caused by various fungal pathogens are the most devastating yield-limiting factors of lentil. Of these, Fusarium wilt, rust and Ascochyta blight are globally important diseases (Bayaa *et al.* 1994), cover a wide range of environments and are addressed by the international breeding programme at ICARDA.

Screening techniques for these diseases have been developed and sources of resistance identified. Fusarium wilt resistant sources have been identified through rigorous screening in a wilt-sick plot at ICARDA, Tel Hadya. Screening is systematically carried out on all new germplasm and breeding lines. Recently, a total of 34 new sources of resistance were identified from 1500 accessions of diverse origin and included in breeding (Sarker *et al.* 2004*a*). Rust resistant lines have been reported from India, Bangladesh and Ethiopia (Agarwal *et al.* 1993; Bakr 1993; Bejiga *et al.* 1998). For Ascochyta blight, about 3000 ICARDA lentil accessions were evaluated at the Victorian Institute for Dryland Agriculture, Australia, and at the National Agricultural research Centre (NARC), Pakistan, against 239 isolates representing 14 pathotypes of Ascochyta blight collected from different countries. About 2·4% of the accessions were identified as having a high level of resistance to foliar as well as to seed infection by Ascochyta blight (Nasir & Bretag 1998). Sources of resistance to minor diseases and viruses have also been reported (Agarwal *et al.* 1993; Bakr 1993; Makkouk *et al.* 2001; Tullu *et al.* 2005). The next frontier is to ensure appropriate multiple disease resistance combinations are available for conditions locally.

Construction of suitable plant type for mechanical harvest

Lentil production in Canada and the USA has been completely mechanized since the introduction of the crop. However, the availability of mechanical harvesters, the tall stature of the crop and large field sizes contrast with the situation in the Mediterranean basin. Lentil cultivation in West Asia and North Africa has been threatened due to the rising cost of agricultural labour, with approximately 0·47 of the total cost of production required for hand-harvesting. Therefore, to reduce costs, it is essential that lentil harvest be mechanized. To address this constraint, ICARDA developed economic machine harvest systems for lentil cultivation involving cultivars with improved standing ability, a flattened seedbed and the use of cutter bars. A survey revealed that by 1998, 0·65 of farmers in Hassakeh Province, Syria, and 0·78 of farmers in South-East Anatolia, Turkey, were machine-harvesting lentil. The Center, with NARS, has developed and promoted a lentil production package that includes mechanization and the use of improved cultivars with good standing ability. Such cultivars include *Idlib-2*, *Idlib-3* and *Idlib-4* in Syria, *Hala* and *Rachayya* in Lebanon, *IPA-98* in Iraq, *Saliana* and *Kef* in Tunisia, and *Firat-87* and *Sayran-96* in Turkey. On-farm trials and demonstrations have verified the value of the mechanization package (Erskine *et al.* 1991). On average, mechanical harvesting combined with improved cultivars having good standing ability reduces harvest costs by 17–20% (ICARDA 2001).

Broadening the genetic base in South Asia

About half of the world's lentil crop is grown in South Asia (FAO 2004). The region grows only small-seeded red lentil, *pilosae* type, an endemic group with a narrow genetic variability, short stature and early maturity. For many years, lentil improvement programmes in South Asia were handicapped due to poor access to sufficient genetic variability for improvement, because of a lack of overlap in flowering with other imported lentils. Most material of West Asian origin, when grown in the short season environments of South Asia, flower when the landraces are maturing (Ceccarelli *et al.* 1994). This observation prompted research on environmental factors, which control flowering in lentil. Summerfield *et al.* (1985) concluded that temperature and photoperiod modulate flowering in lentil. In a comprehensive study with a broad spectrum of lentil germplasm, Erskine *et al.* (1990*a*, 1994) found that germplasm of Indian origin are more sensitive to temperature and less responsive to photoperiod in flowering than germplasm from West Asia.

An early attempt to widen the narrow genetic base of lentil in South Asia utilized *Precoz*, a bold-seeded, early-maturing germplasm of Argentine origin, as well as other early maturing exotic germplasm from ICARDA in breeding programmes in the region (Erskine *et al.* 1998). This led to the development of improved cultivars and a yield jump in Bangladesh (*Barimasur-2* and *Barimasur-4*) (Sarker *et al.* 1999*a*, *c*), Nepal (*Shekher* and *Sital*) and Pakistan (*Manshera-98*, *Shiraz-96*, *Masoor-93* and *Masoor-2002*). The inheritance of flowering in *Precoz* under both Indian and Syrian environments was studied and Precoz was found to have a major gene '*Sn*' for early flowering (Sarker *et al.* 1999*b*).

As a spin-off to the research into broadening the genetic base, and based on findings on quantitative responses to photo-thermal effects, Summerfield *et al.* (1985) proposed a model for flowering in lentil. According to the model, rates of progress towards flowering (i.e. *1/f*, the reciprocal of the time to first flower *f*) in all genotypes, vernalized or not, were linear functions of both mean temperature, *t*, and photoperiod, p, with no interactions between the two terms. So, over a wide range of conditions covering the photothermal regimes experienced by lentil crop worldwide, time to flowering was described by the equation:

$$1/f = a + bt + cp$$

where *a*, *b*, and *c* are constants which differ between genotypes and the value of which provide a sound basis for screening germplasm for sensitivity to temperature and photoperiod. Although these two environmental factors affect the same phenological event, Summerfield *et al.* (1985) suggested that the responses are under separate genetic control.

Development of the International Testing Network

Plant introduction is a key gateway to crop improvement. To ensure widespread availability of improved genetic stocks/promising lines, ICARDA has developed an International Testing Programme for lentil. This vehicle for dissemination includes ICARDA-bred and NARS-bred lines. It comprises nurseries for, e.g. earliness, large seed types, drought tolerance, cold tolerance, rust, Ascochyta blight and Fusarium wilt resistance and segregating populations. Data from international nurseries are compiled and analysed to understand crop adaptation to various agro-ecological niches, and to screen against prevailing stresses in test sites. On the basis of local adaptation and needs, national scientists identify and select promising lines/single plants for eventual release for commercial cultivation. In this endeavour, 91 lentil varieties have been registered to date, by 29 countries, for improved yield, disease resistance and other desirable traits.

PROGRESS IN MOLECULAR RESEARCH

Diversity study

Biochemical and molecular techniques have been used for biodiversity evaluation, assessment of the genetic structure of natural populations, plant systematics and evolution in the genus *Lens* as summarized by Ferguson & Robertson (1996), Abo-Elwafa *et al.* (1995), Sharma *et al.* (1995) and Ford *et al.* (1999). Major investigations were carried out with allozymes, seed protein cDNAs and genomic DNA RFLPs, chloroplast DNA RFLPs, and RAPD analyses of genomic DNA. Even though discrimination between lines is possible, seed proteins have not been extensively used for genetic diversity studies.

Development of lentil linkage map

Establishing linkage maps for agricultural crops is to localize gene(s) for important agronomic traits and to develop tightly linked morphological and molecular markers to enable indirect selection by marker-assisted selection. The first lentil linkage maps using morphological, isozyme and DNA-based markers covered a small number of markers (Havey & Muehlbauer 1989; Tahir *et al.* 1993). Later, a more comprehensive linkage map with more PCR-based markers for lentil genome spanning more than 1073 cM was developed (Eujayl *et al.* 1998*b*). Rubeena *et al.* (2003) reported an intraspecific linkage map in lentil constructed with 114 molecular markers. Recently, two more comprehensive molecular linkage maps were reported, one using an inter-subspecific population (Durán *et al.* 2004) and the other based on intraspecific population (Kahraman *et al.* 2004). The lentil linkage map, produced by Durán *et al.* (2004), contained 62 Random Amplification Polymorphic DNA sequences (RAPDs), 29 Inter Simple Sequence Repeats (ISSRs), 65 Amplified Fragment-Length Polymorphisms (AFLPs), four morphological and one Simple Sequence Repeats (SSR) markers, and spanned a distance of 2172 cM within 10 linkage groups. The map of Kahraman *et al.* (2004) covered 1192 cM within nine linkage groups and comprised a total of 130 RAPDs, ISSRs and AFLPs as markers. More recently, a comprehensive lentil map was developed by enriching the previous map of Eujayl *et al.* (1998*b*) with 39 new lentil-specific SSRs and 50 new AFLP markers spanning 751 cM (Hamwieh *et al.* 2005). To date, all lentil genetic maps have had more linkage groups than the species haploid chromosome number ($n = 7$). The estimated amount of the genome mapped currently varies from 751 cM to 2172 cM with an average marker density of 2·7 cM to 15·9 cM.

Tagging genes of interest with molecular markers

Qualitative traits such as epicotyl colour, seed coat pattern or spotting, pod indehiscence, etc., have been localized and linked DNA markers have been identified (Tahir *et al.* 1993; Vaillancourt & Slinkard 1992). Eujayl *et al.* (1998*a*) identified a RAPD marker (OPK-15_{900}) linked to the single dominant gene (*Fw*) conditioning fusarium vascular wilt resistance at a distance of 10·8 cM. More recently Hamwieh *et al.* (2005), identified an SSR marker and an AFLP marker that flanked the fusarium wilt resistance gene by 8·0 cM and 3·5 cM, respectively. Ford *et al.* (1999) identified RAPD markers, RV01 and RB18, approximately 6 and 14 cM, respectively, from and flanking the foliar Ascochyta blight resistance locus *Ral*1 (AbR_1) in ILL5588. Subsequently, two RAPD markers, $UBC227_{1290}$ and OPD-10_{870}, were identified that flanked and were linked in repulsion phase to the resistance gene *ral*2 in the cultivar Indianhead at 12 and 16 cM, respectively (Chowdhury *et al.* 2001). More recently, molecular markers were developed that were linked to the complementary dominant resistance genes in ILL7537 (Rubeena, unpublished). Thus, there is potential for using markers to pyramid Ascochyta blight resistance genes to develop lentil cultivars with durable resistance to Ascochyta blight. RAPD markers $OPE06_{1250}$ and $UBC704_{700}$ were linked at 6·4 cM and 10·5 cM respectively, to the anthracnose resistance locus, *LCt-2*, (Tullu *et al.* 2003).

Seedling frost tolerance is a major trait for lentil cultivation in cold-prone areas. Successful winter cropping depends on seedling survival and an optimum plant population in the early developmental stages. Eujayl *et al.* (1999) observed that seedling radiation frost tolerance was governed by a single dominant gene *Frt* and that this *Frt* locus was linked to RAPD marker OPS-16_{750} at 9·1 cM. This was the first recorded linkage to an abiotic stress resistance in food legumes.

Most economically important traits are quantitatively inherited and it is important to tag Quantitative Trait Loci (QTL) with molecular markers. QTL tagging is complex and recently started in lentil with only a few QTL studies reported to date. Abbo *et al.* (1992) studied the genetics and linkage of lentil seed weight and reported QTLs affecting seed weight were associated with morphological and RAPD markers, which were distributed over several linkage groups. A total of 22 QTLs were placed upon the map including eight for plant height, five for flowering, seven for pod dehiscence, one for shoot number and one for seed diameter (Durán *et al.* 2002). Kharaman *et al.* (2004) reported five QTLs for winter hardiness distributed on four linkage groups, but one QTL was common across environments. One ISSR marker, ubc808-12, was identified that may be useful for MAS of winter survival. An additional four QTL were reported to influence winter injury at the USA location and together accounted for 0·43 of the trait variation. QTL analysis of the Ascochyta blight resistance in ILL 7537 revealed that two QTLs were located on linkage group 1 and QTL-3 on linkage group 2. The AFLP marker C-TTA/M-AC_{285} was found to be 3·4 cM away from QTL-1 and 12 cM away from QTL-2. The RAPD marker $M20_{700}$ was linked with QTL 3 at a distance of 12 cM (Rubeena *et al.* 2003). It is anticipated that marker-assisted selection will be increasingly employed for key traits in lentil.

Genetic engineering

Resistance to Sitona weevil and *Orobanche* sp., a parasitic angiosperm has not been found in the primary gene pool of the lentil. These two biotic stresses are widespread in West Asia and North Africa, where annual crop losses are substantial. Development of transgenic lentils with the appropriate *Bt* toxin gene for Sitona weevil control and herbicide resistance for Orobanche control is underway at ICARDA. Several constructs have been used in three lentil genotypes, pCGP1258 (ILL 5582), pCGP1258, pROK2/GST9 (ILL 5588), pCGP1258, pROK2/GST (ILL 5883). However, the lack of root system development in the transgenics continues to be a problem (ICARDA 2002). Agrobacterium-mediated and particle bombardment gene transfer protocols have been developed for lentil (Sarker *et al.* 2003 and Gulati *et al.* 2002, respectively) and ultimately these will serve as a means to prove gene function via gene silencing and gene expression in alternate genetic backgrounds.

RESEARCH STRATEGIES

From the onset at ICARDA, a multidisciplinary approach has been followed with breeders, plant protection scientists, agronomists, post-harvest technologists, socio-economists in both international and national programmes working together to develop and transfer improved technology to farmers. The improvement programme also follows a decentralized breeding strategy to develop cultivars for short-season environments of southerly latitude countries and winter-hardy cultivars for the highlands. Among diseases, rust and Ascochyta blight research is being done at hot-spots outside Syria. Recently, the lentil breeding programme has adopted Participatory Varietal Selection (PVS) to enhance adoption of improved varieties as indicated by Witcombe & Joshi (1996). Although over the past two decades a number of lentil cultivars have been released in many countries, their adoption by farmers has been slow for several reasons: poor adaptation to varying environments and vulnerability to pests and diseases, inadequacy of the seed distribution system, lack of extension services and inattention to consumers' tastes. With this background, it is imperative that farmers are involved in the development of high yielding lentil cultivars and production technology right from the start. With their native wisdom, first-hand knowledge of the crop and cropping systems and other local conditions, farmers can be effective collaborators in this endeavour (Ceccarelli *et al*. 2000). Involving farmers early in the process will not only lead to the development of appropriate high-yielding varieties and practices but also facilitate rapid adoption.

CONCLUSION

Before the initiatives of improvement research, farmers of lentil-producing countries used to grow the local lentil landraces, which are very low yielding and vulnerable to a range of biotic and abiotic stresses. With research and development efforts, lentil yields have been increasing globally and production spreading because of several key advances. Agronomic research in tandem with systematic exploitation of germplasm for abiotic stresses (drought and cold), disease resistance, standing ability (machine harvest) and genetic base broadening has led to increases in production. This research has resulted in increased profitability and productivity, leading to a global productivity increase of 58% from 611 to 966 kg/ha and a large increase in cultivated area since the 1970s. Future efforts in research should be focused on molecular breeding to develop multiple stress resistance and higher yield with enhanced nutritional quality, and technology transfer should emphasize further reduction of the yield gap between research and farm production.

REFERENCES

Abbo, S., Ladizinsky, G. & Weeden, N. F. (1992). Genetic analysis and linkage studies of seed weight in lentil. *Euphytica* **58**, 259–266.

Abo-Elwafa, A., Murai, K. & Shimada, T. (1995). Intra-specific and inter-specific variations in *Lens* revealed by RAPD markers. *Theoretical and Applied Genetics* **90**, 335–340.

Agarwal, S. C., Singh, K. & Lal, S. S. (1993). Plant protection of lentil in India. In *Lentils in South Asia: Proceedings of the Seminar on Lentil in South Asia, 11–15 March, 1991, New Delhi, India* (Eds W. Erskine & M. C. Saxena), pp. 147–167. Aleppo, Syria: ICARDA.

Ahad, A. M. & Motior, R. M. (1993). Agronomy of lentil in Bangladesh. Genetic resources and breeding of lentil in Bangladesh. In *Lentils in South Asia: Proceedings of the Seminar on Lentil in South Asia*, 1991, New Delhi, India. (Eds W. Erskine & M. C. Saxena), pp. 128–138. Aleppo, Syria: ICARDA.

Alefeld, F. (1866). *Landwirtschaftliche Flora*. Reprint 1966, Koenigstein, Germany: Koeltz Scientific Books.

Ali, M., Saraf, C. S., Singh, P. P., Riwari, R. B. & Ahlawat, I. P. S. (1993). Agronomy of lentil in India. In *Lentils in South Asia: Proceedings of the Seminar on Lentil in South Asia, 11–15 March, 1991, New Delhi, India* (Eds W. Erskine & M. C. Saxena), pp. 103–127. Aleppo, Syria: ICARDA.

Ali, O., Sarker, A., Rahman, M. M. & Gahoonia, T. S. (2003). Lentil cultivation under relay cropping in Bangladesh. *Krishi Katha* **3**, 12–16.

Ameen, A. (1999). Saline irrigation practices and salt tolerance of lentil varieties. M.Sc. Thesis, Bari, Italy. pp. 1–119.

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

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

Baidya, B. N., Eunus, A. N. & Sen, S. (1988). Estimations of variability and correlation in yield and yield contributing characters in lentil (*Lens culinaris*). *Environment and Ecology* **6**, 694–697.

Bakr, M. A. (1993). Plant protection of lentil in Bangladesh. In *Lentils in South Asia: Proceedings of the Seminar on Lentil in South Asia, 11–15 March, 1991, New Delhi, India* (Eds W. Erskine & M. C. Saxena), pp. 177–186. Aleppo, Syria: ICARDA.

Bayaa, B. & Erskine, W. (1998). Diseases of lentil. In *The Pathology of Food and Pasture Legumes* (Eds D. J. Allen & J. M. Lenne), pp. 423–472. Wallingford, UK: CAB International.

Bayaa, B., Erskine, W. & Hamdi, A. (1994). Response of wild lentil to *Ascochyta fabae* f. sp. *lentis* from Syria. *Genetic Resources and Crop Evolution* **41**, 61–65.

Bayaa, B., Erskine, W. & Hamdi, A. (1995). Evaluation of a wild lentil collection for resistance to vascular wilt. *Genetic Resources and Crop Evolution* **42**, 231–235.

Bhatty, R. S. (1988). Composition and quality of lentil (*Lens culinaris* Medik.): A review. *Canadian Institute of Food Science and Technology Journal* **21**, 144–160.

Barulina, H. I. (1930). Lentils of the U.S.S.R. and other countries. *Bulletin of Applied Botanical Plant Breeding* (*Leningrad*) **40** (*Supplement*), 1–319.

Bejiga, G., Tadesse, N. & Erskine, W. (1998). We fixed rust! Next, wilt and root rots. *ICARDA Caravan* **9**, 12.

Ceccarelli, S., Erskine, W., Hamblin, J. & Grando, S. (1994). Genotype by environment interaction and international breeding programs. *Experimental Agriculture* **30**, 177–188.

Ceccarelli, S., Grando, S., Tutwiler, R., Baha, J., Martini, A. M., Salahieh, H., Goodchild, A. & Michael, M. (2000). A methodological study on participatory barley breeding I. Selection phase. *Euphytica* **111**, 91–104.

Chowdhury, M. A., Andrahennadi, C. P., Slinkard, A. E. & Vandenberg, A. (2001). RAPD and SCAR markers for resistance to Ascochyta blight in lentil. *Euphytica* **118**, 331–337.

Durán, Y., Fratini, P., Garcia, P. & Perez De La Vega, M. (2004). An intersubspecific genetic map of Lens. *Theoretical and Applied Genetics* **108**, 1265–1273.

Durán, Y., Fratini, P., Morales, S., Fernandez, M., Garcia, P. & Perez De La Vega, M. (2002). A genetic map of lentil. In *First International Conference on Legume Genomics and Genetics: Translation to Crop Improvement*. June 2–6, 2002, Minneapolis-St. Paul, MN.

Erskine, W., Myveci, K. & Izgin, N. (1981). Screening a world lentil collection for cold tolerance. *LENS Newsletter* **8**, 5–8.

Erskine, W. & Witcombe, J. R. (1984). *Lentil Germplasm Catalog*. Aleppo, Syria: International Center for Agricultural Research in the Dry Areas (ICARDA).

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

Erskine, W. & Choudhary, M. A. (1986). Variation between and within lentil landraces from Yemen Arab Republic. *Euphytica* **35**, 695–700.

Erskine, W., Adham, Y. & Holly, L. (1989). Geographic distribution of variation in quantitative characters in a world lentil collection. *Euphytica* **43**, 97–103.

Erskine, W., Rihawi, S. & Capper, B. S. (1990*a*). Variation in lentil straw quality. *Animal Feed Science and Technology* **28**, 61–69.

Erskine, W., Ellis, R. H., Summerfield, R. J., Roberts, E. H. & Hussain, A. (1990*b*). Characterization of responses to temperature and photoperiod for time to flowering in a world lentil collection. *Theoretical and Applied Genetics* **80**, 193–199.

Erskine, W., Diekmann, J., Jegatheeswaran, P., Salkini, A., Saxena, M. C., Ghanaim, A. & El-Ahskar, F. (1991). Evaluation of lentil harvest systems for different sowing methods and cultivars in Syria. *Journal of Agricultural Science, Cambridge* **117**, 333–338.

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

Erskine, W., Hussain, A., Tahir, M., Bahksh, A., Ellis, R. H., Summerfield, R. J. & Roberts, E. H. (1994). Field evaluation of a model of photothermal flowering responses in a world lentil collection. *Theoretical and Applied Genetics* **88**, 423–428.

Erskine, W., Chandra, S., Chaudhry, M., Malik, I. A., Sarker, A., Sharma, B., Tufail, M. & Tyagi, M. C. (1998). A bottleneck in lentil: widening the genetic base in South Asia. *Euphytica* **101**, 207–211.

Eujayl, I., Erskine, W., Bayaa, B., Baum, M. & Pehu, E. (1998*a*). Fusarium vascular wilt in lentil: Inheritance and identification of DNA markers for resistance. *Plant Breeding* **117**, 497–499.

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

Eujayl, I., Erskine, W., Baum, M. & Pehu, E. (1999). Inheritance and linkage analysis of frost injury in lentil. *Crop Science* **39**, 639–642.

FAO (2004). *Production Yearbook*. Rome, Italy: FAO.

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

Ferguson, M. E., Maxted, N., Van Slageren, M. & Robertson, L. D. (2000). A re-assessment of the taxonomy of *Lens* Mill. (Leguminosae, Papilionoideae, Vicieae). *Botanical Journal of the Linnean Society* **133**, 41–59.

Ford, R., Pang, E. C. K. & Taylor, P. W. J. (1999). Diversity analysis and species identification in *Lens* using PCR generated markers. *Euphytica* **96**, 247–255.

Gowda, C. L. L. & Kaul, A. K. (1982). *Pulses in Bangladesh*. Joydebpur, Bangladesh: FAO/BARI (Food and Agriculture Organization/Bangladesh Agricultural Research Institute).

Gulati, A., Schryer, P. & Mchughen, A. (2002). Production of fertile transgenic lentil (*Lens culinaris* Medik.) plants using particle bombardment. *In Vitro Cellular & Developmental Biology – Plant* **38**, 316–324.

Haddad, N. I., Muehlbauer, F. J. & Hampton, R. O. (1978). Inheritance of resistance to pea seed-borne mosaic virus in lentil. *Crop Science* **18**, 613–615.

Hamwieh, A., Udupa, S. M., 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. *Theoretical and Applied Genetics* **110**, 669–677.

Hamdi, A., Kusmenoglu, I. & Erskine, W. (1996). Sources of winter-hardiness in wild lentil. *Genetic Resources and Crop Evolution* **43**, 63–67.

Hamdi, A. & Erskine, W. (1996). Reaction of wild species of the genus *Lens* to drought. *Euphytica* **91**, 173–179.

Harris, D., Raghuwanshi, B. S., Gangwar, J. S., Singh, S. C., Joshi, K. D., Rashid, A. & Hollington, P. A. (2001). Participatory evaluation by farmers of on-farm seed priming in wheat in India, Nepal and Pakistan. *Experimental Agriculture* **37**, 403–415.

Havey, M. J. & Muehlbauer, F. J. (1989). Linkage between restriction fragment lengths, isozyme and morphological markers in lentils. *Theoretical and Applied Genetics* **77**, 395–401.

ICARDA (2001). *Germplasm Program Annual Report*. Aleppo, Syria: ICARDA.

ICARDA (2002). *Germplasm Program Annual Report*. Aleppo, Syria: ICARDA.

Johansen, C., Baldev, B., Brouwer, J. B., Erskine, W., Jermyn, W. A., Li Juan, L., Malik, B. A., Miah, A. A. & Silim, S. N. (1992). Biotic and abiotic stresses constraining productivity of cool season food legumes in Asia, Africa and Oceania. In *Expanding the Production and Use of Cool Season Food Legumes* (Eds F. J. Muehlbauer & W. J. Kaiser), pp. 175–194. Dordrecht, The Netherlands: Kluwer Academic Publishers.

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

Khare, M. N. (1981). Diseases of lentil. In *Lentils* (Eds C. Webb & G. Hawtin), pp. 163–172. Farnham, UK: Commonwealth Agricultural Bureau.

Ladizinsky, G. (1979). The genetics of several characteristics in lentil as indicated by crosses between *Lens culinaris* and *L. orientalis*. *Journal of Heredity* **70**, 135–137.

Lakhani, J. P., Holker, S. & Misra, R. (1986). Genetics of seedling vigor and hard seed in lentil. *LENS Newsletter* **13**, 10–12.

Makkouk, K., Kumari, S., Sarker, A. & Erskine, W. (2001). Registration of six lentil germplasm lines with combined resistance to viruses. *Crop Science* **41**, 931–932.

Malhotra, R. S., Sarker, A. & Saxena, M. C. (2004). Drought tolerance in chickpea and lentil – present status and future strategies. In *Challenges and Strategies for Dryland Agriculture* (Eds S. C. Rao & J. Ryan), pp. 257–274. CSSA Special Publication 32. Madison, WI, USA: American Society of Agronomy and Crop Science Society of America.

Nasir, M. & Bretag, T. (1998). Screening lentil for Ascochyta blight resistance. *CLIMA Annual Report*, 2–6.

Neupane, R. K. & Bharati, M. P. (1993). Agronomy of lentil in Nepal. In *Lentils in South Asia: Proceedings of the Seminar on Lentil in South Asia, 1991, New Delhi, India* (Eds W. Erskine & M. C. Saxena), pp. 139–146. Aleppo, Syria: ICARDA.

Ramgiry, S. R., Paliwal, K. K. & Tomor, S. K. (1989). Variability and correlations of grain yield and other qualitative characters in lentil. *LENS Newsletter* **16**, 19–21.

Robertson, L. D. & Erskine, W. (1997). Lentil. In *Biodiversity in Trust: Conservation and Use of Plant Genetic Resources in CGIAR Centres* (Eds D. Fucillo, L. Sears & P. Stapleton), pp. 128–138. Cambridge: Cambridge University Press.

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

Sakar, D., Durutan, N. & Meyveci, K. (1988). Factors, which limit the productivity of cool season food legumes in Turkey. In *World Crops: Cool Season Food Legumes* (Ed. R. J. Summerfield), pp. 137–146. Dordrecht, The Netherlands: Kluwer.

Sarker, A., Erskine, W., Hassan, M. S., Mian, W. & Debnath, A. (1999*a*). Registration of "Barimasur-2" Lentil. *Crop Science* **39**, 875.

Sarker, A., Erskine, W., Sharma, B. & Tyagi, M. C. (1999*b*). Inheritance and linkage relationships of flowering time and morphological loci in lentil (*Lens culinaris* Medikus ssp. *culinaris*). *Journal of Heredity* **90**, 270–275.

Sarker, A., Erskine, W., Hassan, M. S., Afzal, M. A. & Murshed, A. N. M. M. (1999*c*). Registration of "Barimasur-4" Lentil. *Crop Science* **39**, 876.

Sarker, A. & Erskine, W. (2002). Lentil production in traditional lentil world. In *Proceedings for the Lentil Focus National Conference*, pp. 20–25. Horsham, Victoria, Australia.

Sarker, A., Erskine, W. & Saxena, M. C. (2004*a*). Global perspective on lentil improvement. In *Pulses in New Perspective* (Eds A. Masood, B. B. Singh, S. Kumar & V. Dhar), pp. 24–28. Kanpur, India: Indian Society of Pulses Research and Development, IIPR.

Sarker, A., Erskine, W., Bakr, M. A., Rahman, M. M., Yadav, N. K., Ali, A. & Saxena, M. C. (2004*b*). Role of lentil in human nutrition and crop diversification in Asia region. In *Role of Legumes in Crop Diversification and Poverty Reduction in Asia*. Proceedings of the Joint CLAN Steering Committee Meeting, 10–12 November 2003, ICRISAT, India. (Eds C. L. L. Gowda & S. Pande), pp. 182–193. Patancheru, Andhra Pradesh, India: International Crops Research Institute for the Semi-Arid Tropics.

Sarker, A., Erskine, W. & Singh, M. (2005). Variation in shoot and root characteristics and their association with drought tolerance in lentil landraces. *Genetic Resources and Crop Evolution* **52**, 87–95.

Sarker, R. H., Biswas, A., Mustafa, B. M., Mahbub, S. & Hoque, M. I. (2003). Agrobacterium-mediated transformation of lentil (*Lens culinaris* Medik.). *Plant Tissue Culture* **13**, 1–12.

Sarwar, D. M., Kaul, A. K. & Quader, M. (1982). Correlation studies in lentils. *LENS Newsletter* **9**, 22–23.

Savage, G. P. (1988). The composition and nutritive value of lentils (*Lens culinaris*). *Nutrition Abstracts and Reviews* (*Series A*) **58**, 319–343.

Saxena, M. C. (1981). Agronomy of lentils. In *Lentils* (Eds C. Webb & G. C. Hawtin), pp. 111–130. Farnham Royal, UK: Commonwealth Agricultural Bureau.

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

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

Silim, S. N., Saxena, M. C. & Erskine, W. (1990). Seeding density and row spacing for lentil in rainfed Mediterranean environments. *Agronomy Journal* **82**, 927–930.

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

Summerfield, R. J., Roberts, E. H., Erskine, W. & Ellis, R. H. (1985). Effects of temperature and photoperiod on flowering in lentils (*Lens culinaris* Medic.). *Annals of Botany* **56**, 659–671.

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

Tyagi, M. C. & Sharma, B. (1981). Effect of photoperiod and vernalization on flowering and maturity in macrosperma lentils. *Pulse Crops Newsletter* **1**, 10–12.

Tullu, A., Buchwaldt, L., Warkentin, 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). *Theoretical and Applied Genetics* **106**, 428–434.

Tullu, A., Taran, B., Breikreutz, C., Buchwaldt, L., Baninza, S., Warkentin, T. & Vandenberg, A. (2005). A QTL for resistance to Ascochyta blight maps to the same linkage group containing the gene for Anthracnose resistance in lentil. In *Abstracts of the Proceedings of the International Edible Legume Conference, Durban, South Africa, 17–21 April 2005*, p. 22.

Vaillancourt, R. E. & Slinkard, A. E. (1992). Inheritance of new genetic markers in lentil (*Lens* Miller). *Euphytica* **64**, 227–236.

Van Oss, H., Aron, Y. & Ladizinsky, G. (1997). Chloropast DNA variation and evolution in the genus *Lens* Mill. *Theoretical and Applied Genetics* **94**, 452–457.

WESTPHAL, E. (1974). *Pulses in Ethiopia, Their Taxonomy and Agricultural Significance*. Wageningen, The Netherlands: PUDOC.

WILLIAMS, J. T., SANCHEZ, A. M. C. & JACKSON, M. T. (1974). Studies on lentil and their variation. I. The taxonomy of the species. *SABRAO Journal* **6**, 133–145.

WITCOMBE, J. & JOSHI, A. (1996). Farmer participatory approaches for varietal breeding and selection and linkages to the formal seed sector. In: *Participatory Plant Breeding*. *Proceedings of a Workshop on Participatory Plant Breeding, Wageningen, The Netherlands*. *IPGRI, Rome, Italy* (Eds P. Eyzaguirre & M. Iwanaga), pp. 57–65. Rome, Italy: International Plant Genetic Resources Institute.

YAU, S. K. & ERSKINE, W. (2000). Diversity of boron-toxicity tolerance in lentil growth and yield. *Genetic Resources and Crop Evolution* **47**, 55–61.

ZAMAN, A. F. M. & MIAH, A. A. (1989). Effect of different levels of management on the grain yield of lentil. *Advances in Pulses Research in Bangladesh. Proceedings of the Second National Workshop on Pulses, 608 1989, BARI, Joydebpur, Bangladesh*, pp. 67–73. Patancheru, Andhra Pradesh, India: ICRISAT.