CHAPTER 3

ADAPTATION AND ECOLOGY

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Abstract: Worldwide, the major abiotic restrictions on yield of lentil are drought (usually linked with high temperature) and low temperature. LENMOD, a lentil crop growth model, gives greater understanding of how different climatic factors, including water availability and temperature, interact to determine lentil crop growth and yield. This model has considerable potential in predicting where lentil may be grown successfully. Breeding programmes are underway with the objectives of increasing adaptation of lentil to stress environments. The strategy used to combat drought has been to match the crop's development with the period of soil moisture availability. Genotypes with early seedling establishment, early and rapid biomass development and early flowering and maturity have been selected in sites of extremely low rainfall. Also, seed has been sown earlier in the spring or in the autumn. Success in the production of cold tolerant cultivars has been achieved by field screening of lentils in areas prone to extreme cold. High yielding varieties have been released for use in sites which experience over winter temperatures of -12 to $-30°$ C

1. INTRODUCTION

Lentil is a self-pollinating, quantitative long day or day neutral, diploid, annual grain legume suitable for cultivation in warm temperate, subtropical and high altitude tropical regions of the world (Muehlbauer et al. 1995). Currently, it is under cultivation on around 4 million hectares in more than 40 countries and in all continents except Antarctica. Lentil is usually grown alone but can be intercropped with a range of species including wheat, barley, rice, sugarcane, mustard, castor bean and linseed. Lentil seed can be surface broadcast or sown by drilling: it is suitable for direct drilling in areas of relatively high erosion potential (McPhee et al. 2004). 'Optimum' populations in relation to yield are around 100 plants m^{-2} but plants can initiate lateral branches to compensate for poor emergence or thin

S.S. Yadav et al. (eds.), Lentil: An Ancient Crop for Modern Times, 23–32.

stands (McKenzie 1987; Muehlbauer et al. 1995). Lentil can grow on a wide range of soil types and soil pH although there is evidence that, in comparison with a range of other grain legumes including pea, faba bean, chickpea and white lupin, it is more sensitive to waterlogging and soil pH < 6.5 (Tang and Thomson 1996). However, in comparison with these legumes, it would be considered drought and low temperature tolerant (McKenzie and Hill 1990; see below).

The largest collection of lentil genotypes ($> 10,000$) is held at ICARDA (International Centre for Agricultural Research in the Dry Areas, www.icarda.org), Syria (Sarker et al. 2002a). Substantial collections of greater than 2000 genotypes are also held in India, the USA and Russia, while several countries including Bulgaria, China and Spain have much smaller collections (Muehlbauer et al. 1995; Stoilova and Pereira 1999; De La Rosa et al. 2005). Several of these collections have been evaluated for variation in phenology, morphology and growth parameters. Positive correlations have been found between seed size, plant height, plant canopy width, number of productive branches/ pods/ seeds per plant, total biomass, seed yield and residual amounts (Erskine 1985, 1996, 1997; Stoilova and Pereira 1999; Tullu et al. 2001). Genotypic differences were also found in time to flowering and harvest, flowering response to photoperiod, sensitivity to low and high temperatures and disease resistance (Erskine 1985, 1997).

Worldwide, the major restrictions on yield of lentil are drought (usually linked with high temperature), low temperature and disease although other factors such as salt stress, nutrient deficiency and nutrient toxicity are important locally (Muehlbauer et al. 2006; Tivoli et al. 2006). Several breeding programmes are underway in the main lentil growing regions of the world with the objectives of increasing yield and yield reliability, adaptation to stress environments and disease resistance. In particular, ICARDA, which has a worldwide franchise for lentil, is involved with many countries in the development of lentil lines for different agro-ecological niches (Sarker et al. 2002a,b; ICARDA 2005). Here we focus on abiotic effects on lentil growth. Firstly, we take an integrated view of environmental effects on lentil crop growth via a discussion of LENMOD, a lentil crop model, then we consider recent work on selection of plants for drought/high temperature and low temperature tolerance.

2. MODELLING CROP GROWTH AND DEVELOPMENT UNDER DIFFERENT CLIMATIC CONDITIONS

Plant growth is greatly dependent on weather conditions, with physiological processes responding to changes in air and soil temperature, solar radiation, moisture availability and wind speed (Monteith 1981). The effects of individual climatic elements on crop growth during distinct phases of plant development can be quantified allowing the calibration of mechanistic numerical models of crop growth. Such models give greater understanding of how different climatic factors interact to determine crop yield. A lentil crop growth model (LENMOD) was developed and calibrated in experiments carried out on a silt loam soil at Lincoln, Canterbury, New Zealand (43.38° S, 172.30° E, 11 m above sea level) using cv. Titore, a small seeded, red variety of lentil (McKenzie 1987; McKenzie and Hill 1989; McKenzie et al. 1994). The experiments utilized spring, summer, autumn and winter sowing dates and a range of irrigation treatments over different years. The model requires the input of daily values of maximum and minimum air temperature, solar radiation, precipitation, potential evapo-transpiration and daylength and assumes that soil fertility is non-limiting and the crop is free of weeds and disease throughout all stages of growth.

All developmental stages in LENMOD except emergence to flowering depend on accumulated thermal time (TT). Sowing to emergence, flowering to physiological maturity and physiological maturity to harvest date require 115° C, 546° C and 270° C days above the critical temperature respectively. Emergence to flowering is dependent upon accumulated photothermal time and requires 278° C days (photothermal) above the critical temperature. The critical temperature below which growth and development stop is 2° C up to flowering and 6° C after flowering. The equations for relative daily leaf growth (RDLG), leaf area index (LAI) and crop growth rate (CGR) are:

(1) $$\mathrm{RDLG} = -0.0174 + 0.00829 \times \text{daily TT}$$

(2) $$\mathrm{LAI} = \text{previous LAI} \times \mathrm{RDLG} + \text{previous LAI}$$

(3) $$\mathrm{CGR} = 0.5 \times \mathrm{IR} \times \text{fraction IR intercepted} \times \mathrm{RUE} \times \text{drought factor}$$

In Equation(2), LAI is not allowed to exceed seven. In Equation(3), IR equals incident radiation and the drought factor is a ‘switch’ that turns off growth when the limiting deficit is passed. Radiation use efficiency (RUE) is set at 1.7 g DM MJ^{-1} of intercepted radiation. The equation for the fraction of IR intercepted is:

(4) $$\text{Fraction IR intercepted} = 1.0 - \exp(-\mathrm{k} \times \mathrm{LAI})$$

where –k is the extinction coefficient which is usually set at 0.32. The limiting soil moisture deficit is calculated from the relationship between relative yield and maximum potential soil moisture deficit (Penman 1948). When all plant available soil water is depleted, the drought factor becomes zero and thus the CGR becomes zero. After achieving maximum LAI, LAI declines to zero as a parabolic function of TT, based on 650° C days as follows:

(5) $$\mathrm{LAI} = \text{previous LAI} - \text{max LAI} \times [(\text{accumulated TT}/2.5) \times \text{daily TT} \times \text{leaf killer} \times (2/650^2)]$$

Leaf killer is dependent on soil moisture. If the soil moisture goes above the limiting deficit, leaf killer is five, but if it is below the limiting deficit, then leaf killer is one. Soil moisture deficit is based on Penman’s potential evapotranspiration. Total dry matter (TDM) is calculated from daily crop growth rate and the model assumes a stable harvest index of 40% for the calculation of seed yield.

Crop growth models have several practical applications including the prediction of where previously untested crops might be grown (Siddons et al. 1994). LENMOD was used to assess the potential of lentil as a grain legume crop in the UK (Andrews et al. 2001; Joyce et al. 2001). Firstly, the model was validated on one site (Durham, 54.77° N, 1.58° W, 40 m) over different studies. In the main study, predicted and actual time to flowering, and seed yield were determined for five spring sowing dates in 1999 (Table 1).

For the four sowing dates from 21 April to 12 May 1999, predicted flowering date was within 3 days of actual flowering date (Table 1). For the final sowing date (26 May), predicted flowering date was 3–7 days later than actual flowering date. For all sowing dates, predicted seed yields were within 9% of actual seed yields which ranged from 1.40 to 1.65 t ha^{-1}. These yields are substantially greater than average yields obtained in the major lentil producing countries (Muehlbauer et al. 1985). Interestingly, individual seed weight decreased steadily with sowing date from 29.1 mg for 21 April to 24.9 mg for 26 May but seed nitrogen content was similar (4.26–4.41%) for all sowing dates.

LENMOD was then used to predict maximum CGR, flowering date, maximum LAI, radiation intercepted, TDM produced, harvest date and seed yield for spring and autumn sowings of lentil over the period 1987–95 for eight sites selected from the UK Meteorological Office network of climate stations along a transect from NW Scotland to SE England (Andrews et al. 2001). This transect spans 7 degrees of latitude, corresponding to a difference in day length of approximately 1.5 h in mid-summer and is likely to capture the major spatial variability of mean temperature, rainfall and sunshine intensity throughout the year in the UK. Solar radiation and potential evapotranspiration are also likely to vary systematically over the length of the transect. Predicted data for three sites, Fort Augustus (57.13° N 4.68° W, 40 m), Eskdalemuir (55.32° N 3.20° W, 242 m) and East Malling (51.28° N0.45° E, 40 m) are presented to highlight how different climatic conditions would be expected to interact to determine crop growth and yield. In general, over the period 1987–1995, monthly mean daily solar radiation increased in the order Fort Augustus <

Table 1. Actual and predicted flowering date and seed yield and actual individual seed weight of lentil cv Titore for five sowing dates at Durham in 1999

Sowing date	Flowering date		Seed yield (t ha^{-1})		Seed wt (mg)
	Actual	Predicted	Actual	Predicted	Actual
21 April	24 June–28 June	26 June	1.65	1.55	29.1
28 April	29 June–1 July	30 June	1.58	1.47	28.7
5 May	2 July–5 July	4 July	1.55	1.46	26.6
12 May	6 July–10 July	9 July	1.40	1.47	25.4
26 May	11 July–15 July	18 July	1.62	1.48	24.9
SE (10 df)			0.109		0.55

Taken from Andrews et al. (2001)

Eskdalemuir < East Malling but monthly mean daily air temperature during the growing season (May to September) increased in the order Eskdalemuir (11.6° C) < Fort Augustus (12.6° C) < East Malling (15.4° C) (Joyce et al. 2001). Temperatures were lowest at Eskdalemuir because of its greater elevation. Monthly rainfall was generally greater for Fort Augustus and Eskdalemuir than for East Malling. In comparison with mean monthly rainfall, mean monthly potential evapotranspiration was generally less variable across the sites. During May and June for Eskdalemuir, from May to July for Fort Augustus and from April to August for East Malling, mean monthly potential evapotranspiration was substantially greater than mean monthly rainfall.

For the May sowing with 150 or 250 mm PAW, predicted mean values for maximum CGR, maximum LAI, radiation intercepted, TDM and seed yield increased with site in the order Fort Augustus < Eskdalemuir < East Malling (Table 2).

These effects were related to differences in average air temperature and radiation interception. An increase from 150 to 250 PAW with the May 1 sowing had only small effects on growth and yield at Fort Augustus and Eskdalemuir (Table 2). However, for East Malling where potential evapotranspiration was substantially greater than mean monthly rainfall for the longest period, this increase in PAW caused 54% increases in TDM and seed yield. A switch in sowing date from 1 May 250 PAW to 1 October gave small increases in crop growth and yield at Fort Augustus, substantial increases in crop growth and yield at East Malling but substantial decreases in crop growth and yield at Eskdalemuir. The positive effects of autumn sowing at East Malling were due, in part, to greater leaf area duration (LAI × time) and hence greater radiation interception. Also, autumn sowing reduced

Table 2. Predicted mean values for crop growth rate (CGR), flowering date, maximum leaf area index (LAI), radiation intercepted, total dry matter (TDM) produced and seed yield for lentil cv Titore with spring (1 May) and autumn (1 October) sowings at three sites in the UK over the period 1987–1995

	Fort Augustus			Eskdalemuir			East Malling		
	1 May[1]	1 May[2]	1 Oct[1]	1 May[1]	1 May[2]	1 Oct[1]	1 May[1]	1 May[2]	1 Oct[1]
Max CGR ($kg\,ha^{-1}\,d^{-1}$)	93	93	117	100	117	71	162	186	213
Flowering date	3 July	3 July	7 June	9 July	9 July	14 June	28 June	28 June	20 May
Maximum LAI	2.18	2.18	2.66	2.23	2.23	1.08	3.94	3.94	7.35
Radiation intercepted ($MJ\,m^{-2}$)	208	210	262	246	247	166	317	363	704
TDM ($t\,ha^{-1}$)	2.50	2.64	2.96	3.22	3.60	2.42	3.08	4.75	6.94
Seed yield ($t\,ha^{-1}$)	1.00	1.10	1.18	1.29	1.44	0.97	1.23	1.90	2.78

[1] 150 mm plant available water
[2] 250 mm plant available water
Taken from Andrews et al. (2001)

the period of time the crop was exposed to water stress due to its earlier maturation. The negative effects of autumn sowing at Eskdalemuir were due to low temperatures over-winter and in spring which restricted leaf development and hence reduced radiation interception. At all sites, flowering date was unaffected by an increase from 150 mm to 250 mm PAW with the May sowing but was earlier with the October sowing due to photothermal effects. For a 1 May sowing at 150 mm PAW, seed yield was similar at Eskdalemuir and East Malling but for the 1 October sowing, seed yield was three times greater at East Malling. In the case of East Malling, predicted yields for autumn sowing (2.78 t ha^{-1}) are exceptional but not unrealistic as yields of around 2.8 and 2.5 t ha^{-1} were obtained for autumn-sown lentil at Reading in S England over different years (Crook et al. 1999).

3. SELECTION FOR INCREASED DROUGHT TOLERANCE

Drought stress is the major restriction on lentil yield in lentil growing regions, worldwide (Muehlbauer et al. 1995, 2006; McKenzie and Hill 2004). For example, Erskine and El Ashkar (1993) reported that 80% of the variation in lentil seed yield in Mediterranean climates was accounted for by differences in seasonal rainfall. In the Mediterranean regions of West Asia and North Africa, lentil is usually grown in areas of 300–400 mm rain $year^{-1}$ (Erskine et al. 1994). In these areas, the major proportion of the rain falls in winter, and from March until crop maturity in May, the crop experiences water and high temperature stress to an extent that restricts yield.

Lentil is drought tolerant in comparison with other temperate grain legumes. For example, the limiting soil moisture deficit for lentil is similar to that for chickpea and substantially greater than that for pea or faba bean (McKenzie and Hill 2004). However, the amount of yield loss experienced for each mm of drought past the limiting soil moisture deficit was greater for lentil than chickpea or faba bean. Differences in limiting soil moisture deficits across the species are probably due to variation in their rooting depth and root proliferation (McKenzie and Hill 2004). Lentil roots are capable of extracting water from at least 90 cm depth (Sharma and Prasad 1984; McKenzie 1987). The variation in yield loss per mm of drought above the limiting soil moisture deficit was probably caused by factors which can influence water use, such as leaf size and orientation, stomatal number and orientation, and radiation use efficiency. Also, differences in osmotic adjustment could be important (Nielsen 2001). There are reports in the literature that several grain legume species including lentil have a critical period of sensitivity to water stress around time of flowering (Yusuf et al. 1979; McKenzie and Hill 2004). However, McKenzie and Hill (2004) report results from a series of experiments on lentil, chickpea, pea and faba bean which provide evidence that this is not the case. It was found that, throughout the growth of the crops, it was important to ensure that soil moisture was kept above critical deficit levels at which point crop growth stops.

Genetic variation exists in drought tolerance of lentil. For example, small seeded varieties in comparison with large seeded varieties were found to be better adapted to dry environments (Erskine 1996). Also, land races and wild accessions with high levels of drought tolerance but low biomass have been described (Muehlbauer et al. 1995). However, the key strategy used to combat drought has been to match the crop's development with the period of soil moisture availability. This has been achieved in two ways. Firstly, genotypes with early seedling establishment, early and rapid biomass development and early flowering and maturity have been selected (Kusmenoglu and Muehlbauer 1998; Sarker et al. 2002a,b; Muehlbauer et al. 2006). In the case of ICARDA, this has involved the selection of drought tolerant varieties in sites with an average annual rainfall of less than 300 mm (Sarker et al. 2002b). Secondly, seed has been sown earlier in the spring or in the autumn (Kusmenoglu and Muehlbauer 1998). Autumn sowing can result in increased leaf area duration and hence greater radiation interception and it can reduce the period the crop is exposed to water stress due to its earlier maturation (see discussion of LENMOD above). However, low temperatures over winter can restrict leaf development and hence reduce radiation interception (Table 2). Also, if temperatures go below −10° C, leaf damage can occur. In relation to this, selection for drought tolerance is often linked with selection for low temperature tolerance.

4. SELECTION FOR INCREASED LOW TEMPERATURE TOLERANCE

In comparison with other temperate grain legumes, lentil would be considered tolerant of low temperatures. Murray et al. (1988) ranked lentil similar to faba bean and greater than pea or chickpea in relation to winter hardiness. Also, lentil can be autumn sown in areas such as the lowlands of West Asia (< 850 m), which experience minimum temperatures of around −10° C (Sarker et al. 2002a). Agronomic practices, in particular establishment of high stand densities ($\sim$ 400 plants m^{-2}), can to some extent increase low temperature tolerance (Kusmenoglu and Aydin 1995; Crook et al. 1998). However, in the highlands of West Asia which experience overwinter temperatures of around −20° C, lentil is traditionally sown in spring as the risk of low temperature damage is high. Programmes are underway to select lentil varieties for autumn sowing in these environments (Sarker et al. 2002a, 2004).

As for drought stress, genetic variation exists in low temperature tolerance of lentil. For example, photothermally sensitive genotypes are more tolerant of low temperatures (Keatinge et al. 1996). Also, large seeded varieties in comparison with small seed varieties had greater cold tolerance (Erskine 1996). Low temperature tolerance of faba bean is also positively correlated with seed size which in part can be related to greater seed reserves (Andrews et al. 1986). Winter hardiness in lentil has been reported to have low to moderate heritability (Ali and Johnson 2000) and to be conferred by several genes (Kahraman et al. 2004a). Kahraman et al. (2004b) reported that 42% of the variation in winter survival could be explained by the cumulative effects of several quantitative trait loci (QTL). A project is now underway to develop a molecular map of the lentil genome and determine the location of the genes that confer winter hardiness

(Muehlbauer et al. 2004, 2006). An objective of the project is to identify suitable PCR based markers for use in a high throughput procedure for improved winter hardiness. However, it will be several years before this project could result in the release of field material and recent success in the production of cold tolerant cultivars has been achieved by more traditional approaches. In particular, ICARDA carries out field screening of lentils in areas prone to extreme cold and these trials have identified cold tolerant genotypes. As a result of this work, cold tolerant cultivars suitable for early spring sowing have been released in several countries including Afghanistan, Syria, Iran and Turkey; and varieties suitable for autumn sowing have been released in Pakistan, Turkey and Iran (Sarker et al. 2002a). In Turkey, high yielding varieties have been released for use in sites at altitudes of 600 to 1400 m and which experience temperatures of -12 to $-30°$ C in winter (Sarker et al. 2002b, 2004). A complication with autumn sowing is the greater probability of disease, in particular, ascochyta blight. This can be countered by combining high resistance to asochyta blight and other diseases with low temperature tolerance in lentil and/or improved agronomic management (Sarker et al. 2002a, 2004; Ye et al. 2002; Muehlbauer et al. 2006; Tivoli et al. 2006).

5. CONCLUSIONS

Plant growth is greatly dependent on weather conditions, with physiological processes responding to changes in air and soil temperature, solar radiation, moisture availability and wind speed. LENMOD, a lentil crop growth model developed and calibrated in NZ gives greater understanding of how different climatic factors interact to determine lentil crop growth and yield. This model has considerable potential in predicting where lentil may be grown successfully. Worldwide, the major abiotic restrictions on yield of lentil are drought (usually linked with high temperature) and low temperature. The strategy used to combat drought has been to match the crops development with the period of soil moisture availability. This has been achieved in two ways. Firstly, genotypes with early seedling establishment, early and rapid biomass development and early flowering and maturity have been selected in sites of extremely low rainfall. Secondly, seed has been sown earlier in the spring or in the autumn. Success in the production of cold tolerant cultivars has been achieved by field screening of lentils in areas prone to extreme cold. High yielding varieties have been released for use in sites which experience over winter temperatures of -12 to $-30°$ C.

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