CHAPTER 19

ABIOTIC STRESSES

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Abstract: There has been a large focus on biotic stresses in lentil as these cause obvious and serious reductions in yield and quality. However, increasingly abiotic stresses are being identified as major factors involved in the low and unreliable yield of lentils in many countries. Within each growing region, variations in climate, soils, and interactions between climate and soil affect lentil productivity and quality directly, or indirectly though their influence on foliar and soil borne diseases, pests and rhizobia. Furthermore, the impact of a specific stress can be influence by the relative tolerance of a cultivar and/or effect of particular cultural control methods

1. INTRODUCTION

The distribution and quantity of rainfall and the temperature regime are the main determinants of where and in what season lentil is grown around the world. In West Asia and North Africa (WANA) and Australia the climate is characterised by cold, wet winters, rapidly rising temperatures in spring and hot, dry summers (Erskine and Saxena 1993, Erskine *et al.* 1994a, Materne 2003). In winter in these regions low radiation levels and temperatures restrict vegetative growth but increase water use efficiency (Silim *et al.* 1993, Hamdi and Erskine 1996). Lentil is winter sown at altitudes below approximately 850 m, typically in areas that receive an annual rainfall of 300 to 450 mm (Erskine and Saxena 1993, Silim *et al.* 1993, Erskine *et al.* 1994a, Materne *et al.* 2002). However, lentil is spring sown in colder, high altitude areas of West Asia, such as Central Turkey, and in USA, Europe, Canada, Chile and Argentina, where it is grown on stored moisture supplemented by rainfall during the spring and summer growing seasons. In the subtropical regions of Pakistan, India, Nepal and Bangladesh, lentil is grown as a winter ('rabi') crop on residual soil moisture (Ali *et al.* 1993, Muehlbauer *et al.* 1995).

Within each growing region, variations in climate, soils, and interactions between climate and soil affect lentil productivity and quality directly, or indirectly though their influence on foliar and soil borne diseases, pests and rhizobia. Furthermore, the impact of a specific stress can be influence by the relative tolerance of a cultivar and/or effect of particular cultural control methods. For example, late sowing to avoid extremely cold temperatures in the USA and Turkey (Muehlbauer and McPhee, 2002). The influence of abiotic stresses can occur over a broad region such as occurs with drought, or can be highly heterogeneous within a small area such as occurs with soil toxicities in south eastern Australia (Nuttal *et al.* 2003a). To maximize lentil production and quality, the major abiotic stresses must be identified in a particular region and managed through cultural practices to avoid the stress and/or the release of tolerant cultivars.

2. DROUGHT

A lack of water is the major limitation to lentil production worldwide and in it's most severe form drought can result in crops with no economic grain yield. Drought is a regular and severe constraint to crop yields in many areas of the world where lentils are grown (McWilliam 1986). Autumn or winter sown crops in Mediterranean environments are likely to experience intermittent drought during their vegetative growth period and terminal drought during their reproductive period when temperatures are increasing and rainfall is decreasing. Spring sown crops in Mediterranean environments, and winter sown crops in the semi arid tropics, experience progressively increasing drought stress during the growing season. In South Asia, drought may also occur during plant establishment if sowing is delayed and plant roots cannot reach subsoil moisture (Bhattarai *et al.* 1988, Rahman and Mallick 1988).

In order to understand the structure of the world lentil collection, landraces held at the International Center for Agricultural Research in the Dry Areas (ICARDA) were characterised into four major regional groups identified through analysis of variability in quantitative and qualitative morphological traits (Erskine *et al.* 1989). These were the Levantine group (Egypt, Jordan, Lebanon and Syria), the northern group (Greece, Iran, Turkey, USSR, Chile), the Indian subcontinent group and the Ethiopian group. Erskine *et al.* (1994b) later found that the dissemination of lentil around the world has resulted in the selection of different regionally specific balances between photoperiod and temperature for the control of flowering. These regionally specific flowering responses provide the basis for adaptation to the climatic variables of an environment for which abiotic and biotic constraints can be evaluated and addressed. Shrestha *et al.* (2006) found differences in the response of genotypes to water deficits imposed during flowering and podding that also indicate differences between lentil groups in growth and water use. Water deficits reduced seed yield by up to 60% in crossbreds selected for South Asia and the South Asian cultivar, Simal, but seed yield increased with water deficit at flowering in the West Asian genotype, Cassab.

Compared to other pulses, lentil is relatively tolerant of drought and is grown in drier areas of the WANA region than faba bean and chickpea. These lentil growing regions may have as little as 250 mm of annual rainfall (Muehlbauer *et al.* 1985, Saxena 1983, Silim *et al.* 1993, Erskine *et al.* 1994a, Hamdi and Erskine 1996). However, lentil's adaptation to drought is typically through avoidance, with forced senescence and crop maturity induced by high temperatures, severe drought stress or a combination of both (Erskine and Saxena 1993, Erskine *et al.* 1994a).

In the Mediterranean and temperate world regions, lentil yields are very dependent on available soil moisture during the growing season. For example, the total growing season rainfall accounted for 41 to 55% of the total variation in seed yield in lentil in WANA over many sites and seasons (Erskine and Saxena 1993) and 56% of the total variation in seed yield among 11 diverse lentil genotypes grown at two sites in south eastern Australia over four years (Materne 2003). At one site in Syria, total growing season rainfall accounted for up to 80% of the variation in seed yield over several seasons (Erskine *et al.* 1994a). This would also be true of subtropical areas and in cold, high altitude and/or latitude areas, where levels of stored moisture and snow melt and rainfall during the spring and summer growing seasons, respectively, have a major impact on yield.

In Syria and Australia, and most likely all other lentil growing areas, selection for yield under variable rainfed conditions has increased water use efficiency in lentil through an increased response to moisture availability (Murinda and Saxena 1983, Erskine and Saxena 1993, Materne 2003). However, to breed lentil cultivars that are tolerant to drought, it is necessary to identify genetic variability for traits that are associated with low water availability tolerance. Various mechanisms, including high early vigour and early flowering and maturity have been proposed for escaping terminal drought. For example, in a dry year in Syria, the highest yielding lentil genotypes produced a large amount of biomass, flowered early and had a brief, rapid seed-filling phase (Silim *et al.* 1993). Time to flowering accounted for 49% of the variation in seed yield, indicating that avoidance through early flowering, such as with ILL6035, was the key to minimising the effects of drought stress (Silim *et al.* 1993). Early flowering is important for drought escape but it cannot be utilised if genotypes have a relatively low mean yield over many seasons and sites, due to an inability to respond to increasing available soil moisture (Turner *et al.* 2001, Materne 2003). In Syria the medium flowering genotypes ILL4400 and ILL4401 had a high seed yield in most seasons compared to other landraces studied (Murinda and Saxena 1983) but they were intolerant to drought in a separate study (Silim *et al.* 1993). Similarly, early flowering and maturing genotypes were high yielding at low rainfall, low yielding environments in Australia but the yields of these genotypes was low compared to the best medium rainfall genotypes over eight sites and five years (Materne 2003). Inherently late, temperature responsive and photoperiod insensitive genotypes for flowering were the most broadly adapted genotypes in Australia and were proposed for improving drought avoidance as time to flowering is optimal in most years but potentially earlier in drought years when temperatures are often higher (Materne 2003).

Wild lentils, particularly *L. culinaris* ssp. *orientalis*, are often found in habitats characterised by low average rainfall (Erskine and Saxena 1993, Erskine *et al.* 1994a) but they produce markedly less biomass and seed yield than cultivated lentils under dry conditions (Hamdi and Erskine 1996). Hamdi and Erskine (1996) found that the species *L. odemensis* Ladizinsky had the least reduction in seed yield when drought and non drought treatments were compared. However, ILL1861 (cultivated lentil) was the highest yielding genotype under drought conditions.

Lentil, together with chickpea, had a higher degree of osmotic adjustment compared to other grain legumes studied by Leport *et al.* (1998), especially with water deficits during flowering (Shrestha *et al.* 2006). This indicated that avoidance may not be the only mechanism for drought tolerance in lentil and chickpea. Deeper rooting has been advocated as a way of increasing legume productivity under moisture limiting conditions (Buddenhagen and Richards 1988, Turner *et al.* 2001). Genotypic differences in the length and spread of roots have been reported for lentil but not in association with water usage (Saxena *et al.* 1993, Saxena and Hawtin 1981). Short duration cultivars of chickpea and field pea have faster early root growth rates, but this is not sustained during seed fill, leading to early root senescence and the loss of effective root length (Saxena *et al.* 1993). This is also likely to be true of lentil and, as previously shown, early flowering is important for drought avoidance but this may limit the potential for greater root length as a drought tolerance mechanism. In Australia, where subsoils have high levels of boron and salt, cultivars with tolerance to these factors may be better able to utilise subsoil moisture and assist in alleviating drought stress (Materne *et al.* 2002).

Screening for drought tolerance and associated mechanisms may be successfully achieved through limiting water supply but as with early flowering as an escape mechanism, care must be taken in ensuring that selection is not for major regional adaptational traits. Hence, screening multiple genotypes under controlled environment conditions may be an initial useful step, without interference from other potentially adaptive physiological responses. Late sowing was not successful as a screening method in Syria as it altered the vegetative and phenological development of the crop through changes in temperature and photoperiod. (Erskine and Saxena 1993, Erskine *et al.* 1994a). In Australia, late sowing improved the relative performance of late flowering genotypes that perform poorly in drought years (Materne 2003).

Within a defined growing season, the early sowing of lentil often produces the highest seed yield in Mediterranean type environments such as in Italy, Syria, Egypt, Libya and Western Australia, Ethiopia, sub tropical environments in India and Bangladesh, and in North America and South America (Muehlbauer *et al.* 1995, Materne 2003). As with many crops, early sowing has been advocated in many areas to avoid rising temperatures and drought during the reproductive period and maximize yields. However, early sowing can expose crops to increased weed competition, diseases and abiotic stresses. For example in Australia, early sowing increased the prevalence of the diseases *Ascochyta lentis* and *Botrytis spp* and lodging (Materne 2003, Knights 1987). Early sowing increased the incidence of rust (*Uromyces fabae*) (Singh and Dhingra 1980, Mittal 1997), fusarium wilt (*Fusarium oxysporum* f.sp. *lentis*) (Kannaiyan and Nene 1975, Mittal 1997), *Botrytis cinerea* (Knights 1987), root rot (*Rhizoctonia solani* and *Macrophomina phaseolina*), downy mildew (*Peronospora lentis*), ascochyta blight (*Ascochyta lentis* Vassilievsky) (Knight *et al.* 1989, Mittal 1997) and collar rot (*Scerotia sclerotiorum*) (Agrawal *et al.* 1976, Mittal 1997). Early sowing also increased nodule damage by the insect *Sitona crinitus* (Weigand *et al.* 1992), and increased the number and dry weight of weeds (Mishra *et al.* 1996) and infestations of the parasitic weed *Orobanche* spp. in Syria (Silim *et al.* 1991, Hezewijk *et al.* 1987). Excessive vegetative growth and severe lodging due to high rainfall reduced yield of early sown lentil in Ethiopia (Bejiga 1991). In the USA, Turkey (Central Anatolia), Canada, Chile and Argentina, lentil is sown as early as possible in spring provided the soil is not too wet (Muehlbauer *et al.* 1995). In some of these areas, large yield increases can be achieved by sowing lentil in winter rather than spring if problems associated with a lack of winter hardiness, increased incidence of diseases and weed control issues can be addressed (Kusmenoglu and Aydin 1995, Erskine *et al.* 1996, Muehlbauer and McPhee 2002). Thus, addressing constraints to early sowing is another effective method of improving tolerance to terminal drought.

It has also been postulated (see chapter 8) that drought stress may act through reduction in fixation capability either through poorer rhizobium survival in droughted soils or more adverse effects of drought on lentil fixation than total productivity. The proportion of N assimilated from the atmosphere (%Ndfa) may decline with increasing increasing drought stress. This may mean that the symbiosis is preferentially sensitive to drought stress.

3. WATERLOGGING

In comparison with cereals, lentil, field pea and chickpea are intolerant to waterlogging at germination and have severely depressed vegetative growth, especially of roots (Crawford 1977 and Thomson unpublished data in Jayasundara *et al.* 1998). Excess water during winter can reduce lentil yields in Mediterranean environments and likewise if it occurs in late spring and summer in subtropical environments. In Nepal sowing of lentil is delayed to avoid waterlogging and *Lathyrus sativus* is preferred for early sowing. However, in most areas waterlogging can only be avoided by not growing the crop in prone areas or physically altering the environment using drainage systems or raised beds. The sensitivity of lentil (and potentially also lentil nitrogen fixation) to waterlogging and anaerobic conditions accounts for the poor response of the crop to irrigation, but responsive genotypes have been identified with large root parenchyma (Erskine and Saxena 1993, Erskine *et al.* 1994a). Among a range of germplasm, ACC-36115, ACC-215711, ACC-36140, ACC-215348, NEL-944, FLIP-89-63L and FLIP84-78 were most tolerant to waterlogging 30 days after sowing and early maturing lines were more sensitive to waterlogging than late maturing lines (Bejiga and Anbessa 1995). ILL3490 was tolerant to waterlogging in glasshouse studies in Australia (J. Clements pers. comm) but lines with greater field tolerance have been observed in Nepal (D. McNeil pers. comm.).

4. TEMPERATURE

Temperature has a major influence on the growth and development of plants, pathogens and symbiotic organisms such as rhizobia. Temperature has been shown to influence the evolution and adaptation of lentil spread worldwide. For example, Erskine (1996) found that among 171 lentil genotypes from Syria and Turkey, large-seeded (macrosperma) accessions had a longer reproductive period than smallseeded (microsperma) accessions in Syria. They concluded that larger seeded accessions were higher yielding in cooler seasons due to a longer seed filling period, but were lower yielding at higher temperatures. The clustering of traits that define the phenological adaptation of lentil to an ecological environment indicated that local environments have been important in the evolution of the species (Erskine *et al.* 1989). The dissemination of lentil into new environments has thus caused selection for different regionally specific balances between photoperiod and temperature for the control of flowering (Erskine *et al.* 1994b). For example, cultivated lentil spread from West Asia to the Indo-Gangetic plain around 2,000 BC (Erskine and Saxena 1993). Lentil landraces originating from West Asia flower much later in Pakistan and India than the local landraces, and their reproductive development begins when conditions are increasingly hot and dry in that environment (Erskine and Saxena 1993). Similarly, European landraces are too late to flower and mature in West Asia and Australia (Materne 2003). Thus changes in phenology will change the risk of exposure to frost, drought and high and low temperatures during sensitive growth stages. The timing of flowering is a particularly important event as it determines the duration of the vegetative phase (sowing to flowering), which establishes the potential of the crop, and at the same time determines the climatic conditions that the crop will be exposed to during reproductive growth (Lawn *et al.* 1995).

Temperature has a major influence on the general adaptation of lentils but extremes in temperature during the growth and reproduction of lentils can result in a more specific and dramatic effect. High temperatures during spring are major constraints to lentil production in West Asia, North Africa and Australia and cold winters limit production to spring sowing in higher altitude or latitude regions (Erskine and Saxena 1993).

4.1. Low Temperature

In the USA and Turkey (Central Anatolia), large yield increases have been achieved by sowing lentil in winter rather than spring (Saker *et al.* 1988, Erskine *et al.* 1981, Kusmenoglu and Aydin 1995, Erskine *et al.* 1996, Muehlbauer and McPhee 2002).

However, problems associated with a lack of winter hardiness have been encountered and the genetic mechanisms governing tolerance are under investigation (Kahraman *et al.* 2004).

Genotypes that can survive temperatures below freezing during vegetative growth have been selected in field environments in different regions of the world where they survived temperatures as low as -26.8 degrees Celsius (°C)(Erskine et al. 1981, Hambdi *et al.* 1996, Stoilova 2000, Chen *et al.* 2006) and in controlled environment experiments using a cold treatment of -15° C (Ali *et al.* 1999). In the study of Hambdi *et al.* (1996) a total of 245 accessions of wild lentil, 10 of cultivated lentil and three accessions of *Vicia montbretii* (syn. *L. montbretii*) were evaluated for winter hardiness in Syria and Turkey where absolute minimum temperatures were -16 °C and -18.9 °C respectively. Accessions of *L. culinaris* subsp.*orientalis* exhibited the highest level of winter hardiness, on average; whereas, accessions of *L. nigricans* subsp.*ervoides* were the most susceptible. Correlations revealed that winter hardiness was concentrated among accessions originating from high elevation areas. A cold tolerance nursery (LICTN) was established by ICARDA in 1987/88 and the selected tolerant genotypes were distributed internationally for evaluation (Malhotra and Saxena 1993). Efforts to screen for cold tolerance and develop molecular markers have been hindered by the variability in the screening environment caused by large differences between sites and seasons and within sites (Erskine and Saxena 1993, Muehlbauer pers comm). However, Erskine *et al.* (1999) identified one gene that controlled tolerance to radiation frost injury in lentil using recombinant inbred lines. A random amplified polymorphic DNA (RAPD) marker, OPS-16750, was linked to the locus for radiation-frost tolerance (Frt) trait at 9.1 centimorgans (cM). In the USA, winter hardy types have been selected and evaluated with a range of agronomic practices to initiate winter sowing (Chen *et al.* 2006).

In some Mediterranean environments frost during the reproductive period can cause major economic losses by killing flowers, pods and seeds with associated reductions in seed yield and quality. Currently, the only mechanism for limiting frost damage is using later flowering genotypes or delaying sowing to avoid frosts. However in Australia, the benefits of these strategies can be small or non existent in years when frosts occur but they result in lower yields in all other years (Materne 2003).

4.2. High Temperatures

Hot or dry weather during flowering and pod fill present severe constraints to the productivity of lentil crops in many regions of the world, including the Mediterranean (Erskine 1985). Summerfield *et al.* (1989) reported that under controlled conditions, progressively warmer temperatures post flowering restricted vegetative growth, accelerated progress towards reproductive maturity and reduced seed yield. Rhizobia are also susceptible to higher temperatures, particularly when conditions are moist (Malhotra and Saxena 1993). Earlier flowering may be a mechanism for avoiding high temperatures. However, earlier flowering may expose crops to a greater risk of frost damage in some environments, particularly if flowering is early and the crop produces inadequate biomass to sustain large seed yields (Turner *et al.* 2001, Materne 2003).

5. NUTRIENT TOXICITIES

Although generally adapted to alkaline soils, lentil growth can be affected by hostile subsoil factors such as high pH, toxic levels of boron and salinity and sodicity (Nuttall *et al.* 2001, Nuttall *et al.* 2003a, Yau 1999, Yau and Erskine 2000, Saxena *et al.* 1993). Lentil is traditionally grown on neutral to alkaline soils. For example, much of India's lentil is grown in regions with moderate to highly alkaline soils (pH 7.5–9.0) although lentils are also grown on the slightly acidic soils (pH 5.5–6.5) of the Andean foothills (Knights 1987). The crop thrives in warm sandy soils but may produce excessive vegetative growth at the expense of seed yield when grown on rich, moister soils (Smartt 1984, Muehlbauer *et al.* 1995). In Australia, lentil is best adapted to alkaline grey cracking clay and red brown earth soils in medium rainfall (350–450 mm/year) areas (Materne 2002b). However, seed yields have been compromised where soil pH was below 6.0 (CaCl₂) and clay content was less than 15% (Siddique *et al.* 1999). Pulse crops are generally considered to be more sensitive to subsoil constraints than cereal crops (Jayasundara *et al.* 1998). Alleviating such toxicity problems through soil modification is not an economic or practical solution and hence, if lentil is to be grown in these regions, the breeding of more tolerant lentil cultivars is considered the best approach to maximise yields.

5.1. Boron Toxicity

Boron (B) toxicity is increasingly being recognised as a problem in the arid areas of West Asia and Australia where lentil is widely grown (Yau 1999, Yau and Erskine 2000, Hobson *et al.* 2006). In the alkaline-soil cropping regions of southern Australia, high concentrations of soil B have been identified as a limitation to crop growth and grain yield (Ralph 1991). The highest concentrations of B in this region have been found at depths between 40 and 100 cm (Cartwright *et al.* 1984; Nuttall *et al.* 2003b, Hobson *et al.* 2004), although concentrations at shallower depths (10 to 20 cm) may also affect lentil due to their high sensitivity. Levels as low as 4 ppm have produced visual toxicity symptoms on lentil 26 days after sowing (Chauhan and Asthana 1981). In this same experiment, it took 47 and 37 days to see visual symptoms of boron toxicity on barley and oats respectively. The amelioration of B toxicity through soil modification is not an economic or practical solution. Hence the breeding of more tolerant cultivars is considered the best approach to minimise yield losses (Rathjen *et al.* 1999).

High field spatial variability in the distribution of soil B (Ryan *et al.* 1998; Nuttall *et al.* 2003a) makes field screening risky and difficult to interpret. In contrast controlled-environment screening provides an efficient means of identifying tolerant germplasm from large numbers of accessions, prior to confirming results in the field. In glasshouse studies ILL5883 was most tolerant to B as based on seedling symptoms and seed yield (Yau 1999, Yau and Erskine 2000). Accessions from Afghanistan were the most tolerant, followed by those from India, Iraq, Syria, Europe, Ethiopia, and Nepal (Yau and Erskine 2000). Hobson *et al.* (2003) identified lines with better tolerance to B than ILL5883 among landraces from Ethiopia (ILL2024), Afghanistan (ILL213A, ILL1818, ILL1763, ILL1796) and the Middle East (ILL5845), whilst accessions from Europe had the least tolerance. These origins of tolerance are consistent with wheat (Moody *et al.* 1988), winter barley (Yau 2002) and field pea (Bagheri *et al.* 1994). Current Australian lentil cultivars were intolerant to concentrations of soil B that occur in the Mallee region of Australia as reflected in severe effects on both above and below ground biomass accumulation and grain yield (Hobson *et al.* 2006). B-tolerance identified at the seedling stage persisted through to maturity and resulted in higher seed yield. ILL2024 and ILL213A had the least symptoms in the seedling stage and the greatest seed yield in soluble B concentration of 18.2 mg/kg (Hobson *et al.* 2006). While the two tolerant accessions were generally characterised by an ability to partially exclude B from shoot tissues, ILL2024 was more tolerant in terms of leaf toxicity symptoms but ILL213A was more tolerant in terms of growth maintenance at high leaf-B concentrations (Hobson, unpublished data).

When grown in a reconstituted core resembling 'natural' high soil B distribution, ILL2024 had no significant reduction in yield where high subsoil-B occurred (18.2 mg/kg) from 30 or 10 cm in the profile under controlled moisture. In comparison, the current Australian lentil cultivar Cassab, had significantly reduced yields of 32 and 91% when high subsoil-B occurred at 30 and 10 cm respectively (Hobson *et al.* 2004).

The development and release of B tolerant cultivars offers great potential for improving seed yield in large areas of southern Australia and thus for the expansion of the crop. Investigations are currently being conducted in Australia to determine the inheritance and benefits of boron tolerance.

Boron deficiency has been identified as a limitation to lentil production on soils in Nepal (Srivastava *et al.* 1999). Differences in the response of lentil genotypes to applied boron have been reported in the field in India (Sakal *et al.* 1988). Variation in tolerance to boron deficiency has been identified in lentil, with germplasm from South Asia exhibiting the least symptoms and those from the Middle East exhibiting the most severe symptoms (Srivastava *et al.* 2000). Gahoonia *et al.* (2005) found that lentil lines exist with different root morphologies that may be better able to scavenge micronutrients such as B from the soil and give 10–20% yield increases. There is increasing evidence that the same genetic mechanisms are likely to control tolerance to both boron deficiency and toxicity, predominantly boron exclusion (Yau and Erskine 2000, Dannel *et al.* 2002). This dual control may restrict the adaptability of lentils from South Asian countries such as Bangladesh to Australian soils. The two lentil accessions from Nepal that were tested by Hobson *et al.* (2003) were both found to be intolerant of high soil boron.

5.2. Salinity

Salinity occurs mainly in arid and semi-arid regions, where evaporation considerably exceeds precipitation, such as in West and Central Asia and in Australia, and in coastal areas because of the ingress of seawater (Saxena *et al.* 1993). The use of irrigation has also led to salinization of productive lands in the Indo-Gangetic Plain of South Asia, WANA, western USA and Australia (Saxena *et al.* 1993). Secondary salinity is of increasing importance in the dryland cropping areas of Australia, including south eastern and Western Australia where subsoil salinity is a result of cropping on soil laid down over an ancient sea bed (McWilliam 1986). Legumes are relatively sensitive to salt and lentil is comparatively more sensitive than field pea and faba bean and similar to chickpea (Saxena *et al.* 1993). Salinity is not generally considered to be a problem for lentil production worldwide (Erskine *et al.* 1994a), although the major lentil growing areas of the world are regions with a high frequency of saline or sodic soils (Saxena *et al.* 1993). Response to salinity is affected by many other environmental factors such as soil water status, relative humidity, temperature and nutrition (Saxena *et al.* 1993, Lachaal *et al.* 2002).

Variation in tolerance to $MgSO_4$, NaCl, Na₂SO₄ and MgCl₂ was identified in the USDA World Lentil Collection (Jana and Slinkard 1979) but the level of tolerance was considered insufficient for breeding to continue (Muehlbauer and Slinkard 1983). The NaCl tolerant accessions DL443 and Pant L406 (Rai *et al.* 1985), ILL5845, ILL6451, ILL6788, ILL6793 and ILL6796 (Ashraf and Waheed 1990) and LG128 (ILL3534) (Maher *et al.* 2003) have been identified. A positive correlation was observed between degrees of salt tolerance at different stages of growth in the glasshouse (Ashraf and Waheed 1993a) and tolerance was based on the typical halophytic mechanism of salt inclusion (Ashraf and Waheed 1993, Shah and Muhammad 1976). The inheritance of salt tolerance has been investigated but the results were inconclusive, although recessive genes were implicated (Ashraf and Waheed 1998). In the glasshouse, tolerant accessions were unaffected by NaCl concentrations commonly found in the southern Mallee of Victoria but the growth of Australian cultivars was severely reduced (Maher *et al.* 2003). Therefore the development and release of tolerant cultivars offers great potential for improving seed yield in these areas. However, cultivars that are tolerant to both NaCl and B will be required in areas such as the southern Mallee of Victoria where both toxicities occur. High yielding breeding lines have been identified in Australia that have inherited improved NaCl tolerance from ILL6788 (Materne *et al.* 2006) and investigations are currently being conducted to determine the inheritance and importance of the tolerance. Lentils that are growing slowly are more sensitive to salt than those grown rapidly according to Lachaal *et al.* (2002). Breeding for increased vigor and the elimination of other abiotic and biotic stresses may thus offer potential to indirectly reduce the effects of salinity.

5.3. Sodicity

Increasing soil sodicity (10–25 exchangeable sodium percentage, ESP) reduced plant height, leaf area, leaf dry weight, total biomass production and seed yield in lentil, and reduced both the nitrate reductase activity in the leaf and the total concentration of nitrogen in India (Singh *et al.* 1993). PL-406 was most tolerant to sodicity in that study. Gupta and Sharma (1990) found lentil had a sodicity threshold of 14.0 %. When compared to the ESP threshold for wheat (40.2%) , it is clear that pulses are more sensitive to high ESP than cereals. A possible reason for the difference has been suggested to be the cumulative effect of ionic imbalance and water uptake (Gupta and Sharma 1990).

6. CONCLUSIONS

Abiotic stresses have a major impact on lentils worldwide, but when compared to biotic stresses, research and progress have generally been more limited. However, there is now a greater understanding of the general adaptation of lentil and the impacts of drought and waterlogging, high and low temperatures and the major soil toxicities in lentil. In many cases agronomic practices can also add value in addressing abiotic constraints of lentil. In some cases such as with winter hardiness, tolerance to boron and salinity and potentially waterlogging, genetic variability has been identified and selected genotypes will enable the expansion of suitable planting areas and increase the reliability in yield of lentil production. However, genetic improvement for drought, frost and heat has proven more difficult, except where escape is the primary tolerance mechanism. For these, it is likely that further, in depth, studies regarding environment and genetic (multiple gene) components will be required. The identification of the major genetic components governing these important traits, that function in specific environments, will lead to their selection through advanced breeding technologies and the production of superior cultivars.

REFERENCES

- Agrawal, S.C., Khare, M.N. and Kushwaha, L.S. (1976) Effect of sowing dates on the collar rot of lentil caused by Sclerotium Rolf's Sac. JNKVV Research Journal 10: 172–173 CAB abstracts
- Ali, A., Johnson, D.L., Stushnoff, C. (1999) Screening lentil (*Lens culinaris*) for cold hardiness under controlled conditions. Journal of Agricultural Science 133: 3, 313–319
- Ali, M., Saraf, C.S., Singh, P.P., Rewari, R.B. and Ahlawat, I. P. S., S. (1993) Agronomy of lentil in India. In: Lentils in South East Asia, Proceedings of the seminar on lentil in South Asia, 11–15 March 1991, New Delhi, India, pp 103–127 (Eds W. Erskine and M. C. Saxena)
- Ashraf, M. and 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. and Waheed, A. (1993) Responses of some local/exotic accessions of lentil (*Lens culinaris* Medic.) to salt stress. Journal of Agronomy and Crop Science 170: 103–112
- Ashraf, M. and Waheed, A. (1998) Genetic basis of salt (NaCl) tolerance in lentil. LENS Newsletter 25: 15–22
- Bagheri, A., Paull, J.G. and Rathjen A.J. (1994) The response of Pisum sativum L. germplasm to high concentrations of soil boron. Euphytica 75: 9–17
- Bejiga, G. (1991) Effect of sowing date on the yield of lentil (*Lens culinaris* Medik.) Journal of Agronomy and Crop Science 167: 135–140
- Bejiga, G. and Anbessa, Y. (1995) Waterlogging tolerance in lentil. LENS Newsletter 22: 8–10
- Bhattarai, A.N., Bharati, M.P. and Gyawali, B.K. (1988) Factors which limit the productivity of cool season food legumes in Bangladesh. In: World Crops: Cool season food legumes, pp 230–234 (Ed R. J. Summerfield). Kluwer Academic Publishers
- Buddenhagen, I.W. and Richards, R. A. (1988) Breeding cool season food legumes for improved performance in stress environments. In: World Crops: Cool season food legumes pp 81–95. (Ed R. J. Summerfield) Kluwer Academic Publishers
- Cartwright B., B.A. Zarcinas & A.H. Mayfield (1984) Toxic concentrations of boron in a red-brown earth at Gladstone, South Australia. Australian Journal of Soil Research 22: 261–272
- Chauhan R.P.S. and Asthana A.K. (1981) Tolerance of lentil, barley and oats to boron in irrigation water. Journal of Agricultural Science, Cambridge 97, 75–78.
- Chen CC. Miller P. Muehlbauer F. Neill K. Wichman D. McPhee K. 2006) Winter pea and lentil response to seeding date and micro- and macro-environments. Agronomy Journal 98(6):1655–1663
- Dannel, F., Pfeffer, H. and Romheld, V. (2002) Uptake on boron in higher plants uptake, primary translocation and compartmentation. Plant Biology 4: 193–204
- Erskine, W. (1985) Perspectives in lentil breeding. In: Faba Beans, Kabuli Chickpeas and Lentils in the 1980's, pp 91–100 (Eds M. C. Saxena and S. Varma). Aleppo, Syria: ICARDA
- Erskine, W. (1996) Seed-size effects on lentil (*Lens culinaris*) yield potential and adaptation to temperature and rainfall in West Asia. Journal of Agricultural Science, Cambridge 126: 335–341
- Erskine, W. and Saxena, M. C. (1993) Problems and prospects of stress resistance breeding in lentil. In: Breeding for stress tolerance in cool-season food legumes. pp 51–62. (Eds K. B. Singh and M. C. Saxena) John Wiley and Sons
- Erskine, W., Adham, Y. and Holly, L. (1989) Geographic distribution of variation in quantitative traits in a world lentil collection. Euphytica 43: 97–103
- Erskine, W., Myveci, K., and Izgin, N. (1981) Screening a world lentil collection for cold tolerance. LENS Newsletter 13: 19–27
- Eujayl, I.; Erskine, W.; Baum, M.; Pehu, E. (1999) Inheritance and linkage analysis of frost injury in lentil. Crop Science 39: 3, 639–642
- Erskine, W., Tufail, M., Russell, A., Tyagi, M. C., Rahman, M. M. and Saxena, M. C. (1994a) Current and future strategies in breeding lentil for resistance to biotic and abiotic stresses. Euphytica 73: 127–135
- Erskine, W., Hussain, A., Tahir, M., Bahksh, A., Ellis, R. H., Summerfield, R. J., and Roberts, E. H. (1994b) Field evaluation of a model of photothermal flowering responses in a world lentil collection. Theoretical and Applied Genetics 88: 423–428
- Gahoonia, T. S., Omar Ali, Sarker, A., Rahman, M.M. and Erskine, W. (2005) Root traits, nutrient uptake, multi-location grain yield and benefit-cost ratio of two lentil (*Lens culinaris*, Medikus.) varieties. Plant and Soil. 272: 153–161
- Gupta S. K. and Sharma S. K. (1990) Response of crops to high exchangeable sodium percentage. Irrigation Science 11: 173–179.
- Hamdi, A. and Erskine, W. (1996) Reaction of wild species of the genus Lens to drought. Euphytica. 1996. 91: 2, 173–179
- Hamdi, A., Kusmenoglu, I. and Erskine, W. (1996) Sources of winter hardiness in wild lentil. Genetic Resources and Crop Evolution. 1996. 43: 1, 63–67
- Hezewijk, M. J. van, Pieterse, A. H., Saxena, M. C. and Borg, S. J. ter (1987) Relationship between sowing date and *Orobanche* (broomrape) development on faba bean (*Vicia faba* L.) and lentil (*Lens culinaris* Medikus) in Syria. Proceedings of the 4th international symposium on parasitic flowering plants. 1987, pp 377–390. CAB abstracts
- Hobson, K., Armstrong, R., Connor, D., Nicolas, M. and Materne, M. (2003) Genetic variation in tolerance to high concentrations of soil boron exists in lentil germplasm. In: "Solutions for a better environment". Proceedings of the 11th Australian Agronomy Conference. 2–6 February 2003, Geelong, Victoria. Australian Society of Agronomy
- Hobson, K.B., Armstrong, R.D, Nicolas, M.E, Connor, D.J. and Materne, M.A. (2004) Boron tolerance of lentil – highlights of a research program. In: "New directions for a diverse planet". Proceedings of the 4th International Crop Science Congress 26 Sep–1 Oct 2004, Brisbane, Australia.
- Hobson, K., Armstrong, R., Nicolas, M.,Connor, D. and Materne, M. (2006) Response of lentil (*Lens culinaris*) germplasm to high concentrations of soil boron. Euphytica 151, 371–382.
- Jana, M. K. and Slinkard, A. E. (1979) Screening for salt tolerance in lentils. LENS Newsletter 6: 25–27
- Jayasundara, H. P. S., Thomson, B. D. and Tang, C. (1998) Responses of cool season grain legumes to soil abiotic stresses. Advances in Agronomy 63: 77–153
- Kannaiyan, J. and Nene, Y. L. (1975) Note on the effect of sowing dates on the reaction of twelve lentil cultivars to wilt disease. Madras Agricultural Journal 62: 240–242. CAB abstracts
- Karaman A, Kusmenoglu I, Aydin N, Aydogan A, Erskine W, Muehlbauer FJ (2004) Genetics of winter hardiness in 10 lentil recombinant inbred line populations. Crop Science 44:5–12
- Knights, E. J. (1987) Lentil: A potential winter grain legume crop for temperate Australia. Journal of the Australian Institute of Agricultural Science 53: 271–280
- Knight, T. L., Martin, R. J. and Harvey, I. C. (1989) Management factors affecting lentil production in mid Canterbury. Proceedings Annual Conference – Agronomy Society of New Zealand. 1989, 19, pp 17–24. CAB abstracts
- Kusmenoglu, I. and Aydin, N. (1995) The current status of lentil germplasm exploitation for adaptation to winter sowing in the Anatolian highlands. In Autumn-sowing of lentil in the highlands of West Asia and North Africa, pp 63–71 (Eds J. D. H. Keatinge and I. Kusmenoglu) Ankara: CRIFC
- Lachaal, M., Grignon, C. and Hajji, M. (2002) Growth rate affects salt sensitivity in two lentil populations. Journal of Plant Nutrition 25: 2613–2625
- Lawn, R. J., Summerfield, R. J., Ellis, R. H., Qi, A., Roberts, E. H., Chay, P. M., Brouwer, J. B., Rose, J. L. and Yeates, S. J. (1995) Towards the reliable prediction of time to flowering in six annual crops. IV. Applications in crop improvement. Experimental Agriculture 31: 89–108.
- Leport, L., Turner, N. C., French, R. J., Tennant, D., Thomson, B. D. and Siddique, K. H. M. (1998) Water relations, gas exchange and growth of cool-season grain legumes in a Mediterranean-type environment. European Journal of Agronomy 9: 295–303
- Maher, L., Armstrong, R. and Connor, D. (2003) Salt tolerant lentils a possibility for the future? In: "Solutions for a better environment". Proceedings of the 11th Australian Agronomy Conference. 2–6 February 2003, Geelong, Victoria. Australian Society of Agronomy
- Malhotra, R. S. and Saxena, M. C. (1993) Screening for cold and heat tolerance in cool-season food legumes. In Breeding for stress tolerance in cool-season food legumes. Ed Singh, K. B.; Saxena, M. C. John Wiley & Sons Ltd, Chichester, UK: 1993. 227–244.
- Materne, M. A. (2003) Importance of phenology and other key factors in improving the adaptation of lentil (Lens culinaris Medikus) in Australia. Thesis presented for the degree of Doctor of Philosophy at The University of Western Australia, School of Plant Biology and Centre for Legumes in Mediterranean Agriculture (CLIMA), Faculty of Natural and Agricultural Sciences
- Materne, M., McMurray, L., Nitschke, S., Regan, K., Heuke, L., Dean, G. and Carpenter, D. (2002) The future of Australian lentil production. In: Proceedings of Lentil Focus 2002, 14–18 (Ed JB Brouwer) Horsham, Victoria, Australia
- Materne, M., Regan, K., McMurray, L., Nitschke, S., Dean, G., Heuke, L., and Matthews, P. (2006) Breeding for NaCl tolerance and improved adaptation in lentil. In: 'Breeding for success: Diversity in action' (Ed C.F. Mercer) Proceedings of 13th Australiasian Plant Breeding Conference, Christchurch, new Zealand 18–21 April 2006. pp 1198–1203
- McWilliam, J. R. (1986) The national and international importance of drought and salinity effects on agricultural production. Australian Journal of Plant Physiology 13: 1–13
- Mishra, J. S., Singh, V. P. and Bhan, V. M. (1996) Response of lentil to date of sowing and weed control in Jabalpur, India. LENS Newsletter 23: 18–23
- Mittal, R. K. (1997) Effect of sowing dates and disease development in lentil as sole and mixed crop with wheat. Journal of Mycology and Plant Pathology 27: 203–209. CAB abstracts.
- Moody, D. B., Rathjen, A. J., Cartwright, B., Paull, J. G. and Lewis, J. (1988) Genetic diversity and geographic distribution of tolerance to high levels of soil boron. In: Proceedings of the 7th International Wheat Genetics Symposium, Cambridge, UK, p 859–865
- Muehlbauer, F. J. and McPhee, K. E. (2002) Future of North American lentil production. In: Proceedings of Lentil Focus 2002, pp 8–13 (Ed JB Brouwer) Horsham, Victoria, Australia
- Muehlbauer, F. J. and Slinkard, A. E. (1983) Lentil improvement in the Americas. In: Proceedings of the international workshop on Faba beans, Kabuli chickpeas and lentils in the 1980's. pp 351–366. (Eds M. C. Saxena and S. Varma) ICARDA, 16–20 May 1983, Aleppo, Syria.
- Muehlbauer, F. J., Cubero, J. I. and Summerfield, R. J. (1985) Lentil (*Lens culinaris* Medic.) In: Grain Legume Crops. pp 266–311. (Ed R. J. Summerfield and E. H. Roberts) Collins, London
- Muehlbauer, F. J., Kaiser, W. J., Clement, S. L. and Summerfield, R. J. (1995) Production and breeding of lentil. Advances in Agronomy 54: 283–332
- Murinda, M. V. and Saxena, M. C. (1983) Agronomy of faba beans, lentils, and chickpeas. In: Proceedings of the international workshop on Faba beans, Kabuli chickpeas and lentils in the 1980's. pp 229–244. (Eds M. C. Saxena and S. Varma) ICARDA, 16–20 May 1983, Aleppo, Syria.
- Nuttall, J. G., Armstrong, R. D., and Connor, D. J. (2001) Understanding subsoil water-use on southern Mallee soils: I. Spatial characteristics of subsoil constraints. In: Proceedings of the 10th Australian Agronomy Conference pp 51. Hobart. Tasmania (28 January–1 February 2001)
- Nuttall, J., Armstrong, R. and Connor, D. (2003a) The effects of salinity, sodicity and soluble boron on wheat yields in the Victorian southern Mallee. In: "Solutions for a better environment". Proceedings of the 11th Australian Agronomy Conference. 2–6 February 2003, Geelong, Victoria. Australian Society of Agronomy
- Nuttall J.G., R.D. Armstrong, D.J. Connor & V.J. Matassa (2003b) Interrelationships between edaphic factors potentially limiting cereal growth on alkaline soils in north-western Victoria. Australian Journal of Soil Research 41: 277–292.
- Rahman, M. M. and Mallick, R. N. (1988) Factors which limit cool season food legume productivity in Bangladesh. In: World Crops: Cool season food legumes, pp 230–234 (Ed R. J. Summerfield). Kluwer Academic Publishers
- Rai, R., Nasar, S. K. T., Singh, S. J. and Prasad, V. (1985) Interactions between Rhizobium strains and lentil (*Lens culinaris* Linn.) genotypes under salt stress. Journal of Agricultural Science 104: 199–205 Ralph W. (1991) Boron problems in the southern wheat belt. Rural Research 153: 4–8.
- Rathjen A.J., J.D. Brand, C.-Y. Liu, J.G. Paull & D. Cooper (1999) Breeding for tolerance to soil toxicities. *In* 11th Australian Plant Breeders Conference, Adelaide, 19–23 April 1999, 1999. Eds P. Longridge, A. Barr, A. Auricht, G. Collins, A. Granger, D. Handford & J. Paull. pp 34–40. CRC for Molecular Plant Breeding.
- Ryan J, Singh M, Yau SK (1998) Spatial variability of soluble boron in Syrian soils. Soil & Tillage Research 45, 407–417.
- Sakal, R., Singh, A. P. and Sinha, R. B. (1988) Differential reaction of lentil cultivars to boron application in calcareous soil. LENS Newsletter 15: 27–29
- Sakar, D., Durutan, N. and Meyveci, K. (1988) Factors which limit the productivity of cool season food legumes in Turkey. In: World Crops: Cool season food legumes, pp 137–145 (Ed R. J. Summerfield). Kluwer Academic Publishers
- Saxena, M. C. (1983) Food legume improvement program at ICARDA An overview. In: Proceedings of the international workshop on Faba beans, Kabuli chickpeas and lentils in the 1980's. pp 1–13. (Eds M. C. Saxena and S. Varma) ICARDA, 16–20 May 1983, Aleppo, Syria
- Saxena, M. C. and Hawtin, G. C. (1981) Morphology and growth patterns. In: Lentils. pp 39–52 (Eds C. Webb and G. Hawtin) Commonwealth Agricultural Bureaux, ICARDA
- Saxena, N. P., Johansen, C., Saxena, M. C. and Silim, S. N. (1993) The challenge of developing biotic and abiotic stress resistance in cool-season food legumes. In: Breeding for stress tolerance in cool-season food legumes. pp 245–270. (Eds K. B. Singh and M. C. Saxena) John Wiley and Sons
- Shah, M. and Muhammad, Y. N. (1976) Effect of salinity on the chemical composition of three cultivars of lentil (*Lens esculenta*). Journal of Agricultural Research, Pakistan 14: 65–74. CAB abstracts
- Siddique, K. H. M., Loss, S. P., Regan, K. L. and Jettner, R. L (1999) Adaptation and seed yield of cool season grain legumes in Mediterranean environments of southwestern Australia. Australian Journal of Agricultural Research 50: 375–387
- Silim, S. N., Saxena, M. C. and Erskine, W. (1991) Effect of sowing date on the growth and yield of lentil in a rainfed Mediterranean environment. Experimental Agriculture 27: 145–154
- Silim, S.N., Saxena, M.C. and Erskine, W. (1993) Adaptation of lentil to the Mediterranean environment. I. Factors affecting yield under drought conditions. Experimental Agriculture 29: 9–19
- Singh, B. B., Tewari, T. N. and Singh, A. K. (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. Journal of Agronomy and Crop Science 171: 196–205 CAB abstracts
- Singh, G. and Dhingra, K. K. (1980) Effect of sowing dates and varietal reaction on the incidence of lentil rust. Journal of Research, Punjab Agricultural University 17: 233–235
- Smartt, J. (1984) Evolution of grain legumes. I. Mediterranean pulses. Experimental Agriculture 20: 275–296
- Srivastava, S. P., Joshi, M., Johansen, C. and Rego, T. J. (1999) Boron deficiency of lentil in Nepal. LENS Newsletter 26: 22–24
- Srivastava, S. P., Bhandari, T. M. S., Yadav, C. R., Joshi, M. and Erskine, W (2000) Boron deficiency in lentil: yield loss and geographic distribution in a germplasm collection. Plant and Soil 219: 147–151
- Stoilova, T. (2000) Evaluation of lentil germplasm accessions for winter hardness in Bulgaria. Bulgarian Journal of Agricultural Science. 6: 61–164
- Summerfield, R. J., Muehlbauer, F. J. and Short, R. W. (1989) Controlled environments as an adjunct to field research on lentils (*Lens culinaris*). V. Cultivar responses to above- and below-average temperatures during the reproductive period. Experimental Agriculture 25: 327–341
- Turner, N. C., Wright, G. C. and Siddique, K. H. M. (2001) Adaptation of grain legumes (Pulses) to water-limited environments. Advances in Agronomy 71: 193–231
- Weigand, S., Pala, M. and Saxena, M. C. (1992) Effect of sowing date, fertilizer and insecticide on nodule damage by *Sitona crinitus* Herbst (Coleoptera: *Curculionidae*) and yield of lentil (*Lens culinaris* Medik.) in northern Syria. Zeitschrift fur Pflanzenkrankheiten und Pflanzenschutz. 99: 174–181. CAB abstracts.
- Yau, S. K. (1999) Boron toxicity in lentil: yield loss and variation between contrasting lines. LENS Newsletter 26: 14–17
- Yau, S. K. (2002) Comparison of European with West Asian and North African winter barleys in tolerance to boron toxicity. Euphytica 123: 307–314
- Yau, S. K. and Erskine, W. (2000) Diversity of boron-toxicity tolerance in lentil growth and yield. Genetic Resources and Crop Evolution 47: 55–61