Variation in lentil (Lens culinaris Medik) in response to irrigation

Hamdi, Ahmed Hamdi Ismail Hamdi Ahmed

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by

Ahmed Hamdi Ismail Hamdi
Ahmed Hamdi

B.Sc., Cairo University, 1971
M.Sc., Cairo University, 1978

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ABSTRACT

This study aimed to investigate the response of lentil genotypes to different water regimes, providing guide lines, through partitioning the variation, for a selection program for adaptation to irrigated conditions. The research was divided into two main areas; 1) The overall variation in the crop was partitioned into genotypic, environmental and genotype-environmental components in an analysis of adaptation over seasons, irrigation regimes and locations; 2) The genotypic variation was partitioned into its various genetic components in an inheritance study using the diallel mating system.

Pronounced progress should be expected from selection for number of pods/plant, 100 seed weight and straw yield/plant traits, which showed high estimates of $h^2_{b.s}$, C.G.V. and G.S. The two former traits correlated strongly and positively with seed yield, which allowed their use in indirect selection for seed yield. The 35 genotypes used in this study showed wide genetic diversity, allowing selection of high yielding genotypes under irrigation. Environmental variation in water supply, temperature and soil type was found to exert a profound effect on variation in characters measured. This suggests the possibility of raising yield levels through improved management practices. In this study, irrigation repeated twice increased seed yield by 19% over no irrigation, at the same location, and increased the yield by 300% in comparison with a dry location. Seed protein quality was influenced by environments and genotypes. Electrophoretic studies showed that the number and position of the bands could be used to identify genotypes.

Four genotypes showed response to irrigation and could be recommended as promising entries. An anatomical study showed that large air spaces formed in the roots of a responsive genotype, which could be used as a selection criterion for positive response to irrigation.

Seed yield/plant exhibited 31.8% heterosis and showed a predominant role of non-additive genetic variance. Due to the

significance of the non-additive effect, the superior F_1's may be expected to throw out desirable transgressive segregants, provided that the complementary genes and epistatic effects included in the non-additive component are coupled in the same direction to maximize seed yield. Five F_2 crosses showed superiority in seed yield and SCA effects. These crosses should be carried forward in lentil breeding programs.

To my parents

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CHAPTER I

INTRODUCTION

1. History and taxonomy

Lentil (Lens culinaris Medik.) is one of the oldest crops cultivated by man. Lens is a latin word that describes exactly the shape of the seed of the cultigen which nowadays botanists call Lens culinaris, following the name given it in 1787 by Medikus, a German botanist-physician (Cubero, 1981).

Lentils have been found at Mureybit in Syria and at Hazilar in Turkey from levels dated by C^{14} at 8500-7500 and 7000-6500 B.C. respectively. Lentil seeds have been discovered in Egyptian tombs of the 21st dynasty (2400-2200 B.C.), and the preparation of lentil soup is depicted in a fresco of the time of Ramses III (1200 B.C.). The Egyptians mentioned lentils in texts going back to c. 1085 B.C., and it seems that lentils were well appreciated as they were bartered for Lebanese cedar wood and offered as presents to the gods. The ancient Egyptians esteemed it highly and cultivated it carefully and extensively. This has led to the suggestion that it was introduced into Palestine and neighbouring lands from Egypt. The Romans, as is evident from a passage in Martial, regarded it as an Egyptian food plant (Cubero, 1981). In addition, it is also the first legume to be mentioned in the Bible, appearing in Chapter 25 of the Book of Genesis in the familiar story of Jacob and Esau and the mess of pottage. They are also listed in the Koran (Second Surah, Al-Baqarah) as one of the products of the earth which the Jews asked Moses to request from God, following the period in which manna and quails were the only food available to them.

The genus Lens Miller (self-pollinated) belongs to the order Rosales sub-order Rosinae, Family Leguminosae and sub-family Papilionoideae. Within the Papilionoideae, Lens holds an intermediate position between the genera Vicia and Lathyrus, but it is closer to

Vicia (Cubero, 1981). Lens montbretii has recently been transferred to Vicia montbretii (Ladizinsky and Sakar, 1982). There has been a recent taxonomic revision of the genus Lens Miller, this reclassification being based on the crossing relations and chromosome pairing in the F_1 generation. It is now considered to have only two species L. culinaris and L. nigricans, both with the chromosome number 2n = 14. L. culinaris consists of three sub-species; (i) L. culinaris culinaris (cultivated), (ii) L. culinaris orientalis and (iii) L. culinaris odemensis; and Lens nigricans contains two sub-species; (i) L. nigricans nigricans, (ii) L. nigricans ervoides (Ladizinsky et al., 1984). F_1 hybrids within these species have various degrees of fertility, but between the species attempts at hybridization result in pod abortion. Embryo culture has now been employed to produce vegetatively normal hybrids between the two species, L. culinaris ssp. culinaris and L. nigricans ssp. ervoides (Cohen et al., 1984). In particular combinations, fertile hybrids were also produced which gave reasonably fertile F_2 plants (Ladizinsky et al., 1985). Ladizinsky and co-workers excitingly concluded that from a plant breeding perspective the genus Lens may be considered as a single gene pool. Thus any of the variability within the genus may be used by breeders to improve the cultivated lentil. The species L. culinaris spp. culinaris is usually divided into two cross-compatible groups; (i) microsperma , with small rounded seeds, 2-6mm in diameter, yellow or orange cotyledons, and a testa of various colours from pale yellow to black; (ii) macrosperma, with large flattened seeds which normally have yellow cotyledons and a pale green testa, which can be speckled. Plants of the latter group have a more robust vegetative structure than the microsperma and have larger leaflets and pods (Cubero, 1981).

2. Distribution and world production

Lentils are grown in different agro-ecological conditions in the world. They are grown in low elevation areas in Syria, Jordan, Iraq, Lebanon, Cyprus, Turkey and other countries which experience a Mediterranean climate of cold, wet winters followed by hot dry summers. Lentils are also grown in high elevation areas such as the Anatolian plateau in Turkey and the high plateaux in North Africa, where the crop is normally sown during early spring on conserved soil moisture, avoiding the cold winter. Severely cold winters are also responsible

for spring sowing in Idaho, Oregon and Washington states of USA, the western provinces of Canada, the Central plateau and mountainous northern regions of Iran, and the central and eastern areas of Afghanistan. In the Indian subcontinent lentils are grown during the winter on the soil moisture conserved during the preceding monsoon season. If water is available, the crop may be given one or two irrigations. In the Nile Valley in Egypt and northern Sudan, lentils are essentially an irrigated crop grown during winter (Ibrahim et al., 1979 and Salih, 1979). In certain tropical countries such as Colombia, Ecuador and Ethiopia, they are successfully grown at higher altitudes. Production in Ethiopia takes place at altitudes up to 2700m (Westphal, 1974).

With this wide distribution of lentils around the world, the crop also has sizeable differences in production. World production increased from 1,127,000 metric tons in 1974 to 1,538,000 metric tons in 1984, an increase of 36.5%. The area also increased from 1,838,000 ha in 1974 to 2,320,000 ha in 1984, an increase of 26.2%. While Asia produces 81.9% of the world production, Europe produces 5.6%, North of America 5.1%, Africa 4.8%, South of America 2.0% and USSR 0.7% (F.A.O., 1984). Lentils represent about 3% of the total world area sown to pulses (dry beans, dry peas, fababeans, chickpeas, pigeonpeas, cowpeas, vetch and lupins). However, the lentil area, as a percentage of the total pulse area, is much higher in several individual countries, such as in Jordan, where lentils comprise 75% of the total. Other countries with similarly high percentages include Syria (51%), Turkey (28%), Iran (24%), Bangladesh (20%) and Lebanon (18%) (F.A.O., 1977). The areas where lentils are most important are generally those with the lowest yields. The average yield in Asia for the three year period 1980-1982 was only just over half the yield in North America; 597 kg/ha compared with 1099 kg/ha.

3. Lentil production and problems in Egypt

In Egypt, lentils are considered the most important food legume crop after faba bean. The cultivated area in 1960 was 20,400 ha yielding an average of 1,490 kg/ha. The area and seed production were stable until 1974-76. However, from 1977, the area and seed yield has decreased annually; the percentage decreases in the area were 19%, 41%

and 75% in the years 1977-78, 1978-79 and 1979-80. Also, the seed yield/ha declined by 11%, 20% and 27% in the same years. The reduction in the area was continuous and reached 76.4% in 1983. Consequently, seed production decreased to only 7,200 metric tons in 1983, and this amount represents only about 9% of the consumption of lentil in Egypt, which was 80,000 metric tons in 1981. Because of the production shortfall, the Egyptian government increased the amount of lentil imported from 4,000 metric tons in 1970 to 75,000 metric tons in 1983 to compensate for the deficit. The increasing cost of these imports averages about 14 millions U.S. dollars per year (28 million Egyptian pound), (the second conference of ARC in Egypt, 1984).

Several factors have contributed to the decrease in yields and area of cultivation for lentil in Egypt. Prior to the building of the Aswan High Dam in Egypt, lentils were grown on moisture left by the annual flood of the Nile without extra irrigation. After the completion of the dam, irrigation became widely available, but the lentil land races are unadapted to it. Most lentil introductions into Egypt have come from rainfed areas, and they are also ill-adapted to irrigation. A report of food legume improvement in Egypt summarized the problems of lentil in Egypt (the second conference of ARC in Egypt, 1984). The major problems were, (i) the inexperience of farmers in growing lentil under irrigation, (ii) the lack of response of the widespread lentil cultivar (Giza 9) to irrigation. The report concluded that irrigation is the major factor in lentil production in Egypt, and it recommended 1-3 irrigations for lentil under Egyptian conditions. Rizk et al. (1984) described future work needed to improve lentil production in Egypt. They mentioned that there is a need to develop new varieties with early maturity, high yield and good seed quality; and emphasized the importance of screening breeding lines and introductions for adaptation to irrigation.

4. Response to irrigation

Almost all the physio-chemical processes of plants are adversely affected by moisture stress (Slatyer, 1969; Hsiao, 1973) and therefore crop yields are at a maximum when plants never experience water shortage or stress during their growth and development. Lentils are known to use adequate moisture as luxuriantly as wheat or other cereals

Field estimates of the consumptive use of water for lentils have been made for different parts of Egypt and for North India. El-Gibali and Badawi (1978) estimated the consumptive use of lentil for Lower, Middle and Upper Egypt at 365, 364 and 391 mm respectively. In India Saraf and Baitha (1979) computed the water requirement of the lentil crop under different irrigation treatments. The water requirement ranged from about 155 to 214 mm in sandy loam soil.

Various authors have emphasized that inadequacy of soil moisture is one of the major limiting factors to yield in lentils in different season and on different soil types. Many workers studied the agronomic methods of irrigation and they have indicated that the crop responds favourably to irrigation.

In India, lentil is generally grown as a rainfed crop in most of the lentil growing areas. In the absence of stored moisture or winter precipitation, the crop responds very well to supplemental irrigation. Saxena and Yadov, (1976) Mehrotra et al. (1977); Bisen et al. (1980); Verma and Kalra (1981) and Singh et al. (1981) found that two irrigations gave higher seed yield than one irrigation or no irrigation. Saraf and Baitha (1979) mentioned that seed yield of lentil increased by 52% with an increase in the water supply from 115 mm to 228 mm.

In the areas with a Mediterranean-type environment, like Syria, lentils are usually grown in regions of low annual rainfall. A good rainfall distribution during the growing season can give high yields. However, the distribution is sometimes such that all the precipitation occurs in a few heavy rains. This can cause water-logging in lentil fields. In Syria, Saxena and Wassimi in 1980 studied the effect of soil moisture content of eight lentil genotypes under two moisture regimes (i) rainfed i.e. 240 mm rain over the whole season; (ii) two supplemental irrigations after termination of the rain. They reported that grain yield increased with increasing moisture supply, from 9.9g/50cm row segments to 16.5 g/50cm, by 60%. The same trend was obtained by Abdel-Rahman et al. in 1980 in Egypt, who found that irrigation every 20 days gave a higher seed yield than irrigation every 40 or 60 days. Also, in Dongola and adjoining areas of northern Sudan,

where irrigated lentils are grown, irrigation at a frequency of every seven days has been found necessary to obtain high yields (Salih, 1979).

Plant growth in species such as lentil is physiologically more sensitive to moisture stress than others (Salter and Goode, 1967). Therefore, researchers concerned with the response to irrigation of lentils must consider the timing of the irrigation carefully. Pre-flowering (branching/maximum vegetative) and pod filling are critical stages for moisture, and in conditions of insufficient soil moisture, an irrigation at these stages increased seed yield (Dastane et al., 1971; Yusuf et al., 1979; Singh et al., 1979; Saraf and Baitha, 1979; Verma and Kalra, 1981). Irrigation at pod formation is much more important than in the pre-flowering stage (Mehrota et al., 1977). In India, greater yield responses were found with three irrigations applied at seedling, branching and pod development stages than from three irrigations at seedling, branching and flowering (Dastane et al., 1971; Yusuf et al., 1979). Two irrigations at the pre-flowering stage (vegetative phase) and at the pod filling stage gave the highest seed yield (Saraf and Baitha, 1979; Bisen et al., 1980; Verma and Kalra, 1981 and Nema et al., 1984). The same trend has been found by Panwar and Paliwal (1975); Saxena and Yadav (1976); Ojha et al. (1977), who mentioned that the pre-flowering and pod filling stages were the most critical growth stages for application of irrigation. In addition, Panwar and Paliwal found that irrigation at both these stages increased the yield to 100% of the unirrigated check.

In other legume crops, the seed yield increased with the frequency of irrigation. In faba bean (Vicia faba L.), increasing the frequency of irrigation throughout the growing season or irrigation late in the growing season (pod filling) increased seed and straw yield (Krogman et al., 1980). Singh et al. (1978) obtained the highest pea (Pisum sativum L.) seed yield with two irrigations when applied at pre-flowering and pod development stages. Also, irrigation increased pea yield by 78% (White et al., 1982). Twogood and Davis (1979) reported that irrigated green bean (Phaseolus vulgaris L.) plots produced more than twice the yield of unirrigated plots. Seed yield of bean increased from 851 kg/ha with 350mm to 1050 kg/ha with 530mm rain (Frizzone et al., 1982). The response of different growth stages of

soybean (Glycine max (L.) Merr.) to irrigation has also been studied. Seed yield reductions are greatest with moisture stress during late pod-development and pod-fill (Lewis, 1981 and Kanemasu, 1981), and irrigation at these stages increase seed yield (Brady et al., 1974; Constable and Hearn, 1980 and Drummond et al., 1983). Rahman et al. (1983) found that irrigation at the pre-flowering stage is important and gave the highest grain yield of chickpea (Cicer arietinum L.). He mentioned that seed yield was depressed by about 30% when irrigation was given at the flowering stage.

Irrigation, as well as a heavy rain, can cause flooding which leads to deficient aeration as a result of saturation of the soil displacing the soil air. The low solubility and slow diffusion of oxygen in water drastically reduces its supply to the roots (Kramer, 1983). This effect increases in heavy clay soil or when a soil water table is high.

Anaerobic conditions reduce gas exchange and result in decreased oxygen and increased carbon dioxide concentration in the soil (Yelenosky, 1964). However, it appears that under field conditions root growth is more likely to be limited by a low concentration of oxygen than by a high concentration of carbon dioxide (Kramer, 1983).

Injury from flooding has been discussed by many workers. Wilting is likely to be the first symptom, which is generally assumed to result from decreased water absorption caused by a sudden increase in root resistance in the water-saturated soil (Kramer, 1940a). Kramer attributed the increased root resistance to the toxic effect of high carbon dioxide, while Hunt et al. (1981) attributed it to ethylene produced in the soil and the plant. Sojka and Stolzy (1980) reported that oxygen deficiency in the soil causes closure of stomata. There is evidence that products of anaerobic respiration, such as ethanol, aldehydes and lactic acid, accumulate in the roots of flooded plants and presumably cause injury (Crawford, 1967; Bolton and Erickson, 1970; Hook et al., 1972; Francis et al., 1974). However, Jackson et al. (1982) found that the concentrations of ethanol occurring in flooded plants are not toxic and concluded that it probably does not cause injury in this way. Compounds such as methane, sulphides, reduced iron, and other minerals also accumulated in flooded soil and caused injury to roots.

There are wide differences in tolerance to anaerobic condition between species. Plants native to wet habitats tolerate long periods in saturated soil, but some other crops such as corn, wheat and barley are quickly injured or killed. However, adaptations of roots under oxygen deficiency conditions has been found in wheat (Erdmann et al., 1986) and in corn (Kramer, 1983).

One of the principle plant adaptations to oxygen deficiency under saturation conditions is modification of root structure in anaerobic condition (Kramer, 1983). Plants native to wet conditions, such as rice, contain extensive air spaces that form continuous passage ways from shoots to roots. This tissue, called aerenchyma, is usually regarded as an important adaptation that improves the oxygen supply to roots growing in poorly aerated soil. Williams and Barber (1961) showed that the chief function of aerenchyma is provision of anchorage with the smallest possible amount of living, oxygen-consuming tissue. Its function is still under discussion (Crawford, 1983). Roots of mesophytes, such as wheat and corn, also develop large air spaces when grown in anaerobic media. Usually, these air spaces are formed lysigenously by breakdown of masses of cortical cells, leaving spoke-like strands of living cells extending from the outer cortex to the endodermis (Drew et al., 1980). Anatomical parameters under oxygen deficiency have been studied in Corn (Drew et al., 1980) and in wheat (Erdmann, 1986), whereas no such work exists in lentil.

5. Lentil seed quality

As lentil is an important traditional dietary item throughout the Middle East, quality evaluation is considered an important objective in lentil breeding. Protein content, cooking time and seed dehulling are three of the most important quality characters in the crop. On average, lentils provide more than twice the amount of dietary protein of cereals (Pellet and Shadarevian, 1970) and their protein content is comparable to that of faba beans, and higher than chickpeas (Abu-Shakra and Tannous, 1981).

The lentil protein content has been estimated by some workers. In early Russian reports it was revealed that the protein content varied little across locations, but varied from 27.5-31.7% between

varieties (Burulina, 1930). When a world collection of 1688 accessions of lentil was tested for seed protein, a range of 23.4-36.4% was found (Hawtin et al., 1977). More recently Erskine and Witcombe (1984) found a greater variability for protein content, ranging from 18.6-30.2% amongst 1853 lentil accessions of the germplasm collection at ICARDA. Lentil seed protein was not markedly affected by irrigation at any stage (Panwar and Paliwal, 1975; Abdel-Rahman et al., 1980; Eweida et al., 1980 and Saraf and Baitha, 1982), but was influenced significantly by location effects (Erskine et al., 1985).

In addition to the total level of protein in lentil seeds, the amino acid content of the protein is very important in its nutritional quality. To improve the nutritional value of lentil seed meals the levels of the sulphur amino acids need to be increased. This objective may possibly be achieved by breeding. For breeding programs to be successful, the varietal differences and the influence of the environment on protein quality must be established. In such a study, electrophoresis may be a useful technique.

The term electrophoresis is used to describe the migration of a charged particle under the influence of an electric field. Under conditions of constant velocity the driving force on the particle is the product of the effective charge on the particle and the potential gradient and this is balanced by the frictional resistance of the medium (Andrews, 1986). Electrophoretic methodology was introduced by Smithies (1955) who used starch gels as an electrophoretic medium, but this has been largely replaced following the introduction of polyacrylamide gel electrophoresis (PAGE) (Davis, 1964; and Ornstein, 1964). The application of these methods to botanical work and collections of appropriate recipes have been reviewed by Shaw (1965) Makinen and Brewbaker (1967) and Nelson (1967).

There are currently three different geometrical forms in which PAGE is carried out, namely on horizontal slabs, vertical slabs, or vertical cylinders (rods) of gel. Each has its advantages and disadvantages. However, a major advantage of slab gels is that a number of samples can be run side by side under identical conditions and compared without ambiguity. This is particularly useful in

screening procedures where a large number of samples must be examined and compared (Andrews, 1986).

Many different methods have been used to solubilize the constituent lipids and proteins including solvents containing phenol, acetic acid, or high levels of urea, but a large proportion of recent procedures employ detergents. These include non-ionic detergents like; Lubrol W, Brij 35, and the Tween and Triton detergents, cationic detergents such as cetyltrimethyl-ammonium bromide (CTAB) and cetylpryridinium chloride (CPC), and anionic detergents such as deoxycholate (DOC) and sodium dodecylsulphate (SDS). Clearly it is beneficial if the solubilized material can then be utilized directly for further analytical procedures. Not only can this often be done, but when ionic detergents are used most proteins are then separated by PAGE according to molecular size (Andrews, 1986).

Andrews (1986) summarized the factors which should be considered when deciding whether to use detergents and which ones to use. Some detergents, such as SDS, are usually regarded as more strongly denaturing than others (e.g. Lubrol PX). In most cases (particularly if a reducing agent is present to break disulphide bonds) SDS falls into the category of a strongly denaturing detergent and gives rise to essentially random coil configurations.

The use of SDS-PAGE and its theoretical background of molecular weight measurements has been discussed by Andrews (1986), who described the advantages of this method. The apparatus required is readily available in most laboratories and is inexpensive. The procedure is straightforward and highly reproducible, and results can be obtained within a few hours using only a few micrograms of material. As with other PAGE methods, in many cases the sample need not be totally pure. The degree of purity required depends largely upon the sample being studied and the ease with which the component of interest can be identified on the final gel pattern. Due to the benefits of this method, it has become one of the most widely used for measurement of protein molecular weights.

Cooking time is one of the most important aspects of cooking quality. Normally dry legume seeds require a long cooking time.

Lentils are quicker to cook than faba bean or chickpeas and good cooking lentil seeds are sold at a higher price than those with poorer cooking quality (Abu-Shakra and Tannous, 1981).

The cooking process makes hard seeds soft by improving the plasticity of the cell wall, thus facilitating cell expansion and reduction of intercellular adhesion. Lentil seeds which are difficult to cook are thought to be influenced by the presence of insoluble pectins in the middle lamella of the cell wall. Large amounts of insoluble calcium and magnesium pectates are formed in the middle lamella of the cell walls when the seeds are rich in Ca and Mg or when the cooking water is rich in these elements (Abu-Shakra and Tannous, 1981). The importance of adequate levels of both major and trace elements in affecting the cooking quality of lentils has been emphasized by Wassimi et al. (1978). In particular, high levels of potassium and sodium, together or separately, in the seed were associated with shorter cooking times. In another study, the major significant correlation obtained was between cooking quality and $(Ca^{2+} + Mg^{2+})/P$ content (Bhatty, 1984). A further review of the influence of mineral ions on cooking time in lentil is given by Summerfield and Muehlbauer (1982). The need for a rapid and repeatable method for screening for cooking quality has been highlighted by Abu-Shakra and Tannous (1981). Suitable procedures have been developed at ICARDA (Erskine et al., 1985).

Erskine et al. (1985) found differences between locations in cooking time, but the range in cooking time was greater between genotypes than locations.

In many countries of the world, grain legumes are initially processed by removing the hull (seed coat) and splitting the seed into its dicotyledenous components (Siegel and Fawcett, 1976). In the Middle East, lentils are a major constituent of two common dishes named 'koshari' or 'mujaddarah' (lentil and rice) and lentil soup. Decorticated dry seeds are usually used in the preparation of these dishes.

Removal of the hull (dehulling) results in a reduction of fibre and tannin content in the seeds (Deshpande et al., 1982a) and an

improvement in appearance, texture, cooking quality (Kon et al., 1973) and functional properties, palatability and digestibility of the seeds (Deshpande et al., 1982b).

There are two main types of lentil marketed, large-seeded and small-seeded types. The large seeded are usually marketed whole, undehulled, while small-seeded genotypes are graded, dehulled and split before marketing. Within the limits of size of small-seeded lentils (2.5-4.5 mm in diameter), the larger the seed, the lower is the percentage loss during decortication. In a study at ICARDA, seeds with an average size of 4 mm lost an average of 8.19% of their weight during dehulling. This rose to 9.8% for seeds with a mean diameter 3 mm, representing a loss equivalent to about U.S.$6 per tonne. The larger seeds also command a higher price than the smaller seeds (Erskine et al., 1985).

6. Variance components, heritability and genetic advance from selection

Effective selection is dependent on the existence of genetic variability. The extent of the genetic variability in a specific breeding population depends on the germplasm included in it and its selection history (Hallauer, 1981). In investigations with lentil accessions, a wide range of variation for yield, yield components and other lentil characters was observed (Malhotra et al. (1973); Sharma and Kant (1975); Kant and Sharma (1975); Tiwari and Singh (1980); Prem Sagar (1980); Solh and Erskine (1981); Sindhu and Misra (1982) and Sinha and Chowdhary (1984)).

Various authors have emphasized the utility of estimates of variance components, as a basis for predicting the response of quantitative characters to selection in plant breeding. Selection in a given population is based on the phenotypic value of individuals while only a portion of the phenotypic value is transmitted to the following generation. Thus, it is of primary importance to know the relative magnitudes of the different components of the phenotypic value. The phenotypic expression of a character can be considered as the sum of a genetic effect and a deviation attributable to environment and

interaction between the genotype and the environment involved. Wright (1921, 1935) considered the genetic variation to consist of three components:

a) additive genetic variance (σ^2_A).

b) variance due to dominance deviations from the additive scheme (σ^2_D).

c) Variance due to epistatic deviations from the additive scheme (σ^2_I).

Estimates of variances due to the different sources of variation contributing to differences between individuals as described above are important for plant breeders to develop their breeding strategies. Comstock and Moll (1963) outlined three advantages of knowing the true magnitudes of genetic variation:

a) over estimation of genetic variation would in some cases lead to investment of time and effort not justified by the real potential for improvement of genetic stocks employed.

b) Optimum procedures may vary significantly, depending on the magnitude of genetic variances.

c) There is a danger that sound breeding programs may be abandoned prematurely or unwisely because of results that are disappointing relative to unwarranted expectations based on erroneous estimates of genetic variance.

In general, the different procedures suggested by plant breeders for partitioning the phenotypic variance of quantitative characters in a population carry the following biological assumptions : (1) normal diploid behaviour at meiosis; (2) no maternal effects; (3) absence of multiple alleles; (4) linkage equilibrium; (5) random selection; (6) no epistasis. However, under certain circumstances, models are available in which one or more of these restrictions may be eliminated (Sprague, 1966). These procedures have been discussed by Anderson and Kempthorne (1954); Griffing (1956a, 1956b); Hayman (1958, 1960);

Kempthorne and Curnow (1961); Crumpacker and Allard (1962); Cockerham (1963); Gardner (1963); Matzinger (1963); Sprague (1966); Dudley and Moll (1969) and Mather and Jinks (1971).

Knowledge of the heritability of quantitatively inherited attributes has been useful as a tool for improving selection efficiency. Progress under selection in breeding programs depends on the magnitude of heritability for the trait under selection. Estimates of genetic variance and phenotypic variance are used by plant breeders to estimate heritability.

The heritability concept and its implications in plant breeding have been discussed by several workers (Burton, 1952; Warner, 1952; Hanson, 1963; Robinson, 1963; Dudley and Moll, 1969 and Falconer, 1981).

The phenotypic expression of any particular character can be visualized as the sum of a general population mean, a genotypic effect, an environmental effect, and an interaction effect. Allard (1960) explained the importance of these factors when heritability has been estimated. Also, Robinson (1963) stated that heritability estimates must be treated with some caution because they depend on the choice of plot size, planting density and number of replications. Since an estimate of heritability is as restricted in its application and since a ratio is not as informative as a knowledge of its two components, he questioned whether there was value in estimating heritability. However, he stated that a meaningful estimate of heritability is of use in estimating expected progress when pursuing the programme, and it is also a very useful concept in determining the relative importance of genetic effects which may be passed on to offspring, even in cases where it would be difficult to extrapolate to other populations.

The variance components method proposed by Comstock and Robinson (1948, 1952) has been used extensively in estimating heritabilities. This method could be applied to either genetically different cultivars or families from a given generation. The major problem encountered in using the variance components method to estimate heritability is that the estimate of additive variance so obtained is quite likely to

contain fractions of epistatic variances and genotype-environment interactions which, if present, would inflate the estimate.

As soon as heritability is estimated for a quantitative trait in a population, the question is raised as to what progress would be expected under selection in that population. The estimate of such progress is called the genetic advance. Falconer (1981) defined the expected genetic advance from selection as the products of selection intensity, the estimate of phenotypic standard deviation and the heritability estimate. Expected genetic advance has been estimated by most authors who have investigated heritability of quantitative characters.

Comstock and Robinson (1952) stated that the essential aspects of most, if not all, breeding programs are : (1) selection within a base population of genetically variable individuals or families, and (2) utilization of the selected material for the creation of new populations to be employed either as potential new commercial varieties or as the base for a new cycle of selection. It is apparent that genetic advance under selection, as represented by improvement in the genotypic value, in the new population as contrasted to the base population will depend on (1) the amount of genetic variability, that is, the magnitude of the differences in genotypic value among different individuals (or families) in the base population, and (2) the magnitude of the masking effect of the environmental and interaction components of variability on the genetic variability. A third factor, the intensity of the selection that is practised, will also influence the rate of genetic advance under selection. Burton (1952) emphasized the importance of using the genetic coefficient of variation, together with heritability estimates. He mentioned that both gave the best picture of the genetic advance to be expected from selection. Therefore, Johnson et al. (1955) in their studies in soybean have found that heritability value along with the genetic gain is more useful than the heritability estimates alone in predicting the resultant effects of selecting the best individuals.

In the literature of lentils, some workers studied the genetic variation in only one location. In this situation, Johnson et al. (1955) reported that serious misjudgements may arise because the

genotypic variance estimated on the basis of a single location also includes the variance due to genotypic-environment interactions, and the conclusions based on the inflated estimates of genotypic variance may not hold good at other locations.

Allard (1960) stated that genotypic values must be measured with reference to some particular group of environments, usually the ones occurring over a period of years at a number of locations within some comparatively homogeneous geographical area. Experimental measurements of genotypic values, no matter how extensive (within practical limits), can only sample the population of environments occurring within this grographical area. Hence the plant breeders must usually be satisfied with an attempt to identify the effect of the environmental components that are likely to be important in determining the agricultural value of genotypes, for example, soil fertility, rainfall, and temperature. In practice, these items are usually identified with years and locations.

Comstock and Robinson (1952) and Johnson, Robinson and Comstock (1955) also emphasized the importance of evaluating the interaction between the genotype and the environment. It is clear, therefore, that the evaluation of strains under diverse conditions of environment provides sound estimates of genetic variability which exclude the effects of year-environment interactions.

A genotype-environment interaction analysis was undertaken with 30 varieties of lentils under three environments (sowing dates) by Pandey et al. in 1982, who mentioned that the differences due to varieties, environments and environment-varieties were highly significant. The component analysis revealed a higher value for the genotype-environment interaction component than for the genotypic component, indicating a major effect of the environment on the evaluation of genotypes for seed yield per plant.

In lentils, widely varying estimates of heritability, variability and genetic advance for different characters have been reported. A summary of literature on broad sense, narrow sense heritability, phenotypic and genotypic coefficient of variation are given in Tables 1 and 2.

Table 1 Estimates of heritability% for lentil characters

Population	Seed yield (kg/ha)	Seed yield/ plant	No. of pods/ plant	No. of seeds/ plant	No. of seeds/ pod	Average seed weight	Plant height	No. of branch/ plant	Time to flow.	Time to mat.	Reference
40 strains	-	97.3	97.3	-	-	94.6	55.6	48.4	95.8	-	Singh and Singh, 1969
47 promising lines:											Malhotra et al., 1974
g-e interaction included	-	48.8	43.5	-	-	47.2	61.5	26.1	-	-	" " "
g-e interaction excluded	-	2.2	18.7	-	-	40.9	34.6	7.1	-	-	" " "
45 cultivars	46.9	21.9	45.0	52.7	73.6	94.9	-	-	-	-	Muelbauer, 1974
11 cultivars	30.5	-	39.7	-	15.8	74.6	23.1	-3.7	-	-	Lal and Chandra, 1978
63 cultivars : 1978	-	99.0	79.8	-	-	91.1	36.1	86.1	-	-	Pandey et al., 1980
1979	-	72.7	91.2	-	-	-	70.8	-	-	-	" " "
23 F_4 Bulks + 3 cultivars	57.0	42.0	80.0	-	-	75.0	83.0	-	74.0	96.0	Prem Sagar, 1980
$h^2_{n.s}$ of $3F_6$: cross 1	-	-	-	-	-	0.0	0.0	-	3.0	0.0	Haddad et al., 1982
" 2	-	-	-	-	-	32.0	24.0	-	38.0	25.0	" " "
" 3	-	-	-	-	-	5.0	8.0	-	10.0	0.0	" " "
Range of 8 F_2 crosses =	-	24-65	19-71	18-65		19-91	62-85	33-78	28-95	-	El-Hady, 1983
$h^2_{b.s}$ / $h^2_{n.s}$	-	4.5-55.5	3.7-45.9	2.5-81	-	5.1-72	2.3-35.5	6.4-23.4	11-85.8	-	" "
F_2 cross : $h^2_{b.s}$	-	2.0	-	-	-	60.0	47.0	-	64.0	46.0	Sakar, 1983
F_2 cross : $h^2_{n.s}$	-	17.0	-	-	-	62.0	43.0	-	56.0	39.0	
F_4 cross : $h^2_{b.s}$	-	39.0	-	-	-	80.0	48.0	-	76.0	59.0	
24 genotypes	50.0	-	-	-	-	98.0	-	-	-	-	Erkine et al., 1985

All these studies were carried out at one location except Malhotra et al., (1973)and Erskine et al., (1985), that were at 3 locations.

Table 2 Estimates of phenotypic and genotypic coefficient of variation for lentil characters

Population		Biolog. yield (kg/ha)	Seed yield/ (kg/ha)	Seed yield/ plant	No. of pods/ plant	No. of seeds/ pod	Average seed weight	Plant height	No. of branch./ plant	Time to Flow.	Time to Mat.	Reference
40 strains	G	-	-	79.0	82.5	-	41.0	9.3	22.7	8.6	-	Singh and Singh, 1969
47 promising lines:												Malhotra et al. 1973
g-e interaction included	G	-	-	30.9	27.1	-	14.8	12.6	14.4	-	-	" " "
g-e interaction excluded	G	-	-	6.5	18.5	-	14.3	9.8	8.6	-	-	" " "
11 cultivars	P	29.0	53.9	-	40.3	8.7	20.3	13.7	26.7	-	-	Lal and Chandra, 1978
" "	G	4.8	29.8	-	26.1	0.44	2.4	3.9	0.99	-	-	" " "
63 cultivars:1978	P	-	-	30.4	26.5	-	13.9	16.7	62.6	-	-	Pandey et al., 1980
" " "	G	-	-	30.1	23.7	-	13.1	15.5	58.1	-	-	" " "
63 cultivars:1979	P	-	-	23.7	44.4	-	-	21.8	-	-	-	" " "
" " "	G	-	-	20.2	40.5	-	-	15.4	-	-	-	" " "
23 F_4 bulks + 3 cultivars	P	15.5	26.6	32.6	26.3	-	26.6	10.1	-	3.5	5.3	Prem Sagar, 1980
	G	13.4	20.0	21.2	23.6	-	23.1	9.2	-	3.0	5.2	" " "

P : Phenotypic coefficient of variation

G : Genotypic coefficient of variation

The range of broad sense heritability for seed yield (kg/ha) was from 30.5-57% with an average of 46.1%. The broad sense heritability of biological yield (kg/ha) ranged from 28.4-71% (Lal and Chandra, 1978 and Prem Sagar, 1980); the average of this character (49.7%) was lower than the value for seed yields (kg/ha). Seed yield per plant had a wide range of broad sense heritability of 2-99% with an average of 51.2%. This wide range of heritability may be due to the nature of populations used for estimation. The lowest broad sense heritability was estimated from only the F_2 generation of one cross (Sakar, 1983), whereas the highest value was obtained from 63 cultivars (Pandey et al., 1980). Also estimates of broad sense heritability are strongly influenced by environments (seasons and locations). For example, Pandey et al. (1980) found that the broad sense heritability of seed yield per plant was 99% in one season, but this decreased in the subsequent season to 72.7% with the same material. Malhotra et al. (1973) showed the effect of genotype-environmental interaction on heritability and genetic variation estimates. They found that the mean of broad sense heritability of seed yield per plant was 48.8% (average of 3 locations), but when they eliminated the effect of genotype-environmental interaction, the heritability value decreased to only 2.2%, and the coefficient of genetic variation decreased from 30.9% to 6.5%.

The narrow sense heritability of seed yield per plant also varied greatly. In a study of El-Hady (1983) the narrow sense heritability of yield per plant ranged from 4.5-55.5%; it was above 50% for only one cross and lower than 50% for seven crosses. Also, a low narrow sense heritability of yield per plant (17%) has been found (Sakar, 1983). These low narrow sense heritability values were probably due to dominance effects.

The range of phenotypic coefficients of variation for seed yield (kg/ha), seed yield per plant and biological yield per plant were 27-54%, 24-29% and 16-29% with averages of 40.3%, 28.9% and 22.3%, respectively. Whereas genotypic coefficients of variation ranged from 20-30%, 20-30% and 5-14% for seed yield per plant, seed yield (kg/h) and biological yield (kg/h), with averages of 36.3%, 24.9% and 9.1%, respectively.

Heritability estimates varied across characters. The ranges of broad sense heritability for days to flowering, days to maturity, seed weight, plant height and number of pods per plant were; 28-96, 59-96, 19-98, 23-85 and 19-97 with averages of 73.6%, 67%, 65.2%, 64.2% and 61.6%, respectively. Number of branches per plant, number of seeds per pod and number of seeds per plant had generally lower broad sense heritability values ranging from 26-86, 16-74 and 18-65 with averages of 56.2%, 44.7% and 38.7%, respectively. The highest value of narrow sense heritability was for days to flowering (45.4%), whereas the lowest value was for branches per plant (12.3%). Haddad et al., (1982) found low narrow sense heritability (including zero values) for days to flowering and maturity and plant height in two crosses, with sizeable dominance effects of these characters. In comparison, the third cross showed higher values of narrow sense heritability with more additive genetic variation. For seed protein content and cooking quality, Erskine et al., (1985) found that broad sense heritability of these characters were 71% and 82%, respectively.

Genetic advance in percentage of mean for different characters is given in Table 3. The highest percentages of genetic advance were for pods per plant and seed yield per plant, with averages of 66.6% and 65.9% respectively. These characters had also the highest values of coefficient of genetic variation (Table 2), whereas time to flowering and plant height had low estimates of genetic advance and coefficient of genetic variation.

7. Phenotypic and genotypic correlation and selection criteria

Knowledge of the magnitude and type of relationships between plant characters has theoretical and practical implications in plant breeding. For example the correlation between complex characters of low heritability, such as yield, and less complex characters which may have much higher heritabilities, would benefit the breeder to the extent that it may be easier to select for the complex character indirectly by practising selection on the highly heritable characters. In fact, in some cases it might be possible to achieve more rapid progress under selection for a correlated response than from selection for the desired trait itself (Falconer, 1981). Grafius (1956) considered that the response to direct selection for yield has often

Table 3 Genetic advance in % of mean for lentil characters

Population	Biolog-yield (kg/ha)	Seed yield/ (kg/ha)	Seed yield/ plant	No. of pods/ plant	No. of seeds/ pod	Average seed weight	Plant height	No. of branch./ plant	Time to Flow.	Time to Mat.	Reference
40 strains	-	-	160.5	167.2	-	82.9	14.4	22.5	17.4	-	Singh and Singh, 1969
47 promising lines :											Malhotra et al., 1973
g-e interaction included	-	-	43.6	37.1	-	20.8	20.3	16.0	-	-	" " "
g-e interaction excluded	-	-	2.0	16.5	-	18.8	11.9	4.7	-	-	" " "
11 cultivars	16.9	33.4	-	32.9	2.4	31.1	6.5	-	-	-	Lal and Chandra, 1978
63 cultivars : 1978	-	-	62.1	43.6	-	26.0	29.6	111.0	-	-	Pandey et al., 1980
" " : 1979	-	-	35.5	76.0	-	-	22.6	-	-	-	" " "
23 F_4 Bulks + 3 cultivars	23.0	31.0	28.0	43.0	-	41.0	17.0	-	5.0	10.0	Prem Sagar, 1980

been found to be slow because of the low heritability of yield. He emphasized that selection for yield should be based on the other characters which are relatively simply inherited and associated with yield (indirect selection).

The genetic relationship among quantitative characters is of considerable interest to plant breeders. Falconer (1981) stated three reasons for determining such relationships, which were: (a) to determine the changes brought about in a given character when selection is practised on another character; (b) to study the genetic causes of correlation through the pleiotropic action of genes; and (c) to examine the relationship between a metric character and fitness of that character in a natural population. The phenotypic correlation is a linear combination of genetic and environmental correlations. However, the contributions which genetic and environmental correlations make up to the phenotypic correlations is variable depending on the magnitude of the heritabilities of both characters.

Adams (1967) stated that the attainment of characteristic form and function in a crop plant depends upon a chain of interrelated events which are sequential in time, gene regulated at critical sites and times, and subject to the modifying influences of nongenetic forces. Moreover, these events do not occur haphazardly, but follow an integrated pattern. He stated that seed yield is an obvious example of integration in which the components of seed yield are to some extent interdependent in their development.

The correlations between quantitative traits in lentil have been estimated by many workers including; Singh and Singh (1969), Singh et al. (1970), Malhotra et al. (1973), Tikka et al. (1973), Dixit (1974), Muehlbauer (1974), Singh and Singh (1975), Singh and Dixit (1976), Chandra and Lal (1977), Wilson (1977), Narsinghani et al. (1978), Nandan and Pandya (1980), Todorov (1980), Chauhan and Sinha (1982), Basant et al. (1983), El-Hady (1983), Erskine (1983), and Erskine et al. (1985). In summary, radically different coefficients of correlation have been found between the same characters in these different studies. For ease of discussion the interrelationships between characters have been classified into four groups : (i) relationship between seed yield, on the one hand, and yield components,

such as number of pods per plant, number of seeds per pod and seed weight, on the other hand; (ii) relationship between seed yield on the one hand and between morphological and phenological characters such as, plant height, number of branches per plant, days to flowering and days to maturity, on the other hand; (iii) relationship between seed yield and seed quality characters such as protein content and cooking quality; (iv) relations between yield components, phenological and seed quality characters.

The relationships between seed yield and yield components were studied by most of the authors mentioned above. In general, strong positive correlations were found between seed yield and number of pods per plant. The Phenotypic and genotypic correlations between both characters were ranged from 0.61-0.95 and from 0.63-1.0, respectively; within 45 lentil lines, pods per plant only accounted for 45% of the observed variation in yield (Muehlbauer, 1974), and it was 49.3% in another study (Basant et al., 1983). Positive correlation was shown between seed yield and seeds per pod, however, in path analysis, seeds per pod had a positive direct effect on the seed yield (Basant et al., 1983). Zero or negative correlation coefficients have been reported between seed yield and average seed weight (Singh and Singh, 1969; Muehlbauer, 1974 and Basant et al., 1983). The negative association may be due to a lack of sufficient yield compensation for fewer seeds/pod and fewer pods/plant in large seeded types (Muehlbauer, 1974).

Seed yield had a positive and significant correlation with plant height (Malhotra et al., 1973 and Narsinghani et al., 1974). The coefficients varied from 0.23 to 0.71 for phenotypic correlation and from 0.003 to 0.96 for genotypic correlation. The relationship between yield and time to flowering varied between investigations. On the one hand, Singh and Singh (1969) found strong negative phenotypic and genotypic correlations with seed yield (-0.50 and -0.58, respectively). Whereas the relations were found positively and significantly correlated with seed yield by others (Narsinghani et al., 1978 and Tikka et al., 1973). Again, both positive and negative correlations have been reported between seed yield and time to maturity (Narsinghani et al., 1978 and Basant et al., 1983). The relationship between number

of branches per plant and seed yield was positive and significant (Singh et al., 1970 and Tikka et al., 1973).

The relationships between seed yield and seed quality characters have been studied by Todorov (1980) and Erskine et al. (1985). Contrasting positive and negative correlations between seed yield and cooking quality have been reported by Erskine et al. (1985) and Todorov (1980), respectively. However for the relationship between seed yield and seed protein content both studies showed negative correlations.

The relationships between all the previously mentioned characters are labyrinthine in complexity, particularly because the studies conducted in different places on different material usually for only one season show contrasting results. The relationship of pods per plant with other characters are summarized because of its major importance and constant strong association with seed yield. The relationship between other characters are mentioned as necessary during the results and discussion section.

Number of pods per plant exhibited a strong negative relationship with seed weight and had phenotypic and genotypic correlation values of (-0.63) and (-0.64) respectively (Singh and Singh, 1969), (-0.39) and (-0.37) (Narsinghani et al., 1978). Pods per plant was positively correlated with plant height, number of branches per plant and days to maturity (Singh and Singh, 1969; Singh et al., 1970; Tikka et al., 1973; Narsinghani et al., 1978 and Basant et al., 1983). Pods per plant showed strong negative phenotypic and genotypic correlations with time to flowering (Singh and Singh, 1969), but Tikka et al. (1973) and Basant et al. (1983) found positive and significant correlations between both characters.

8. Adaptability and phenotypic stability

The seed yield of lentil was closely related to total seasonal moisture supply in Northern Syria (ICARDA annual report, 1984). However, because the rainfall, and thus soil moisture content, varies from location to location and from season to season, it is difficult to demonstrate the significant superiority of any variety when compared over a series of environments and years. The genotype-environment

interaction usually causes the relative rankings of varieties to differ (Eberhart and Russell, 1966). Since little additional progress can be expected in reducing genotype-environment interaction by the stratification of environments (Allard and Bradshaw, 1964), other methods need to be investigated. Any such method aims to rank varieties for stability.

The existence of interactions between genotypes and environmental factors has long been recognised, the earliest reference, which precedes the analysis of variance, being Fisher and Mackenzie (1923). In considering the manurial responses of different potato varieties they concluded that "the yields of different varieties under different manurial treatments are better fitted by a product formula than by a sum formula." The methods used here foreshadowed those developed many years later, but were apparently completely forgotten. Sprague and Federer (1951) separated out the effects of genotypes, environments and their interaction by equating the observed mean squares in the analysis of variance to their expectations on the random model. This approach emphasized the overall importance of the genotype-environment interaction, but did not fix interest on the response of individual genotypes to a set of environments. Many others followed this method including Miller, Williams and Robinson (1959); Miller, Robinson and Pope (1962). However, Plaisted and Peterson (1959) computed an analysis of variance for each possible pair of genotypes in turn in order to find an estimate of the interaction due to every paired combination. The mean of the interaction variances associated with an individual genotype was then taken as a gauge of its contribution to the overall genotype-environment variance.

The next development in the analysis of genotype-environment interaction was to focus on the response of individual genotypes to environments, and can be described as the identification of patterns of response across environments. It is, of course, basic to this approach that underlying patterns do exist which reflect heritable differences between genotypes. This technique was applied by using the linear regression, and used first by Yates and Cochran (1938), who showed that regressions accounted for a large part of the interaction, but their ideas were not really taken up until Finlay and Wilkinson (1963) rediscovered the same method and used it for an analysis of adaptation

in a barley trial. This method has subsequently been developed into a powerful and informative method of genotype-environment analysis (Eberhart and Russell, 1966; Perkins and Jinks, 1968; Breese, 1969). A basic objective of this technique is to identify systematic variation in performance, and it can be very informative where genotype-environment interactions have high linear association with environmental index (Byth et al., 1976).

This linear relation usually accounts for most of the variation over environments of a genotype and as a result it is possible to predict its phenotype under further related environmental conditions (Breese, 1969; Jinks and Perkins, 1970).

The statistical validity of these methods has been questioned by Freeman and Perkins (1971), because the yields of separate varieties (y) are not statistically independent of the mean yield of all the varieties (x) when the mean yield of all the genotypes at a site is used as the environmental index. But Freeman stated that if the model is fixed and that inferences are only made about the particular set of environments and genotypes sampled, then the method is valid. Since the independence of the y variable from the x increases with the number of genotypes under test, the use of many genotypes will partially circumvent the criticism. Fripp and Caten (1971) and Eberhart, Penny and Harrison (1973) mentioned that the criticisms of non-independence have prompted the use of independent physical and biological measures of the environment. Another problem with this approach, as pointed out by Freeman and Perkins (1971), is that the x variate in the regression is subject to error, but Hill (1975) reported that this problem is probably not serious when large numbers of genotypes are used.

Some biological criticism has also been levelled at the joint regression analysis because the underlying response of genotypes to changes in an environmental factor may be non-linear (Knight, 1970 and Witcombe and Whittington, 1971) and efforts to force such patterns into a linear straitjacket can lead to erroneous conclusions. Given that joint regression analysis is a totally empirical method, it does, however, have a safety valve in the test of adequacy of the linear model. If the response of genotypes to one environmental factor is

non-linear or equally if there is variation over environments in more than one factor, then the model will prove unsatisfactory.

The application of genotype-environmental interaction parameters has been reported to be useful also for measuring of the stability by various workers (Immer, Hayes and Powers, 1934 and Horner and Frey, 1957). Some stability parameters are obtained from the regression approach. Thus, Finlay and Wilkinson (1963) used the regression coefficient as a measure of stability. Eberhart and Russell (1966) also used the regression coefficient as a first measure of stability but go further and regard the sum of squared deviations as a second measure.

The application of this technique in lentils has been used by some workers; Malhotra et al. (1971); Mehra and Pahuja (1979); Sagar and Lal (1980); Pandey et al. (1982) and Ahmed and Pandey (1983).

9. Genetic analysis by the diallel system

In any plant breeding program, the aim of selection is to identify superior genotypes which will transmit their desirable characteristics to future generations. Hence any overall genetic evaluation which is useful in identifying in the early generations the crosses of potential value is of considerable value. The approach relies on the fact that estimates of genetic parameters allow the choice of parental material showing non-allelic interaction. In subsequent generations transgressive segregants may be produced from this material for the characters under selection (Lupton and Whitehouse, 1957).

Several mating systems can be employed, but two, which offer both a systematic experimental approach and also an overall genetic evaluation in the early generations following crosses between inbred genotypes, are the test-cross analysis (Jinks, Perkins and Breese, 1969) and the diallel cross (Hayman, 1954a and b; Jinks, 1954). The test-cross analysis requires fewer crosses than the diallel. Two tester inbred genotypes are crossed with the remaining n inbred lines in the test population, giving 2n crosses, whereas in the diallel analysis, n (n-1) crosses are needed between n parents. However, the test-cross analysis requires that the two tester genotypes are the

extreme selections from the population under test. If the two testers are not extreme selections and have the same allele for loci controlling the character under analysis, then additive and dominance effects will be underestimated. In the present study yield was the primary selection criterion. However, it was decided to study the inheritance of other characters of potential importance in indirect selection for yield, based on response to irrigation. It was not possible to find two tester genotypes which were extreme for all the characters under consideration, so this precluded the use of the test-cross analysis.

The diallel cross mating system was first discussed by Schmidt (1919), and the application of diallel-cross technique for evaluation of quantitative variability in self-pollinated crops was developed by Hayman (1954), Jinks (1954) and Griffing (1956a, b).

Sprague and Tatum (1942) defined the terms general and specific combining as follows; the term 'general combing ability' is used to designate the average performance of a line in hybrid combination, and the term 'specific combining ability' is used to designate those cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved.

Griffing (1956b) was concerned with the definitions of general and specific combining ability when the testing procedure utilizes a diallel crossing system. He stated that the proper interpretation of the genetical parameters from the diallel analysis depends on the particular diallel method, the assumptions regarding the experimental material, and the conditions imposed on the combining ability effects. In this respect, four different experimental methods of diallel cross were suggested by the author. These methods vary with inclusion or absence of parental inbreds and/or reciprocal F_1's and with sampling assumptions (models). Following the classification of Griffing (1956b), the four possible diallel crossing methods are : (1) parents, one set of F_1s, and reciprocal F_1's are included (all P^2 combinations); (2) parents and one set of F_1's are included but reciprocal F_1's are not (1/2 P(P+1) combinations); (3) one set of F_1's and reciprocal F_1's are included but not the parents (P(P-1) combinations); and (4) one set

of F_1's but neither parents nor reciprocal F_1's are included (1/2P(P-1)). For each method, there are two alternative models depending on whether the genotypes are assumed to be (a) a chosen or fixed set and cannot be regarded as a random sample from any population (Model I), or (b) a random sample from a population about which inferences are to be made (Model II). These four different diallel crossing methods with two different models for each, result in eight different situations, each requiring different analysis.

Several other methods of diallel cross analysis have been developed (Jinks and Hayman, 1953; Hayman, 1954; Jinks, 1954; Allard, 1956; Kempthorne and Curnow, 1961, Fyfe and Gilbert, 1963). In the early 1950's, Jinks and Hayman, from the Biometrical Genetics Unit of the University of Birmingham, published a series of papers on the analysis and interpretation of data from diallel crosses. Hayman extended the statistical analysis by subdividing the interaction term into three subcomponents. At the same time, he and Jinks were developing a theory for interpreting diallel statistics in terms of gene frequencies and gene effects. The Jinks-Hayman (1953) diallel analysis of parental and F_1 generations from a set of diallel crosses appeared to provide a rapid evaluation of the genetic relationships among a number of parents. This method thus seemed to offer promise in identifying parents whose hybrids are most likely to respond to selection (Crumpacker and Allard, 1962). This analysis includes parents and one or both sets of F_1 crosses. Thus, with respect to Griffing's classification of diallel crossing techniques, it is applicable to both experimental methods I and II.

The diallel analysis procedures have been used to obtain information concerning the inheritance of quantitative traits, and for the prediction of segregation in the F_2 and later generations. The Hayman-Jinks analysis makes the following genetic assumptions : (1) homozygous parents; (2) diploid segregation; (3) no reciprocal differences; (4) gene frequencies equal to 0.5 at all segregating loci; (5) genes independently distributed between the parents (no-linkage); (6) no epistasis (no non-allelic interaction); and (7) no multiple alleles.

With lentil, assumptions 1 and 2 are the usual ones and could be assumed from its history of self-pollination. The last five assumptions are not so easily accepted and they are difficult to evaluate independently. They are tested by the analysis as the null hypothesis. Hayman (1954, 1957) developed two methods for testing some of the assumptions mentioned above. He stated that he could always detect epistasis, and multiple allelism in the absence of epistasis, and when both of these factors are absent gene correlation may be exposed. Hayman (1954b) showed that multiple allelism is unimportant until the F_2 generation. Nevertheless it was felt that the diallel cross mating system and its analysis offered the best properties for a genetic evaluation of early generations of an underexploited crop species with a view to identifying promising crosses.

The application of diallel crosses in lentils has been given by some workers; Malhotra et al. (1973); Singh et al. (1975) and Goyal et al. (1977). But two only are available. Malhotra et al. (1973) found that general combining ability effects were more important than specific combining ability effects for all the characters studied. Graphical and component analyses indicated partial dominance for seed yield, partial to no dominance for pod number, partial dominance for days to flower, over-dominance for plant height and partial to over dominance for secondary branches. The combining ability, graphical and component of variance analyses suggested predominance of additive gene action for the characters excepting plant height, where non-additive gene action was more pronounced.

Singh et al. (1975) studied 15 one-way diallel crosses for primary and secondary branches, pods/plant, 100-seed weight and grain yield in lentil. They observed significant variance due to hybrids for all the characters, but variance due to hybrids vs parents (heterosis) was significant only for grain yield, pods/plant and secondary branches. Of the 15 crosses, 3 exhibited significant heterosis over the mid-parent and superior parent for yield as well as for pods/plant and secondary branches. For all the characters general combining ability and specific combining ability variances were observed to be important. They suggested that selection of superior segregants should be based on the number of secondary branches during the early stages of growth and on pod number per plant at the time of maturity.

* * * * *

The problem of adaptation to different soil moisture regimes, particularly in Egypt, has been highlighted already. This study aimed to investigate the response of lentil genotypes to different water regimes to provide guidelines, through partitioning the variation, for a selection program for adaptation to irrigation conditions. The research was divided into two main areas; 1) The overall variation in the crop was partitioned into genotypic, environment and genotype-environment components in an analysis of adaptation over seasons, irrigation regimes and locations. 2) The genotypic variation was partitioned into its various genetic components in an inheritance study using the diallel mating system.

These investigations were planned to provide estimates of expected response of yield to selection either for seed yield per se, or for indirect selection for other traits associated with yield. Additionally, many agronomic and quality characters were studied to monitor indirect effect of selection for yield on these traits.

CHAPTER II

MATERIALS AND METHODS

1. Plant materials

Thirty five genotypes of lentil, selected from the international germplasm collection at ICARDA, primarily on the basis of diversity of origin and agronomic characteristics, were included in this study. However, amongst these genotypes, three lines were chosen on account of their known positive or negative response to irrigation. Family 370, a new Egyptian line, and FLIP 84 – 1 L produced high yield under irrigation in Egypt; therefore they were considered responsive to irrigation. The third genotype was the local Egyptian cultivar Giza 9, which showed no response to irrigation. The origin, the international legume lentil number (ILL) and some other characters of the genotypes are given in Table 4.

2. Experimental procedures

2.1 Description of trial sites and environments

A study of the adaptation to moisture supply requires testing under different water levels, hence, experiments were conducted in three contrasting rainfed locations in Syria and Lebanon, spanning the range in rainfall found in the main production areas in the Middle East.

These locations were: (i) Tel Hadya, the ICARDA farm, in North Syria with long-term average seasonal rainfall of 350mm; (ii) Breda (the dry site, with an average rainfall of 250mm) in North Syria; (iii) Terbol in the Biqa'a Valley in Lebanon, the cold wet site with an average rainfall of 550mm. A summary of the location data is given in Table 5.

To extend the range of moisture supply at one location, three water regimes were used at Tel Hadya. Accordingly, there were five

Table 4 Description of the genotypes

Genotype	ILL*	Country of origin	Plant height	Flower earliness	Seed size	Cotyledon colour	Comments
Giza 9	784	Egypt	Tall	Early	Small	Red	Local cultivar
Family 370	5486	"	Tall	Early	Small	Red	Selection from local material
Family 130	813	"	Very tall	Very late	Very small	Yellow	Selection from local material
Selaim	1861	Sudan	Short	Medium	Very small	Red	Local cultivar
-	1693	Ethiopia	Short	Early	Very small	Red	-
-	1983	"	Short	Early	Very small	Red	-
-	40	Syria	Tall	Medium	Small	Red	-
-	241	"	Tall	Medium	Medium	Yellow	-
Local large	4400	"	Tall	Medium	Large	Yellow	Selection from local material
Local small	4401	"	Tall	Medium	Small	Red	" " "
Jordanian loc.	4354	Jordan	Short	Medium	Medium	Yellow	Local cultivar
76TA66005	5562	"	Tall	Early	Medium	Yellow	Selection from local material
78S26003	5583	"	Medium	Medium	Medium	Yellow	" " "
78S26004	5584	"	Medium	Medium	Medium	Yellow	" " "
76TA66088	5572	Iran	Tall	Medium	Small	Red	" " "
-	357	Algeria	Short	Medium	Small	Yellow	-
-	4349	USSR	Very tall	Very late	Large	Yellow	Selection from local material
-	121	Turkey	Tall	Late	Very small	Red	-
74 TA161	5516	"	Short	Very late	Medium	Red	Selection from local material
Lenka	5480	Czechoslovakia	Very tall	Late	Medium	Yellow	-
Okula	5481	"	Very tall	Very late	Large	Yellow	-
74TA276	5527	Hungary	Tall	Medium	Large	Red	Selection from local material
74TA212	5519	Greece	Tall	Very late	Small	Yellow	" " "
-	274	"	Tall	Very late	Small	Yellow	-
-	355	Mexico	Tall	Very late	Large	Yellow	Promising line in Ethiopia
-	358	"	Tall	Early	Very small	Red	" " "
Precoz	4605	Argentina	Medium	Early	Large	Red	Promising line in Pakistan
Pant.L.406	2501	India	Short	Early	Very small	Red	-
-	2526	"	Short	Early	Very small	Red	-
-	2573	"	Short	Early	Very small	Red	-
74TA264	5523	Australia	Tall	Medium	Large	Yellow	Selection from local material
FLIP84-1L	5674	Icarda	Tall	Late	Large	Red	Selection from Icarda cross
FLIP84-27L	5699	"	Tall	Early	Medium	Yellow	" " "
FLIP84-67L	5737	"	Tall	Early	Medium	Yellow	" " "
FLIP84-78L	5748	"	Tall	Early	Large	Yellow	" " "

* International Legume Lentil collection number at ICARDA.

Table 5 Summary of the location data

Description		Tel Hadya	Breda	Terbol
Latitude		35°55'N	35°55'N	33°55'N
Longitude		36°55'E	37°10'E	36°00'E
Altitude (sea level, m)		362	350	950
* Soil classification		Crumsol Soil	Reddish Brown	-
Long term average rainfall (mm)		342	283	551
Seasonal rainfall	) 1984-85	373	277	489
(mm)	) 1985-86	316	218	396
Date of planting	) 1984-85	28 Nov.	21 Nov.	18 Nov.
	) 1985-86	5 Dec.	28 Nov.	25 Nov.

* Soil classified according to USA system.

environments which varied in moisture supply. These environments were as follows:

i (T_1) Tel Hadya rainfed only.

ii (T_2) Tel Hadya under rainfed + one supplementary irrigation with 50mm at pre-flowering stage.

iii (T_3) Tel Hadya under rainfed + two supplementary irrigations (50mm/each) at pre-flowering stage and at pod filling stage.

iv (Br) Breda rainfed only.

v (Ter) Terbol rainfed only.

These five environments were used in two growing seasons 1984-85 and 1985-86 and the water supply for all environments is shown in Table 6. Air temperature and rainfall distributions for two growing seasons at all locations will be presented with the results.

2.2 Field processes

At Breda and Terbol, randomized complete block designs were used with 35 genotypes with three replications. At Tel Hadya, a split-plot design was used with three replications; the three water regime treatments were in the main-plots and the 35 genotypes were in sub-plots. In all experiments, the sowing was done at the recommended crop density with intra-row spacing of 2cm with 25cm between rows and 4 meter long rows. A sowing depth of 4-6cm was maintained at all sites. Dates of sowing are given in Table 5. No inoculation was used in any of the trials, and nodulation was adequate throughout. Fertilizer at 50 kg P_2O_5/ha was added to all experiments and 30 kg N/ha was used at Tel Hadya and Breda only (Terbol already having a high nitrogen status). At all locations, fertilizers were added to the soil prior to planting. In all experiments, herbicide mixtures of Pronamide (trade mark, Kerb, marketed by Rohm and Haas Co.) and Cyanazine (trade mark, Bladex, marketed by Shell Research Ltd.) were both used at pre-emergence at the same rate of 1 kg/ha against broad-leaved weeds. Thereafter, hand-weeding was undertaken as necessary. Furrow

Table 6 Water supply of the environments during lentil growing period (22 Oct. - 2 June) for two seasons

Environments	Water supply (mm)	
	1984-85	1985-86
T_1	346	306
T_2	396	356
T_3	446	406
Br	253	203
Ter	433	358

irrigation with gated pipes system was used at Tel Hadya with hydrometer to control the amount of water for each experimental plot. The irrigation systems have been described by Hagan et al. (1967).

At harvesting 30 pods from every experimental plot were collected at random, then the central $3m^2$ of plots was pulled by hand, placed in cotton sacks, dried in the sun, weighed, then threshed by machine and the clean seeds weighed.

2.3 Laboratory techniques (seed protein quality and content, cooking time and dehulling characteristics)

Seed protein content, cooking time and a dehulling test for all experimental plots in five environments were all analyzed at ICARDA's Quality Laboratory in the 1984-85 and 1985-86 seasons. Investigation of the effect of environmental conditions on seed protein quality was carried out by gel-electrophoresis at the Science Laboratory of Durham University, Botany department, England during October-November, 1985.

For seed protein content (N x 6.25), samples were analyzed for the test after grinding 20g seed in a U.D. cyclone sample mill fitted with a 1.0mm screen. Testing for protein was carried out on a Neotec model 5Q A51A analyzer, which uses the principle of near-infrared reflectance spectroscopy. As a check, every tenth sample was also analysed by a macro-Kjeldhal procedure (AACC, 1969) using 0.5/g/sample. Data for protein are reported on an "as is" basis with respect to moisture since this is the state in which lentils are traded and used by the consumer. Moisture content was determined by drying a 2g sample of ground lentils at 130°C for 65 minutes, cooling and weighing. Moisture was very consistent and the range was from 9.0 to 9.5% with a mean of 9.27% (Erskine et al., 1985).

Seed protein quality

A study of the total storage protein in lentil seeds as affected by irrigation and environmental conditions was made for 35 genotypes at 5 environments by the polyacrylamide gel electrophoresis technique according to the method of Davis (1964) and Ornstein (1964).

A seed sample of 20g/genotype was selected from every environmental treatment at random. Any off-type seeds were discarded from the sample and one seed was chosen at random to represent the population. Seed coat was removed, then the cotyledons were cracked and 10 mg seed meal was extracted in 0.2 M Chilled Tris/HCl buffer (pH 6.8), in the ratio rate of 1 : 5 (W/V), containing 10% (W/V) Sucrose and 2% (W/V) SDS. The crude extract was centrifuged for 3 minutes at 500 r.p.m. and the clear supernatant was separated and 10 µl Mercaptoethanol was added, then the extract used for electrophoretic analysis.

The analysis was done by SDS/poly acrylamide-gel electrophoresis in slab gels using a Pharmacia GE-4 slab gel apparatus. A few drops of bromophenol blue were added to the upper electrode compartment and the crude extract loaded on top of the gel in the wells using a 10 µl syringe with a long needle. Gels were run at room temperature (20-25°C) initially at 15mA for 30 mins. then at 30mA at constant current. The run was terminated as the tracking dye reached the bottom of the gel.

Following electrophoresis, the gel was incubated in the staining solution overnight, then removed to the destaining solution until photographed. The position of each band was calculated as an Rf value, relative to the Bromophenol Blue (BPB) front (Rf = migration distance of the band/migration distance of BPB). Each gel was dried between two sheets of uncoated cellophane in a gel drier. The following chemicals were used to prepare the gel and solutions:

Separating gel:

The 17% (W/V) separating gel contained in a total volume of 59.5 mL, the following:

1. Acrylamide stock
   30g acrylamide plus 135 mg N, N, N methylene bis acrylamide (BIS) and distilled water up to 100 mL. — 25 mL

2. 1M Tris/HCl buffer (PH 8.8) with distilled water up to 1000 mL. — 22.5 mL

3.	Distilled water (degassed)	9.9 mL
4.	1% (W/V) ammonium persulphate (freshly prepared)	1.5 mL
5.	10% (W/V) sodium dodecyl sulphate (SDS)	0.6 mL
6.	N, N, N', N' tetramethyl ethylene diamine (TEMED)	20 µl

Spacer gel

1.	Acrylamide stock 30g acrylamide plus 435 mg bis and distilled water up to 100 mL	3 mL
2.	IM Tris/HCl (PH 6.8)	2.5 mL
3.	Distilled water (degassed)	13.8 mL
4.	1% Ammonium persulphate (freshly prepared)	0.5 mL
5.	10% (W/V) SDS	0.2 mL
6.	TEMED	10 µl

Development buffer

Glycine	141 g
Tris	30 g
SDS	10 g

Distilled Water up to 1000 mL

(This solution was diluted 10 times before using)

Staining solution

Coomassie blue	0.5 g
Methanol	500 mL
Acetic acid (glacial)	70 mL

Distilled Water up to 1000 mL

Destaining solution

Methanol	500 mL
Acetic acid	70 mL
Distilled Water up to 1000 mL	

The chemicals used in this study and their suppliers are listed in Appendix Table 6.

For measuring cooking quality, 6-8 g of seeds were boiled to softness in 100 mL water using a Labconco Crude Fibre Digestion apparatus (Erskine et al., 1985). The progress toward cooking could be followed through the glass of the Bercelius beaker. The boiling liquor darkened in colour and froth developed. Ruptured seed coats sometimes separated. To establish the stage of cooking, after 15 minutes 5 seeds were removed from the beaker and pressed by the finger to test the seed consistency. When all 5 seeds were soft, more seeds were tested for softness until it had been verified that 80% of seeds were cooked. If the tested seeds were not soft, the sampling was repeated every 2 minutes until cooking was complete. Prior to measuring cooking quality, the lentils had been stored for approximately 2 months at room temperature (22-23°C). Relative humidity at that time of year (June-October) in Northern Syria is very low (30-40%), and the storage conditions used were unlikely to lead to increased cooking time (Jones and Boulter, 1983).

To test the dehulling characteristics, 200g seeds from every experimental plot were sieved with 5, 4.5, 4 and 3.5mm sieves for small and medium seeded genotypes and with 6, 5, 4.5 and 4mm sieves for large seeded genotypes. Then, 10g of seeds are taken from the larger fraction. The production model of the Tangential Abrasive Dehulling Device (TADD), complete with a 12-sample plate which allows up to 12 different samples of grain to be dehulled simultaneously, was used (Reichert et al., 1985).

Because different seed sizes require different treatments, genotypes were classified into three groups; small seeded with 100 seed weight up to 3.9g, medium seed size, from 4-4.4g and large seeded with a seed weight of more than 4.5g. Samples of small seeded, medium

size and large seeded genotypes were applied in the machine for 25, 20 and 15 seconds, respectively, using the automatic timer. After dehulling for the appropriate time, the dehulled seeds were removed from the sample cups using the vacuum aspirator. This device simultaneously collected and cleaned the dehulled grain, removing any residual fine material that had not escaped under the sample cups. The dehulled and non-dehulled seeds were weighed and then the percentage of dehulled seeds was calculated as:

$$\text{percentage of dehulled seed} = \frac{\text{weight of dehulled seed (g)}}{\text{weight of seed sample (10g)}} \times 100$$

2.4 Root system and structure study

In order to study variated differences in root morphology and anatomy under anaerobic conditions, two genotypes were selected, viz, 74TA264 and ILL 121. Sixty seeds of each genotype were sown in 20cm diameter plastic pots at the rate of 10 seeds/pot, in the greenhouse of the Botanic Garden in Durham University during November 1986. Oxygen deficiency was induced by flooding of heavy clay soil (treatment W), allowing the comparison of oxygen free (treatment D) with well-aerated soil, Levington peat based soil. For every genotype, three pots were subjected by treatment (W) and three to treatment (D). The pots of (W) were irrigated every day until saturation, while pots of (D) were irrigated as required. All pots were grown at 18-22°C in 16 h. days.

Eighteen days after sowing, seedlings were removed from the soil carefully avoiding damage in roots, which were washed in water then photographed. Cross sections of about 40 µm thick were taken from roots using a rotating razor blade, 2cm below the root tip. Sections were examined using a Nikon Diaphot fluorescence microscope with non-fixed fresh sections stained with Calcofluor M2R and illuminated with ultra-violet light. Photographs were taken on Kodak Technical Pan film (125 ASA), processed according to the manufacturer's instructions.

2.5 Genetic analysis by diallel technique

The parents used in this study were selected from the 35 genotypes detailed in Table 4. Eight genotypes (parents given in Table 7) were chosen on the basis of predicted response to irrigation, but care was taken to ensure a wide genetic base.

The 28 possible crosses were made between the eight parents (p = 8) to complete the half diallel mating system (P(P-1)/2), excluding reciprocals (Table 8). These crosses were made both in the plastic house and at ICARDA, Tel Hadya farm, in 1984-85 to ensure adequate hybrid seed supply. The hybridization method is described in Muehlbauer and Slinkard (1981).

At maturity, the hybrid pods of each cross were harvested separately, then threshed by hand. The seeds of each cross were divided to two groups; the first one, not less than 15 seeds, was grown at Shaubak in Southern Jordan in June 1985, to produce F_2 seeds. The second set was fumigated with phostoxine for storage. In September 1985, the F_1 plants, at Shaubak, were harvested then threshed.

In December 1986, the parents, F_1 and F_2 generation were sown at Tel Hadya in a completely randomized block design with two replications. Each replicate consisted of 64 lines (28 F_1's, 28 F_2's and 8 parents) distributed at random. The field processes were identical to that mentioned in section 2.2. However, due to limitation in the number of F_1 seeds and to ensure crop plant density, the row lengths for the F_1 generation varied depending on seed availability per cross. These lengths ranged from 30cm with 15 seeds (the minimum/plot) to 126cm with 63 seeds (the maximum/plot). Plastic sticks marked each end of F_1 rows and a black seed genotype (ILL2526) was sown in remaining ends of the row as a common competitor to, and the marker of, F_1 plants under study giving the crop density of 200 plants/m^2. This experiment was irrigated twice as in environment T_3.

At harvesting, 30 pods from every plot were collected at random, then the middle 15 plants from each plot were pulled by hand and put together in a cotton sack, dried in the sun, weighed, then threshed by hand and the clean seeds weighed.

Table 7 Parental lines in the diallel

Parent	Selection	Country of origin	Comments
1	Giza 9	Egypt	Local variety.
2	Family 370	Egypt	Egyptian selection, high yield in Egypt.
3	78S26004	Jordan	Adapted to dry conditions in Tel Hadya.
4	Precoz	Argentina	High yield in Syria and early maturity.
5	Pant.L,406	India	High yield in India and early maturity.
6	FLIP84,1-L	ICARDA	Hybridization line, high yield in Egypt.
7	ILL 274	Greece	High protein content.
8	ILL 121	Turkey	High protein content.

Table 8 Description of crosses made in 1984-85

Cross No.	Female parent	x	Male parent
1	1		2
2	1		3
3	1		4
4	1		5
5	1		6
6	1		7
7	1		8
8	2		3
9	2		4
10	2		5
11	2		6
12	2		7
13	2		8
14	3		4
15	3		5
16	3		6
17	3		7
18	3		8
19	4		5
20	4		6
21	4		7
22	4		8
23	5		6
24	5		7
25	5		8
26	6		7
27	6		8
28	7		8

3. Data measured

Yield component characters are measured on 10 individual plants selected at random from each plot. But, because phenotypic plasticity of lentil is high, the use of individual plants to represent the population leads to high experimental error. Aristarkhova and Voluzneva (1982) found that yield-related characters in lentil cannot safely be characterized on the basis of averages calculated using samples of only 10 plants. Accordingly, the yield component characters were calculated in the basis of the average of all plants in each plot. However, plant height and number of branches per plant still had to be measured on 10 random plants from each plot.

The following characters were estimated throughout:

1. Biological yield (kg/ha).
2. Seed yield (kg/ha).
3. Straw yield (kg/ha).
4. Biological yield per plant in grams (g).
5. Seed yield per plant (g).
6. Straw yield per plant (g).
7. Harvest index (%).
8. Number of pods per plant.
9. Number of seeds per pod.
10. 100-seed weight in gram (g).
11. Plant height (cm).
12. Number of branches per plant.
13. Time to flowering (days).
14. Time to maturity (days).
15. Seed protein content (%).
16. Cooking quality (minutes).
17. Dehulling (%).

Plant height was measured from ground level to the apex of the plant. Number of branches per plant included primary and secondary branches. Both characters were measured during the pod-filling stage. Time to flowering was recorded by calculating the time from the first day of soil wetting sufficient for germination to when 50% of the plants in the plot started to flower. Time to maturity was also calculated as

number of days from this date to when 90% of the pods in a plot were mature (when foliage colour became yellowish, lower leaves on stem started shedding and pods and seeds hardened). To calculate number of seeds per pod, the 30 pods collected at harvest from every plot were threshed by hand and then the number of seeds counted; then the number of seeds per pod was calculated from the number of seeds of 30 pods. An average of two counts of 100 seeds are taken from each plot at random to calculate 100-seed weight. At harvesting, the number of plants in each plot was counted. Biological yield, seed yield and straw yield per plant were calculated as follows : Biological yield per plant = Biological yield per plot/number of plants per plot, Seed yield per plant = seed yield per plot/number of plants per plot and straw yield per plant = (biological yield per plot - seed yield per plot)/number of plants per plot. Number of pods per plant was calculated by the formula = (seed yield per plant x 100/100 seed weight)/number of seeds per pod. Harvest index was calculated as : (seed yield per plot/biological yield per plot) x 100. Seed protein content, cooking time and dehulling percent were estimated as described in 2.3.

4. Statistical analyses

The plot mean for each character was used for statistical analysis. Data was analysed on a VAX/VMS computer at ICARDA, using the CRISP package. There was cold damage to genotype Family 370 at all locations and on 21 experimental plots at Tel Hadya, due to the early frost which occurred in the 1984-85 season. Therefore, Family 370 was ignored in both seasons and the 21 plots were estimated as missing data. The statistical analysis was carried out as follows:

4.1 Environmental trial

4.1.1 Analysis of variance and estimation of genetic components

The analysis of variance was performed for each environment in every year separately with a randomized complete block design (Snedecor and Cochran, 1967). Then Bartlett's test was used to examine the homogeneity of error variances of each environmental trial before combining them (Gomes and Gomes, 1984). Since we obtained homogenous error variances, a combined analysis of variance of two years was

Table 9 Form of variance analysis and mean squares expectations

Source	D.F.	Mean square	Expectation of mean square
Years	y-1		
Environments	E-1		
Environments - years	(E-1)(y-1)		
Reps. in environments and years	Ey(r-1)		
Genotypes	g-1	M_5	$\sigma^2 e + r\sigma^2_{gEy} + ry\sigma^2_{gE} + rE\sigma^2_{gy} + rEy\sigma^2_{g}$
Genotype-year	(g-1)(y-1)	M_4	$\sigma^2 e + r\sigma^2_{gEy} + rE\sigma^2_{gy}$
Genotype-environment	(g-1)(E-1)	M_3	$\sigma^2 e + r\sigma^2_{gEy} + ry\sigma^2_{gE}$
Genotype-environment-year	(g-1)(E-1)(y-1)	M_2	$\sigma^2 e + r\sigma^2_{gEy}$
Pooled error	Ey(r-1)(g-1)	M_1	$\sigma^2 e$

applied by split-split plot design using a fixed model (genotypes fixed and environments random). The genotypic mean square was tested against pooled error. The expectation of mean squares were derived from the plot data (Table 9), then equated to the observed values to estimate the components of variance.

In Table 9, g, r, E and y are numbers of genotypes, replicates, environments and years, respectively and $\sigma^2 e$ is pooled error variance, $\sigma^2 g$: genotypic variance, $\sigma^2 gE$: variance due to genotype-environment interaction, $\sigma^2 gy$: variance due to genotype-year interaction and $\sigma^2 gEy$: variance due to genotype-environment-years interaction.

These variance components were estimated by the following formulae (Miller et al., 1959):

$$\text{Genotypes } (\sigma^2 g) = \frac{M_5 + M_2 - M_3 - M_4}{rEy}$$

$$\text{Genotypes - years } (\sigma^2 gy) = \frac{M_4 - M_2}{rE}$$

$$\text{Genotype-environment } (\sigma^2 gE) = \frac{M_3 - M_2}{ry}$$

$$\text{Genotype-environment-year } (\sigma^2 gEy) = \frac{M_2 - M_1}{r}$$

$$\text{Pooled error } (\sigma^2 e) = M_1$$

The importance of genotypic component of variance in relation to phenotypic variance (overall variance $\sigma^2 ph$) was assessed as broadsense heritability ($h^2_{b.s.}$) (Allard, 1960) as:

$$\sigma^2 ph = \sigma^2 g + \frac{\sigma^2 gE}{E} + \frac{\sigma^2 gy}{y} + \frac{\sigma^2 gEy}{Ey} + \frac{\sigma^2 e}{gEr}$$

$$h^2_{b.s.} = \frac{\sigma^2 g}{\sigma^2 ph}$$

The coefficient of variation was estimated by using the formula suggested by Burton (1952) as:

$$\text{Genetic coefficient of variation (G.C.V.)} = \frac{(\text{genetic variance})^{\frac{1}{2}}}{\text{overall mean}} .100$$

The genetic advance under selection was calculated by using the method suggested by Allard (1960) as:

$$Gs = K. (\sigma^2_{ph})^{\frac{1}{2}} . h^2_{b.s.}$$

With Gs represents the expectation of genetic advance under selection. It measures the difference between the mean genotypic value of the selected genotypes, and the mean genotypic value of the original genotypes. $(\sigma^2 ph)^{\frac{1}{2}}$ or σph is the phenotypic standard deviation of the mean character of the original genotypes and $h^2_{b.s.}$ is the broad sense heritability. Whereas K is a selection differential (Allard, 1960). In the present study K value is considered to be 2.06.

4.1.2 Estimation of phenotypic and genotypic correlations

Covariance estimates obtained by the analysis of covariance between each pair of traits, followed the same form as the analysis of variance in Table 9. Then the phenotypic and genotypic correlations were calculated as follows:

$$\text{Phenotypic correlation (rph)} = \frac{M_{1.2}}{[(M_1)(M_2)]^{\frac{1}{2}}}$$

Where $M_{1.2}$ is the phenotypic mean product between pairs of traits 1 and 2, M_1 and M_2 are the phenotypic mean squares of the two traits, respectively.

$$\text{Genotypic correlation } (rg) = \frac{\sigma^2 g\ 1.2}{[(\sigma^2_{g1})(\sigma^2_{g2})]^{\frac{1}{2}}}$$

where $\sigma^2_{g1.2}$ is the genetic covariance between two characters and σ^2_{g1} and σ^2_{g2} are the genotypic variances of the two traits respectively. (Bliss *et al*., 1973).

4.1.3 Stability analysis

The plot data was used for statistical analysis. Genotype, Family 370 was discarded from this analysis because it was omitted in the first season trials due to cold damage, and an equal number of genotypes at all environments in all seasons is required in this analysis.

Stability parameters suggested by Eberhart and Russell (1966) were calculated. The stability analysis was made in two ways; firstly with 6 environments; T_1, T_2 and T_3 in each year separately to study the genotype-irrigation interaction. The second stability analysis was made using all environments, T_1, T_2, T_3, Breda, and Terbol in each year (10 environments) to study the adaptation of lentil under different agro-climatic environments.

The linear regression technique developed by Finlay and Wilkinson (1963) was also used to describe various types of variety adaptability to the irrigation and range of environments. To evaluate the efficiency of the regression analysis for genotype-environment interaction, the linear proportion of variance accounted for by regression was estimated by the following formula (Fripp and Caten, 1971):

$$\frac{100L}{L+nL}$$

where L is the difference between the mean square of heterogeneity of regression and the pooled mean square, and nL is the difference between the mean square of the deviations from regression and the pooled mean square.

Another approach, which is useful also to investigate the interaction effect was used. This was the simple expedient of the variance of individual genotypes over environments. This variance was calculated with the mean over replicates and measures the variability of performance of genotypes (Erskine, 1979).

In addition to previous approaches and to evaluate the genotypes for drought resistance under water stress conditions the drought

susceptibility index was used. The calculation of this index was made according to Fischer and Maurer (1978) using their formula as follows:

$$Y_d = Y_p (1 - SD)$$

where Y_d is variety yield under stress condition, Y_p is potential yield under non stress condition, S is susceptibility index and D is drought intensity. D is calculated as $1 - (Y_d / Y_p)$ where Y_d and Y_p are the average yields over all genotypes tested under stress and non stress environments.

4.2 Genetic analysis by diallel (parents and F1 and F2 generations)

4.2.1 Analysis of variance and combining ability analysis

The plot mean was used for statistical analysis. The analysis of variance for the completely randomized block design was performed for each character in each of the parents, parents with F_1's and parents with F_2's generations separately. Differences between the genotypes were tested using the error mean squares.

When the analysis of variance showed significant differences between genotypes over replications, general combining ability (GCA) and specific combining ability (SCA) variances and effects for the eight parental genotypes and their crosses were estimated according to Griffing's (1956b) combining ability analysis method 2, model I, using the computer program "Diall 12" for each of parents and one set of F_1 and parents and one set of F_2 generations separately. In this model, genotypes were considered fixed (fixed model). The analysis of variance and the expectations of mean squares for this model are shown in Table 10.

4.2.2 Estimation of heterosis and inbreeding depression

The heterosis and inbreeding depression were calculated by the following formulae:

$$\text{Heterosis} = \frac{\text{F1 - Mid parent}}{\text{Mid parent}} \times 100$$

Table 10 Analysis of variance for general and specific combining ability and expectations of mean squares for the assumptions of method 2, model I

Source of variance	D.F.	Expectation of mean squares
General combining ability	P-1	$\sigma^2 e + \frac{P+2}{P-1}\sigma^2 g$
Specific combining ability	$\frac{P(P-1)}{2}$	$\sigma^2 e + \frac{2}{P(P-1)}\sigma^2 s$
Error	m	$\sigma^2 e$

Where $\sigma^2 g$, $\sigma^2 s$ and $\sigma^2 e$ were the general, specific combining abilities and error variances respectively for crosses amongst P parents.

$$\text{Useful heterosis} = \frac{\text{F1 - better parent}}{\text{better parent}} \times 100$$

$$\text{Inbreeding depression} = \frac{\text{F1 - F2}}{F_1} \times 100$$

A test of significance for the F_1 cross mean from the mid-parent values was conducted by the following "t" value as suggested by Wynne et al. (1970).

$$t = (F_{1ij} - MP_{ij}) \; / \; (\tfrac{3}{8}\sigma^2 e)^{\frac{1}{2}}$$

Where :

F_{1ij} = the mean of the ijth F_1 cross.

MP_{ij} = the mid parent value for the ijth cross.

$\sigma^2 e$ = estimate of error variance.

A "t-test" was used to examine if F_2 cross means were statistically different from F_1 values according to the following formula suggested by Al-Rawi and Kohel (1969).

$$t = F_2 - F_1 \; / \; (\sigma^2 eF_1 + \sigma^2 eF_2)^{\frac{1}{2}}$$

Where :

F_2 = the mean of the F_2 cross.

F_1 = the mean of the F_1 cross.

$\sigma^2 eF_1$ = estimates of F_1 error.

$\sigma^2 eF_2$ = estimates of F_2 error.

4.2.3 Estimation of genetic components

The variance components were calculated from both the Griffing and the Jinks-Hayman diallel analyses. In the first, variance components were calculated according to the method described by Kempthorne and Curnow (1961). In the latter method (Jinks-Hayman), variance components were estimated according to the formula proposed by Crumpacker and Allard (1962). Assuming the model is adequate, the components of variance were calculated for the two methods of analysis from the expectation shown in Table 11.

Narrow sense ($h^2_{n.s.}$) and broad sense ($h^2_{b.s.}$) heritabilities were estimated from the Griffing analysis, as described by Kempthorne and Curnow (1961), as follows:

$$h^2_{n.s.} = 2\sigma^2 gca/[(2\sigma^2 gca + \sigma^2 sca) + \sigma^2 E]$$

$$h^2_{b.s.} = (2\sigma^2 gca + \sigma^2 sca)/[(2\sigma^2 gca + \sigma^2 sca) + \sigma^2 E]$$

While in the Jinks-Hayman analysis, only narrow sense heritability was calculated; the method followed that used by Mather and Jinks (1971); i.e.

$$h^2_{n.s.} = \tfrac{1}{2}D + \tfrac{1}{2}H_1 - \tfrac{1}{2}H_2 - \tfrac{1}{2}F/\tfrac{1}{2}D + \tfrac{1}{2}H_1 - \tfrac{1}{4}H_2 - \tfrac{1}{2}F + E$$

Table 11 Expectations of the variance components from the Griffing and the Jinks-Hayman diallel analyses

Variance component		Griffing	Jinks-Hayman
General combining ability variance	(σ^2gca)	$\frac{\text{GCA.MS-Error MS}}{\text{(No. of parents +2)}}$	-
Specific combining ability variance	(σ^2sca)	SCA.MS-Error MS	-
Additive variance	(σ^2A)	$2\sigma^2$gca	1/4 D
Non-additive variance	(σ^2NA)	σ^2sca	$1/4(H_1 - F)$
Genetic variance	(σ^2G)	$\sigma^2A + \sigma^2NA$	$1/4(D+H_1-F)$
Environmental variance	(σ^2E)	Error MS	Error MS
Phenotypic variance	(σ^2ph)	$\sigma^2G + \sigma^2E$	$1/4(D+H_1-F)+E$

CHAPTER III

RESULTS AND DISCUSSION

1. Genetic variation in lentil genotypes

The individual analysis of variance for each environment in every year showed significant differences among the genotypes with respect to all the characters studied. Since Bartlett's test indicated the homogeneity of experimental errors across all environments, combined analyses of variance for five environments were made for each year separately. Then, a combined analysis of variance for 14 characters across all ten environments was made over the two years.

The analysis of variance in the seasons 1984-85 (Table 12) and 1985-86 (Table 13) showed highly significant differences between all sources of variance, environment, genotype and genotype-environment interaction. But for most traits, the variance due to environmental effect was greater than the variance of either genotype or genotype-environment interaction, because the water supply differed radically over the five environments. The highly significant genotype-environment interaction variances for all characters reflect the differing performance of genotypes depending on water supply.

Similarly, the combined analysis over both years showed that all sources of variance for the main effects (Genotypes (G), Years (Y) and Environments (E) and first order interactions (Y - E, Y - G and G - E) were highly significant (Table 14). The relative magnitudes of these various sources of variance will be discussed later in this chapter and discussion will now continue on the genetic variance.

Estimates of the components of variance of phenotypic and genotypic effects over two seasons are shown in Table 15. The relative magnitude of the components of variance of i) genotype-environment interaction, ii) genotype-year interaction, and iii) genotype-environment-year interaction in comparison to overall phenotypic variance are presented as three ratios in Table 15 for the

14 characters. The range, mean, coefficient of genetic variation, broad sense heritability and expected genetic advance from selection as a percent of the mean are given for each trait in Table 16. The interpretation of these genetic parameters will be discussed for every group of traits as follows:

1.1 Yield characters and harvest index

In this section the following characters related to yield are discussed : biological yield/plant, seed yield/plant, straw yield/plant and harvest index.

Straw yield per plant had the widest range, followed by biological yield per plant then seed yield per plant, with mean values of 2.43, 3.65 and 1.22g respectively. The genetic variance component comprised the major proportion of the phenotypic variance component for the four yield characters. Seed yield had the lowest broad sense heritability (76.4%) among these traits. Straw yield had a high heritability estimate (82.1%) because of the lower magnitude of its interaction variance components in comparison to the other two characters. Also, straw yield per plant had a relative higher coefficient of genetic variation and consequently higher genetic advance than biological and seed yield per plant. Harvest index had the highest heritability (95.3%), but a lower coefficient of genetic variation than straw yield thus a lower expected genetic advance.

Moderate broad sense heritability for seed yield per plant has been reported by Pandey et al., 1980 ($h^2_{b.s.}$: 72.7%) and El-Hady, 1983 ($h^2_{b.s.}$: 65%). Prem Sagar (1980) found broad sense heritability for biological yield was 71%. These estimations were comparable with broad sense values estimated in this study. The broad sense heritability of harvest index was estimated by Prem Sagar, 1980 ($h^2_{b.s.}$: 73%).

1.2 Yield component characters

The number of pods per plant, number of seeds per pod and 100 seed weight were studied as yield component characters. Number of pods per plant showed a wide range of 9.74 - 32.96 compared with the range of 1.1 - 1.9 and 1.99 - 6.55 for number of seeds/pod and 100 seed weight

Table 12 Mean squares for combined (pooled) analysis of variance for 14 lentil characters in 1984-85 season

Source of variance	D.F.	Biological yield per plant	Seed yield per plant	Straw yield per plant	Harvest index
Environment (E)	4	352.72**	43.91**	147.88**	0.0126*
Genotype (G)	33	16.32**	1.91**	10.32**	0.0505**
G - E	132	2.08**	0.30**	1.16**	0.0045**
Pooled error	330	1.27	0.18	0.61	0.0021

*, ** Significant at 0.05 and 0.01 level of probability, respectively.

Table 12 (continued)

Source of variance	D.F.	No. of pods per plant	No. of seeds per pod	100 seed weight	Plant height	No. of branches per plant
Environment (E)	4	13802.81**	0.157**	5.31**	3446.17**	1219.83**
Genotype (G)	33	627.93**	0.990**	25.07**	198.74**	62.61**
G - E	132	121.73**	0.035**	0.130**	15.87**	9.19**
Pooled error	330	69.75	0.023	0.027	6.29	3.73

Table 12 (continued)

Source of variance	D.F.	Time to flowering	Time to maturity	Seed protein content	Cooking time	Dehulling
Environment (E)	4	** 2,166.65	** 3,718.34	** 243.60	** 995.38	** 4,570.11
Genotype (G)	33	** 541.02	** 512.95	** 21.45	** 765.96	** 447.26
G - E	132	** 9.30	** 13.91	** 0.949	** 20.08	** 85.51
Pooled error	330	0.57	2.46	0.484	2.29	12.09

Table 13 Mean squares for combined (pooled) analysis of variance for 14 lentil characters in 1985-86 season

Source of variance	D.F.	Biological yield per plant	Seed yield per plant	Straw yield per plant	Harvest index
Environment (E)	4	161.73**	14.10**	81.25**	0.0289**
Genotype (G)	34	4.10**	0.64**	3.37**	0.0590**
G - E	136	0.55**	0.08**	0.35**	0.0027**
Pooled error	340	0.33	0.04	0.20	0.0015

** Significant at 0.01 probability level.

Table 13 (continued)

Source of variance	D.F	No. of pods per plant	No. of seeds per pod	100 seed weight	Plant height	No. of branches per plant
Environment (E)	4	5853.13**	0.325**	7.01**	4590.05**	753.90**
Genotype (G)	34	293.50**	0.996**	23.69**	163.98**	18.83**
G - E	136	37.31**	0.037**	0.14**	14.13**	4.00**
Pooled error	340	19.12	0.020	0.03	8 41	2.23

Table 13 (continued)

Source of variance	D.F.	Time to flowering	Time to maturity	Seed protein content	Cooking time	Dehulling
Environment (E)	4	11808.93**	18982.12**	38.80**	596.52**	7922.09**
Genotype (G)	34	762.23**	688.54**	16.21**	800.35**	1872.23**
G-E	136	10.64**	12.01**	2.03**	8.59**	238.59**
Pooled error	340	1.23	3.39	0.36	0.84	57.71

Table 14 Mean squares for combined (pooled) analysis of variance over two seasons of 1984-85 and 1985-86 for 14 lentil characters

Source of variance	D.F.	Biological yield per plant	Seed yield per plant	Straw yield per plant	Harvest index	No. of pods per plant	No.of seeds per pod	100 seed weight
Reps. in environment	20	3.18	0.35	1.47	0.003	140.98	0.012	0.084
Year (Y)	1	185.53**	48.90**	43.93*	0.458**	16016.21**	0.453**	1.679**
Environment (E)	4	437.70**	48.87**	195.48**	0.038**	15769.06**	0.378**	11.979**
Y - E	4	72.39**	8.69**	31.65**	0.003**	3626.83**	0.085**	0.360*
Genotype (G)	33	17.21**	2.08**	12.16**	0.107**	770.31**	1.873**	48.66**
Y - G	33	3.33**	0.49**	1.62**	0.004**	153.66**	0.121**	0.218**
G - E	132	1.67**	0.186**	1.04**	0.004**	81.80**	0.043**	0.195**
Y - E - G	132	0.98	0.188**	0.48	0.003**	77.52**	0.030**	0.072**
Pooled error	660	0.80	0.11	0.41	0.002	44.58	0.021	0.031

*, ** Significant at 0.05 and 0.01 level of probability, respectively.

Table 14 (continued)

Source of variance	D.F	Plant height	No. of branches per plant	Time to flowering	Time to maturity	Seed protein content	Cooking time	Dehulling
Reps. in environment	20	64.74	21.05	2.02	20.17	2.47	3.77	77.91
Year (Y)	1	3093.64**	507.72**	171307.01**	123895.39**	342.60**	284.71**	388212.27**
Environment (E)	4	7302.13**	1359.06**	10322.98**	16376.14**	168.21**	1516.62**	8679.65**
Y - E	4	620.39**	587.44**	3281.79**	5787.80**	112.59**	87.70**	3525.87**
Genotype (G)	33	337.39**	65.56**	1249.94**	1172.19**	34.15**	1529.32**	1668.59**
Y - G	33	29.94**	16.30**	41.54**	48.80**	3.94**	23.96**	706.84**
G - E	132	16.67**	8.10**	9.31**	13.32**	1.68**	14.97**	194.97**
Y - E - G	132	13.17**	5.0**	10.41**	12.64**	1.35**	13.17**	134.26**
Pooled error	660	7.28	2.97	0.90	2.86	0.42	1.56	35.05

Table 15 Estimates of phenotypic ($\sigma^2 ph$) and genotypic ($\sigma^2 g$) variance components and ratio of genotype-environment ($\sigma^2 gE$), genotype-year ($\sigma^2 gy$) and genotype-environment-year ($\sigma^2 gEy$) to phenotypic variance for 14 lentil characters

Character	$\sigma^2 ph$	$\sigma^2 g$	$\frac{\sigma^2 gE/E}{\sigma^2 ph}$	$\frac{\sigma^2 gy/y}{\sigma^2 ph}$	$\frac{\sigma^2 gEy/Ey}{\sigma^2 ph}$
Biological yield/plant	0.57	0.44	0.04	0.14	0.01
Seed yield/plant	0.07	0.05	0.00	0.15	0.04
Straw yield/plant	0.41	0.33	0.05	0.09	0.01
Harvest index	0.004	0.003	0.01	0.01	0.01
No. of pods/plant	25.68	20.41	0.01	0.10	0.04
No. of seeds/pod	0.062	0.058	0.01	0.05	0.01
100 seed weight	1.62	1.61	0.00	0.00	0.00
Plant height	11.25	10.13	0.01	0.05	0.02
No. of branches/pl.	1.96	1.54	0.05	0.08	0.04
Time to flowering	41.67	40.32	0.00	0.03	0.01
Time to maturity	5.74	4.09	0.00	0.21	0.06
Seed protein	1.19	1.00	0.06	0.07	0.03
Cooking time	50.98	50.12	0.00	0.01	0.01
Dehulling	55.62	30.05	0.04	0.34	0.06

Table 16 Genotypic range, mean, coefficient of genetic variation (CGV) heritability ($h^2b.s$) and expected genetic advance from selection (GS%) of 14 lentil characters

Character	Genotypic range	Mean	C.G.V	$h^2b.s$	GS%
Biological yield/plant	2.07 - 5.08	3.65	18.2	76.7	32.8
Seed yield/plant	0.77 - 1.61	1.22	18.9	76.4	34.0
Straw yield/plant	1.26 - 4.11	2.43	23.8	82.1	44.4
Harvest index	19.51 - 40.09	34	17.2	95.3	34.5
No. of pods/plant	9.74 - 32.96	22.65	20.0	79.5	36.6
No. of seeds/pod	1.1 - 1.9	1.45	16.6	92.9	32.9
100 seed weight	1.99 - 6.55	4.05	31.4	99.3	64.4
Plant height	25.5 - 41.5	33.22	9.6	90.1	18.7
No. of branches/pl.	5.4 - 11.7	7.42	16.7	78.5	30.5
Time to flowering	117 - 137	126.25	5.0	96.8	10.2
Time to maturity	157 - 178	166.91	1.2	71.3	2.1
Seed protein	22.1 - 26.9	24.73	4.0	83.5	7.6
Cooking time	25.2 - 48.5	36.12	19.6	98.3	40.0
Dehulling	37.2 - 75.0	57.31	9.6	54.0	14.5

respectively. The variance component due to the three interaction effects for pods/plant was represented by 15% overall phenotypic variance, whereas this estimate was only 7% and almost zero (0.7%) for number of seeds/pod and 100 seed weight traits, respectively. These results obviously indicate that number of pods/plant was much more influenced by environment and year effects than the other two characters. 100 seed weight, which was unaffected by environment or year factors, had the highest estimates of coefficient of genetic variation (31.4) and broad sense heritability (99.3%) among the components characters. These high values make the expected genetic advance estimate for this character very high (64.4%). Amongst the other two yield components, the number of pods/plant was more affected by environmental variation (year, environment) than seeds per pod, but both characters had lower heritability and coefficient of genetic variation than 100 seed weight.

Broad sense heritabilities estimated in this study were in agreement with the estimates found by many workers. Broad sense heritabilities of number of pods per plant were 79.8% and 71%, calculated by Pandey et al. (1980) and El-Hady (1983), respectively. Number of seeds per pod had a broad sense heritability value of 73.6 (Muehlbauer, 1974); this value was less than the value estimated in this study. Many researchers have found high broad sense heritability for average seed weight. The heritability values ranged from 91% to 98% (Singh and Singh, 1969; Muehlbauer, 1974; Pandey et al., 1980; El-Hady, 1983 and Erskine et al., 1985). Lal and Chandra (1978) found the genetic advance of number of pods per plant was 32.9%.

1.3 Morphological characters

Plant height and number of branches per plant had wide and narrow ranges among all characters studied, (25.5 - 41.5 and 5.4 - 11.7 respectively). The broad sense heritability was greater for plant height (90.1%) than for number of branches/plant (78.5). The differences in these heritability values were due to the high estimates of interaction variance components in number of branches/plant (17%). This indicates that this character was more influenced by changes in environment and season than plant height. The coefficient of genetic variation was low for plant height (9.6) and moderate for number of branches per plant (16.7) compared with other traits.

Broad sense heritability of plant height was found to be high by Prem Sagar (1980) and El-Hady (1983). Their estimates of heritability were 83% and 85%, respectively. El-Hady (1983) estimated a broad sense heritability of number of branches per plant, in irrigated lentil in Egypt, of 78%, which is equal to the heritability estimate in this study. Estimates of genetic advance for plant height in previous studies varied from 7% to 30% with an average of 18.4% which is comparable with genetic advance calculated for plant height in this study.

1.4 Phenological characters

The ranges of days to 50% flowering and days to maturity characters were 117-137 and 157-178, respectively. The variance component due to genotype-environment effect was very low for both characters. The genotype-year interaction variance component was equal to only 3% of the overall phenotypic variance for time to flowering, whereas this ratio was greater, at 21%, for time to maturity, indicating that this character was much more influenced by seasons than time to flowering. These phenological characters had the lowest coefficient of genetic variation values of all the characters measured. Time to maturity also had a relatively low broad sense heritability (71.3%) and it had the lowest genetic advance estimate (2.1%) among all characters, whereas time to flowering had a higher broad sense heritability (96.8%), but also a low genetic advance percentage of 10.2%.

Singh and Singh (1969) and El-Hady (1983) obtained high values of broad sense heritability for time to flowering, 95.8% and 95% respectively, in agreement with the results in this study. For time to maturity, broad sense heritability ranged from low values of 46% and 59% (Sakar, 1983) to a high estimate of 96% (Prem Sagar, 1980). The heritability estimation of time to maturity in this experiment was within the range of those values. In previous studies, Singh and Singh (1979) and Prem Sagar (1980) reported that the genetic advance of time to flowering was low, again in agreement with this study.

1.5 Seed quality characters

Seed protein content, cooking time and dehulling characters had varied ranges of values. Amongst these characters seed dehulling was the character most influenced by seasons. The genotype-year interaction variance component represented 34% of phenotypic variance for dehulling, whereas this ratio was 7% and 1% for seed protein and cooking time respectively. Accordingly, the broad sense heritability was relatively low for dehulling (54%) and higher for both seed protein (83.5%) and cooking time (98.3%). Low estimates of coefficient of genetic variation were obtained for seed protein and dehulling, but the value was moderate for cooking time. Hence, the expected genetic advance was higher for cooking time (40%) than for seed protein (7.6%) and dehulling (14.5%).

Erskine et al. (1985) found that the broad sense heritability of cooking time (82%) was higher than in protein content (71%), in agreement with the results of this study.

There are highly significant differences among genotypes averaged over the environments for all characters in this study. There were also highly significant genotype-environment interactions which revealed that the performance of the genotypes in this study varied with different water levels. Thus these experiments make it clear that there are opportunities for improving lentil characters by selection within the population.

Estimates of broad sense heritability showed that 100 seed weight, cooking time, time to flowering, harvest index, number of seeds per pod and plant height had high values of >90%. Other characters had moderate heritability values, except dehulling which had the lowest broad sense heritability estimate. The magnitudes and trends of heritability and genetic advance estimates are comparable to those previously reported in lentil.

Heritability is useful for comparing traits with respect to their usefulness as aids to selection. The genetic advance from selection depends on the heritability estimate, the magnitude of phenotypic variance and the proportion selected (Burton, 1952). In order to

determine the validity of selection, expected genetic advance should be obtained.

In addition, Johnson et al. (1955) stated that heritability estimates together with genetic gains are more useful than the heritability values alone in predicting the resultant effect of selecting the best individuals. In this study, time to flowering, which had a very high broad sense heritability (96.8%) had a very low genetic advance (10.2%) because its coefficient of genetic variation was low (5.0). In comparison straw yield per plant, which had a lower heritability (82.1%), had a high genetic advance percentage of 44.4% due to its high coefficient of genetic variation (23.8%).

The 100 seed weight trait was found to be the most heritable and stable character. It was relatively uninfluenced by environment or season and had the highest coefficient of genetic variation, broad sense heritability and genetic advance amongst all characters studied. Also, straw yield per plant and number of pods/plant had moderate values of coefficient of genetic variation with high to moderate values of heritability and high values of genetic advance.

On the basis of the relatively high heritability, coefficient of genetic variation and genetic advance, pronounced progress should be expected from selection for 100 seed weight, straw yield per plant and number of pods/plant. Moderate progress from selection between genotypes should be expected with seed yield per plant, biological yield per plant and harvest index. However lower genetic advance should be expected from selection between genotypes for time to maturity, seed protein and dehulling.

2. Inter-relationships between characters

Associations between plant characters are of value in breeding programs helping in their planning and evaluation. The matrices of both Phenotypic and genotypic correlation coefficients between 14 lentil characters are presented in Table 17.

In general, the genetic correlation coefficients were slightly higher than, but in the same sign as, the corresponding phenotypic coefficients indicating that significant phenotypic correlations were largely due to genetic causes. Many reports provide evidence of the comparatively higher value of genotypic than phenotypic correlations (Singh and Singh (1969) and Singh et al. (1970) in lentil and Johnson et al. (1955) in soybean).

Throughout the remainder of this section references will be made to genotypic correlations in order to avoid unnecessary repetition.

Seed yield per plant correlated positively and significantly with harvest index, number of pods/plant, 100 seed weight and cooking time, but was negatively and significantly correlated with number of seeds/pod. The correlation coefficient values between seed yield and other traits were low in magnitude and non-significant. The correlations between seed yield and each of the following characters, straw yield/plant, plant height and time to flowering were intermediate in magnitude and non-significant, but may be referred to as positive relationships.

The positive correlations between seed yield per plant and harvest index and number of pods/plant are comparable to those previously reported for lentil. Tejinder Singh (1977) found a strong positive correlation between seed yield per plant with harvest index, and Singh and Singh (1969), and Tikka et al. (1973) reported that number of pods per plant is one of the most important components determining seed yield per plant in lentil.

A positive correlation between seed yield per plant and seed weight has been found in lentil by Singh and Singh (1975) under Indian conditions and also by El-Hady (1983) in irrigated lentil under

Table 17 Phenotypic (rph) and genotypic (rg) correlations for 14 lentil characters grown under different water supply in two seasons

		Seed yield/ pl.	Straw yield/ pl.	Harvest index	No.of pods/ pl.	No.of seeds/ pod	100 seed weight	Plant height	No.of branches/ pl.	Time to fl.	Time to mat.	Protein	Cooking time	Dehulling
Biological yield/plant	rph	0.57**	0.94**	-0.46**	0.13	-0.64**	0.65**	0.72**	0.27	0.54**	0.68**	0.46**	0.56**	0.44**
	rg	0.55	0.94	-0.51	0.06	-0.70	0.70	0.77	0.26	0.57	0.74	0.53	0.60	0.50
Seed yield/plant	rph		0.25	0.44**	0.67**	-0.47**	0.41*	0.24	0.07	-0.27	-0.10	-0.01	0.37*	0.15
	rg		0.23	0.45	0.65	-0.51	0.42	0.27	0.04	-0.29	-0.12	-0.02	0.41	0.20
Straw yield/plant	rph			-0.76**	-0.13	-0.54**	0.60**	0.75**	0.32	0.76**	0.84**	0.55**	0.49**	0.45**
	rg			-0.78	-0.19	-0.59	0.63	0.78	0.32	0.80	0.91	0.64	0.53	0.50
Harvest index	rph				0.59**	0.18	-0.31	-0.58**	-0.22	-0.91**	-0.88**	-0.57**	-0.23	-0.28
	rg				0.62	0.19	-0.32	-0.63	-0.24	-0.96	-0.93	-0.61	-0.24	-0.34
No.of pods/plant	rph					-0.12	-0.27	-0.13	0.17	-0.33	-0.35*	-0.15	-0.26	-0.04
	rg					-0.11	-0.29	-0.15	0.18	-0.37	-0.40	-0.18	-0.27	-0.04
No.of seeds/pod	rph						-0.83**	-0.53**	0.24	-0.24	-0.42*	-0.16	-0.41*	-0.35*
	rg						-0.85	-0.56	0.28	-0.24	-0.44	-0.19	-0.45	-0.37
100 seed weight	rph							0.59**	-0.26	0.26	0.48**	0.17	0.95**	0.35*
	rg							0.61	-0.29	0.27	0.49	0.18	0.96	0.37
Plant height	rph								-0.11	0.62**	0.74**	0.52**	0.54**	0.34*
	rg								-0.17	0.65	0.80	0.58	0.56	0.36
No.of branches/plant	rph									0.37*	0.20	0.23	-0.33	0.09
	rg									0.40	0.21	0.26	-0.38	0.10
Time to flowering	rph										0.92**	0.59**	0.19	0.24
	rg										0.95	0.63	0.20	0.27
Time to maturity	rph											0.59**	0.40*	0.35*
	rg											0.64	0.42	0.40
Protein	rph												0.15	0.14
	rg												0.17	0.19
Cooking time	rph													0.25
	rg													0.27

Egyptian conditions. However, some other researchers found negative or no correlation between both characters (Singh and Singh, 1969; Singh et al., 1970; Muehlbauer, 1974 and Tejinder Singh, 1977) in lentil. An explanation of the significant and positive correlation between seed yield and 100 seed weight obtained in the present study should be attempted. The 34 genotypes in this study can be divided, on the basis of 100 seed weight, overall environments and years, into four groups; (1) 100 seed weight less than 3g (7 genotypes), (2) 3.1 - 4g (9 genotypes), (3) 4.1 - 5g (11 genotypes) and (4) above 5.1g (7 genotypes). These four groups produced average seed yield/plant of 0.90, 1.27, 1.37 and 1.27g respectively. The average numbers of pods/plant for these groups were: 22, 24, 23 and 18 respectively. These data indicate that the increase of 100-seed weight increased number of pods/plant and thus seed yield for the first three groups. In comparison, low yield in group 4 was due to fewer pods/plant and fewer seeds/pod in relation to the large seeded types (above 5.1g/100 seeds). Consequently, a significant and positive correlation between seed yield and seed weight occurred in this study, but it was not high in magnitude.

The positive and significant correlations between seed yield and both 100-seed weight and number of pods/plant, in addition with the high heritabilities of these traits, suggests the use of these two characters in indirect selection for seed yield.

In order to compare the efficiency of indirect selection through selection for 100 seed weight or for number of pods/plant, the ratio of expected response was calculated according to the following formula suggested by Falconer, 1981; $CR_x/R_x = rg_{xy}/(ixhx/iyhy)$, where R_x is the direct response of the seed yield, if the selection was applied directly to it, and CR_x is the correlated response of the seed yield/plant resulting from selection applied to the other trait, rg_{xy} is the genotypic correlation coefficient between seed yield and the other trait, ix and iy are the respective intensities of selection for yield and the other trait, hx and hy are the respective heritabilities for yield and the other trait.

The ratio was 0.55 if indirect selection was applied to 100-seed weight, whereas it was 0.69 if selection was performed on number of pods/plant. These results indicate that improving seed yield by selection for pods per plant should be more efficient than selection for seed weight. Malhotra et al. (1973) also reported that maximum weight should be given to pod number and cluster number during selection for high yielding lines in lentil. It should be mentioned, however, that counting the number of pods on a plant is a more laborious operation than measuring its seed yield.

Biological yield and straw yield/plant shows similar relationships with other characters. Both traits had strong positive correlations with 100 seed weight, plant height, time to flowering, time to maturity, protein, cooking time and dehulling per cent and strong negative correlations with harvest index and number of seeds/pod. The correlation coefficient between straw and biological yield/plant was 0.94, unsurprisingly high in view of the fact that most of the biological yield is straw.

Although the correlation between seed yield and straw yield was not significant, it was positive and was 0.25 and 0.23 for phenotypic and genotypic correlation respectively, revealing that it is possible to select for high seed yield and straw yield plants. Erskine (1983) found the genotypic correlation between seed yield and straw yield was 0.76.

The relationships among the three yield components, number of pods/plant, 100 seed weight and number of seeds/pod, showed no association between number of pods/plant with either of the other components. Moreover, there was a strong negative correlation between 100 seed weight and number of seeds/pod. These results indicate that it would be difficult to achieve a response to selection for high levels of these two characters simultaneously.

Number of pods per plant was correlated negatively with time to flowering, indicating the possibility of selecting for earliness and high number of pods. Singh and Singh (1969) also found strong negative correlation between time to flowering and number of pods per plant. Number of seeds per pod showed significant negative correlations with

plant height, time to maturity, cooking time and seed dehulling percent. Basant et al. (1983) also found negative correlation between seeds/pod and time to maturity, and seeds/pod was unrelated with most other characters. 100 seed weight was strongly correlated with cooking time, plant height, time to maturity and dehulling. These results agreed with those previously reported in lentil.

Number of branches per plant (primary and secondary branches) was only correlated, negatively, with harvest index and 100 seed weight. Its correlation coefficient with seed yield/plant was very low in magnitude. Tejinder Singh (1977) found that number of primary and secondary branches had negative direct effects on seed yield. She observed that a bushy plant type results in relatively more plant dry matter than seed yield, and hence lower harvest index. She suggested it would thus be desirable to develop varieties with less branching to allow better light penetration through the plant canopy for good pod formation. In the present investigation, the results indicate that it is possible to select for high seed yield/plant with a reduced number of branches/plant.

Some other correlations were positive and relatively large. These were: plant height with time to flowering, time to maturity, protein, cooking time and dehulling. Also, time to flowering and time to maturity were strongly correlated together and both characters were positively correlated with protein.

No relationship was detected between seed quality characters, protein, cooking time and dehulling, but high biological yield and straw yield per plant correlated positively and significantly with these traits.

The similarity in the signs and magnitudes of phenotypic and genotypic correlations indicated that visual selection of characters positively correlated with seed yield was of value in identifying high yielding genotypes.

The results suggested that selection for medium-large seeded genotypes and high number of pods per plant would be an efficient method for improving seed yield.

3. Exploitation of the genetic variation in response to irrigation

The combined analysis of variance (Table 14) showed that all sources of variance were highly significant, indicating the importance of genotype, year, environment and genotype-environment and genotype-year interactions as factors affecting the lentil under different water supply regimes. The relative size of the variance due to these various factors differed from trait to trait.

In this section, the variation due to each factor and its effect on different lentil characters will be presented to direct a lentil breeding programme for response to irrigation.

3.1 Variation between genotypes

As the results in Table 14 showed there were highly significant differences among the genotypes, for all characters, when tested against pooled error, and when tested against genotype-environment and genotype-year interactions. These results confirmed the presence of substantial differences among genotypes for all characters.

The average performances of the 34 genotypes, over all environments and years, for 17 lentil characters are given in Table 18.

The average seed yield over all genotypes, environments and years was 1707 kg/ha. The highest yielding genotypes were FLIP84-67L, ILL241 and FLIP84-27L with no significant differences between them, followed by 74TA264. These genotypes have average 100 seed weights between 4 to 5g. In comparison, the lowest seed yield was obtained from genotypes, ILL1983, Pant.L,406 and ILL2573, which have 100 seed weight of less than 2g. Indeed no small seeded genotypes (less than 2g/100 seeds) showed superiority of seed yield (kg/ha). However, several large seeded genotypes also produced low yield, such as Okula (6.04g/100 seed) which yielded 1099.3kg/ha.

The high yielding genotypes showed also high biological and straw yield. ILL241, 74TA264 and FLIP84 — 67 L gave the highest biological yield of above 6100 kg/ha. The average harvest index for these

Table 18 The overall means of 34 genotypes evaluated in 5 environments in two seasons

Genotype	Seed yield kg/ha	Biological yield kg/ha	Straw yield kg/ha	Seed yield /plant	Biological yield/plant	Straw yield /plant	Harvest index	Pods /plant
Giza 9	1855.24	5430.46	3575.22	1.33	3.85	2.52	0.36	24.82
Family 130	1432.53	5046.36	3613.84	1.14	4.00	2.85	0.29	29.05
Selaim	1793.41	5306.85	3513.44	1.08	3.15	2.08	0.35	19.45
ILL 1693	1283.41	3257.66	1974.26	0.90	2.31	1.41	0.39	19.01
ILL 1983	1071.97	2890.19	1818.22	0.76	2.07	1.31	0.38	19.44
ILL 40	1842.29	5214.23	3371.95	0.23	3.48	2.25	0.36	21.71
ILL 241	2242.41	6492.57	4250.15	1.46	4.21	2.75	0.35	32.96
SLL,ILL 4400	2080.39	6007.41	3927.02	1.61	4.53	2.93	0.36	23.03
SLS,ILL 4401	1769.83	4970.83	3201.0	1.23	3.42	2.19	0.36	23.04
Jord. Loc.	2010.32	5340.0	3329.69	1.51	3.97	2.45	0.38	27.80
76TA66005	2143.80	5597.87	3454.07	1.46	3.77	2.32	0.38	25.28
78S26003	1956.07	4960.37	3004.30	1.36	3.41	2.05	0.40	29.11
78S26004	2025.04	5403.70	3378.67	1.50	4.02	2.53	0.39	29.93
76TA66088	2153.26	5724.36	3571.09	1.43	3.77	2.34	0.38	27.01
ILL 857	2135.33	5703.52	3568.19	1.48	3.93	2.45	0.38	25.29
Laird	1242.13	577.32	4528.20	1.01	4.69	3.67	0.21	14.38
ILL 121	1362.93	5358.66	3995.73	0.99	3.84	2.85	0.27	23.70
74TA 161	1018.66	5373.15	4354.49	0.97	5.08	4.11	0.20	14.55
Lenka	1282.12	4580.05	3297.93	0.95	3.36	2.41	0.28	16.52
Okula	1099.30	5268.20	4168.91	0.77	3.75	2.98	0.20	9.74
74TA 276	2001.92	5536.62	3534.70	1.53	4.18	2.65	0.37	24.47
74TA 212	1614.90	5655.31	4040.41	1.29	4.38	3.09	0.28	24.68
ILL 274	1603.89	5628.12	4024.24	1.18	4.07	2.89	0.28	23.53
ILL 355	1308.39	4880.19	3571.80	1.01	3.72	2.71	0.27	14.28
ILL 358	1844.19	4655.82	2811.63	1.27	3.19	1.92	0.40	25.51
Precoz	1527.55	3929.91	2402.36	1.22	3.11	1.89	0.39	16.69
Pant.L,406	1144.60	2929.80	1785.21	0.82	2.07	1.26	0.40	22.38
ILL 2526	1352.32	3423.96	2071.64	0.88	2.25	1.37	0.39	21.30
ILL 2573	1150.46	3046.06	1895.60	0.77	2.07	1.29	0.38	20.68
74TA264	2138.39	6242.78	4104.40	1.51	4.35	2.84	0.34	23.32
FLIP 84,1-L	1970.81	5728.29	3757.48	1.35	3.91	2.56	0.34	23.77
FLIP 84,27-L	2200.66	5851.27	3650.62	1.49	3.96	2.47	0.38	26.07
FLIP 84,67-L	2349.17	6163.33	3814.17	1.50	3.97	2.46	0.38	27.18
FLIP 84,78-L	2015.87	5593.52	3577.65	1.48	4.09	2.61	0.36	20.35
SE±	84.52	208.39	156.62	0.09	0.23	0.16	0.01	1.72

Table 18 (Continued)

Genotype	Seeds /pod	100 seed weight	Plant height	Branches /plant	Days to flow.	Days to mat.	Seed protein content	Cooking time	Dehulling
Giza 9	1.67	3.33	31.88	9.54	125.30	165.77	24.57	29.43	53.91
Family 130	1.67	2.43	37.67	7.25	137.07	174.71	25.87	27.49	52.02
Selaim	1.73	3.30	31.04	8.41	125.13	164.30	24.96	31.70	56.24
ILL 1693	1.73	2.76	28.65	7.20	118.40	156.30	24.27	27.14	53.99
ILL 1983	1.85	2.13	26.26	6.64	119.63	158.14	23.23	27.22	52.86
ILL 40	1.68	3.46	31.67	8.52	125.10	164.94	24.55	31.74	57.66
ILL 241	1.13	4.09	31.99	9.39	128.37	168.61	24.37	33.24	59.58
SLL,ILL 4400	1.11	6.55	35.82	7.74	126.33	168.93	24.48	48.63	69.07
SLS,ILL 4401	1.67	3.29	31.58	8.18	124.50	164.47	24.86	32.53	57.46
Jord. Loc.	1.31	4.28	33.40	7.01	123.00	164.53	24.27	36.47	56.12
76TA66005	1.37	4.30	33.09	6.23	120.03	165.47	23.28	36.93	63.03
78S26003	1.06	4.48	32.66	6.20	123.00	164.13	23.96	41.37	56.31
78S26004	1.07	4.76	31.59	7.52	122.40	163.97	24.28	40.33	64.68
76TA66088	1.44	3.68	34.18	6.72	123.37	162.49	25.81	33.75	49.60
ILL 857	1.37	4.39	33.12	6.95	122.27	165.17	24.39	38.17	58.89
Laird	1.10	6.37	41.50	6.20	136.16	176.92	24.55	47.07	75.04
ILL 121	1.61	2.65	35.22	9.54	134.20	173.36	25.94	25.98	61.17
74TA 161	1.56	4.23	33.38	11.69	139.50	178.26	26.45	35.23	60.57
Lenka	1.42	4.08	38.41	5.38	130.99	173.55	26.94	39.33	53.51
Okula	1.29	6.04	36.04	5.88	137.43	177.50	25.39	46.53	55.26
74TA 276	1.16	5.48	32.45	7.57	124.00	166.24	25.37	46.82	51.59
74TA 212	1.42	3.59	35.18	10.27	136.20	174.44	26.45	34.64	64.77
ILL 274	1.40	3.58	35.24	9.71	135.30	173.97	26.19	33.03	62.32
ILL 355	1.22	5.83	35.43	6.06	134.37	176.00	25.72	46.83	55.91
ILL 358	1.69	3.02	32.90	6.93	122.23	162.87	24.26	37.03	55.54
Precoz	1.52	4.97	30.86	7.05	116.53	159.02	24.77	45.07	50.26
Pant.L,406	1.80	2.07	26.78	6.17	119.40	160.37	23.28	26.07	53.55
ILL 2526	1.85	2.28	31.38	6.76	122.20	158.37	24.06	25.24	37.22
ILL 2573	1.88	1.99	25.52	6.90	119.20	156.79	22.12	25.37	56.51
74TA264	1.15	5.82	36.85	6.62	126.80	168.69	24.24	45.50	72.85
FLIP 84,1-L	1.53	3.83	34.24	8.14	128.87	167.73	23.54	36.02	41.32
FLIP 84,27-L	1.34	4.41	33.13	6.04	120.47	163.79	25.27	35.77	58.33
FLIP 84,67-L	1.30	4.38	33.64	5.99	119.93	163.13	25.32	37.81	59.46
FLIP 84,78-L	1.32	5.70	36.81	5.81	124.70	172.03	23.73	42.50	61.91
SE±	0.04	0.05	0.70	0.45	0.25	0.44	0.17	0.32	1.53

genotypes ranged from 34-38%. The genotypes 78S26003, ILL358 and Pant.L,406 gave the highest harvest index ratios, of 40%, among all lines, but their yields were not high. In comparison, Laird, 74TA161 and Okula gave the lowest harvest index ratios of 20-21% and, therefore, produced the highest straw yield (kg/ha). These genotypes showed the same trend for their per plant seed, biological and straw yields as in their yield per unit area (Table 18).

The average seed yields and straw yields (kg/ha) in this study were higher than those previously reported in lentil. The mean seed yield and straw yield of 24 genotypes grown in Tel Hadya (Syria) and Terbol and Kfardan (Lebanon) were 1223 kg/ha and 3166 kg/ha, respectively (Erskine,1983), compared to 1707 and 3381 kg/ha in this study.

Genotype ILL241 exhibited the highest number of pods per plant (33 pods) among all genotypes. In comparison, Okula and Laird produced 9 and 14 pods/plant and ranked last. The average number of pods/plant in this study was 23 pods. This mean value with the overall mean of seed yield/plant in this study was lower in magnitude than those found in the literature. This was due to the fact that the estimation of those traits in this study was done on crop density, and not on the basis of individual spaced plants as in most previous studies in lentil.

The genotypes varied widely in plant height, number of branches per plant, time to flowering and time to maturity as showing by their mean values presented in Table 18.

The overall mean of seed protein content was 24.7% giving a protein yield of 422 kg/ha. There were consistent differences between genotypes in protein content, but only a small range of 22.1 to 26.9%. Four lines exhibited a protein percentage above 26%, these being 74TA161, Lenka, 74TA212 and ILL274. Erskine et al. (1985) also found differences between lentil genotypes for protein content and these averaged 27% with 330 kg/ha protein yield.

The overall mean time for cooking was 36.1 minutes. The large seeded genotypes took a longer time to cook than small seeded entries. Laird and ILL4400 which had the highest seed weight took the longest time to cook, with 47.1 and 48.6 minutes respectively. In contrast, the quickest genotypes to cook were small seeded entries such as ILL2526 (25.2 min.). These results agreed with those of Erskine et al. (1985).

The results in Table 18 showed consistent differences between genotypes in dehulling percent. In general the large-seeded genotypes dehulled more easily than small seeded ones and thus large seeded lines had higher dehulling percent values. However, there were consistent differences between genotypes within each group. For example, in the large seeded group, Laird and 74TA264 had average seed weights of 6.37 and 5.82g/100 seeds respectively and exhibited dehulling percentage of 75 and 73%. In comparison, ILL355 and Okula also had high 100 seed weight of 5.83 and 6.04g, but their dehulling percentages were only 56 and 55%. Similar differences were observed in small seeded genotypes; ILL121 (2.65g/100 seed) exhibited 62% dehulling seeds, while ILL2526 (2.28g/100 seed) showed a dehulling percentage of only 37% and was the lowest recorded value among all genotypes.

These results confirmed that there were intergenotypic differences in the ease of removing the seed coat and splitting the seed into its dicotyledonous components (dehulling). The degree to which seeds are able to resist splitting is at least partly related to seed morphology and anatomy (Reichert et al., 1984). The very poor dry-dehulling characteristic of some cowpea varieties was observed by Dedah and Stanley (1979a, b), who suggested that varieties with thick, smooth seed coats (highly organized palisade cells) dehulled more satisfactorily than those with thin, rough seed coats (amorphous seed coat structure). Reichert et al. (1984) observed that a black-eyed cowpea which had somewhat thicker seed coat also had a higher dehulling efficiency than did the brown cowpea variety. Another relevant morphological aspect is the large cavity between the cotyledons of kidney beans (Bourne, 1967), probably responsible for the total splitting of the seeds of this crop during dehulling (Reichert et al., 1984).

It is worthwhile noting that ILL2526, which had the lowest dehulling percent among all genotypes in this study, is a black seed coat genotype. Because lentils with black seed coats are generally high in tannin content (Vaillancourt and Slinkard, 1983), consequently the high content of tannins may have caused difficulty in removal of the seed coat.

In general the results indicated that the genotypes differed significantly in seed yield and all other characters, reflecting the presence of wide genetic diversity under different water supply regimes. These results, with the high genotypic variance for seed yield, allow selection for higher-yielding genotypes under irrigation.

3.2 Seasonal effects

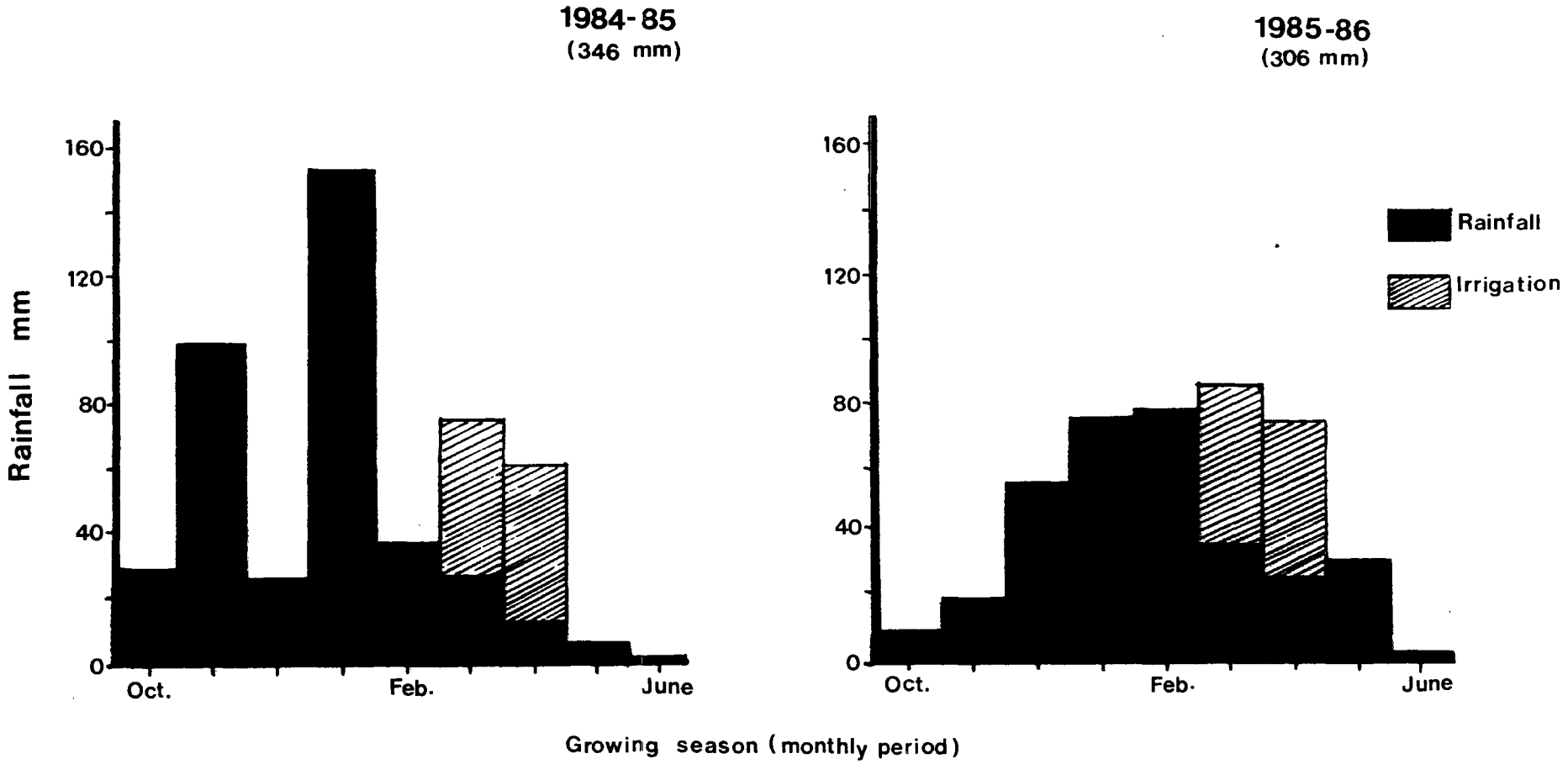
Rainfall and air temperature and their distribution during the crop growth periods of 1984-85 and 1985-86 seasons at the three locations are presented in Figures 1 and 2. The mean performance for 17 lentil characters, over all genotypes and environments are given in Table 19. The mean performances, over all genotypes, for all characters at the five environments in these two seasons are shown in Table 20.

In general, the mean performances decreased in the second season for all characters, except plant height, time to flowering, time to maturity and cooking time (Table 19). These revealed that the growth conditions were more favourable in the first season.

The season 1984-85 was wetter at all sites than the following season with 373 and 316mm rain received in the two seasons respectively in Tel Hadya. Terbol and Breda received 433 and 253mm of rainfall in the first season, whereas in the same period in the second season they received 358 and 203mm of rain respectively (Figure 1). Consequently the yield characters, as well as most of the other characters, decreased in the second season in Tel Hadya and Breda, but not in Terbol. For example, seed yields at Breda and Tel Hadya (unirrigated) were 599 and 2195 kg/ha in 1984-85 (Table 20), but in the following season the trial means had dropped to 531 and 1931 kg/ha respectively, representing declines in yield of 11 and 12%.

Seed yield (kg/ha) was closely related to seed yield/plant. Except, in the second season, at Terbol where there was the highest seed yield/plant, but a lower seed yield (kg/ha) than in Tel Hadya. This was due to low number of plants/plot at Terbol, resulting from an early dry spell of 18mm after sowing (during November 1985) compared with 70mm during November 1984 (Figure 1) which reduced germination.

Although biological yield (kg/ha) was not affected significantly by season, harvest index decreased in the second season because of the increase of straw yield and decrease of seed yield (kg/ha) (Table 19).



Tel- Hadya

Figure 1 . Distribution of rainfall during growing seasons in Tel-Hadya, Terbol and Breda

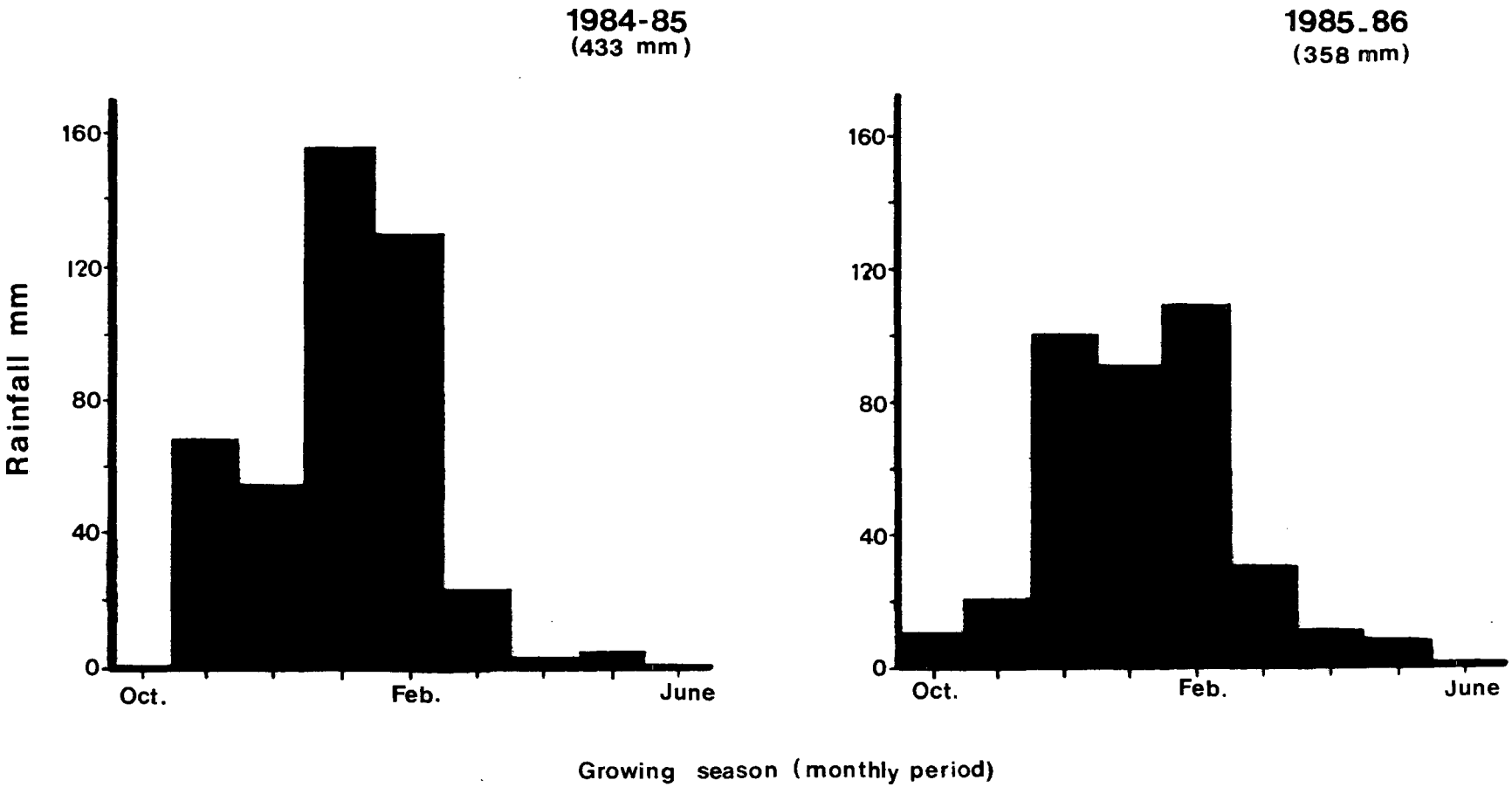


Figure 1. Continued

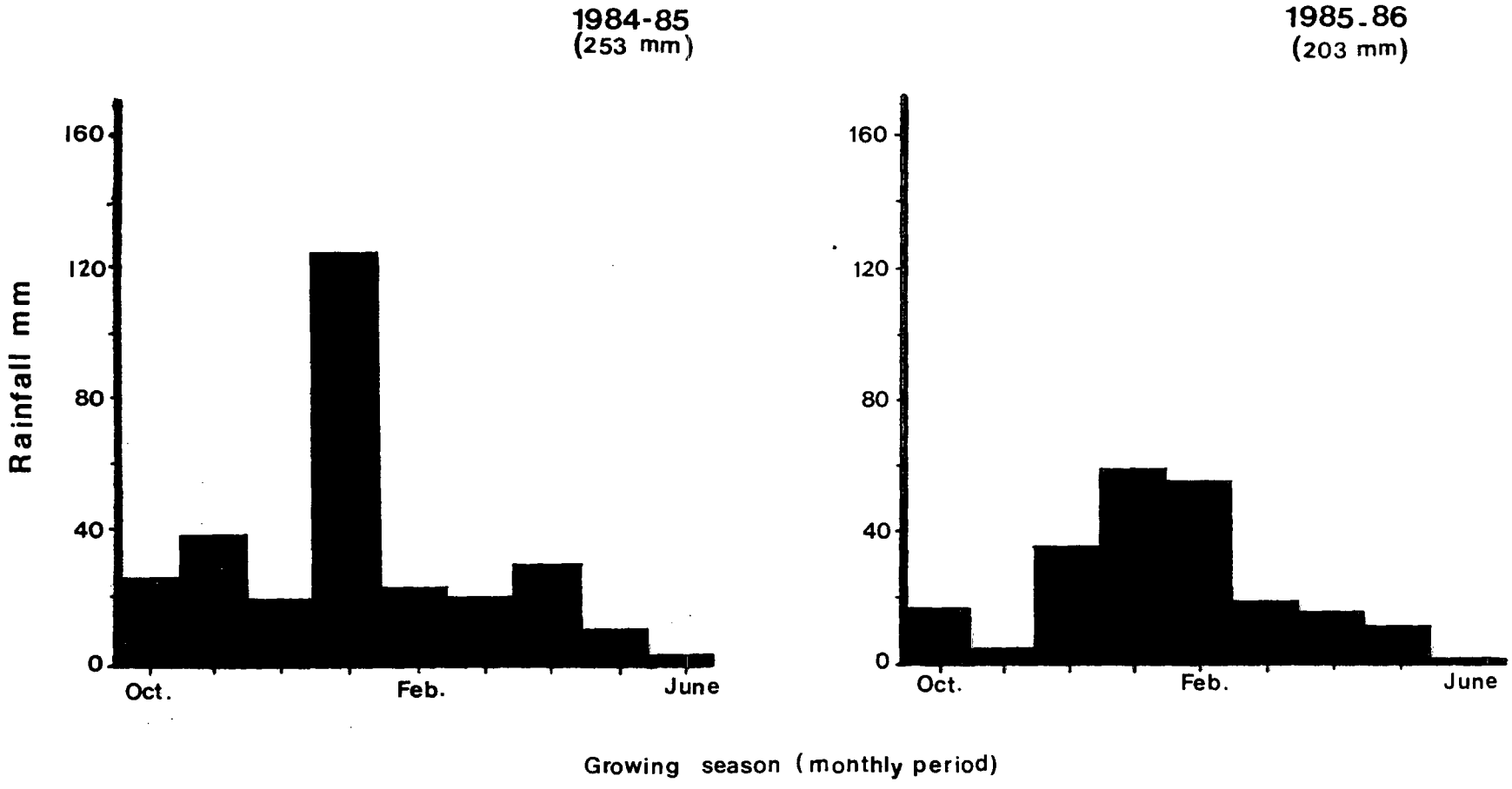


Figure 1 Cohtinued

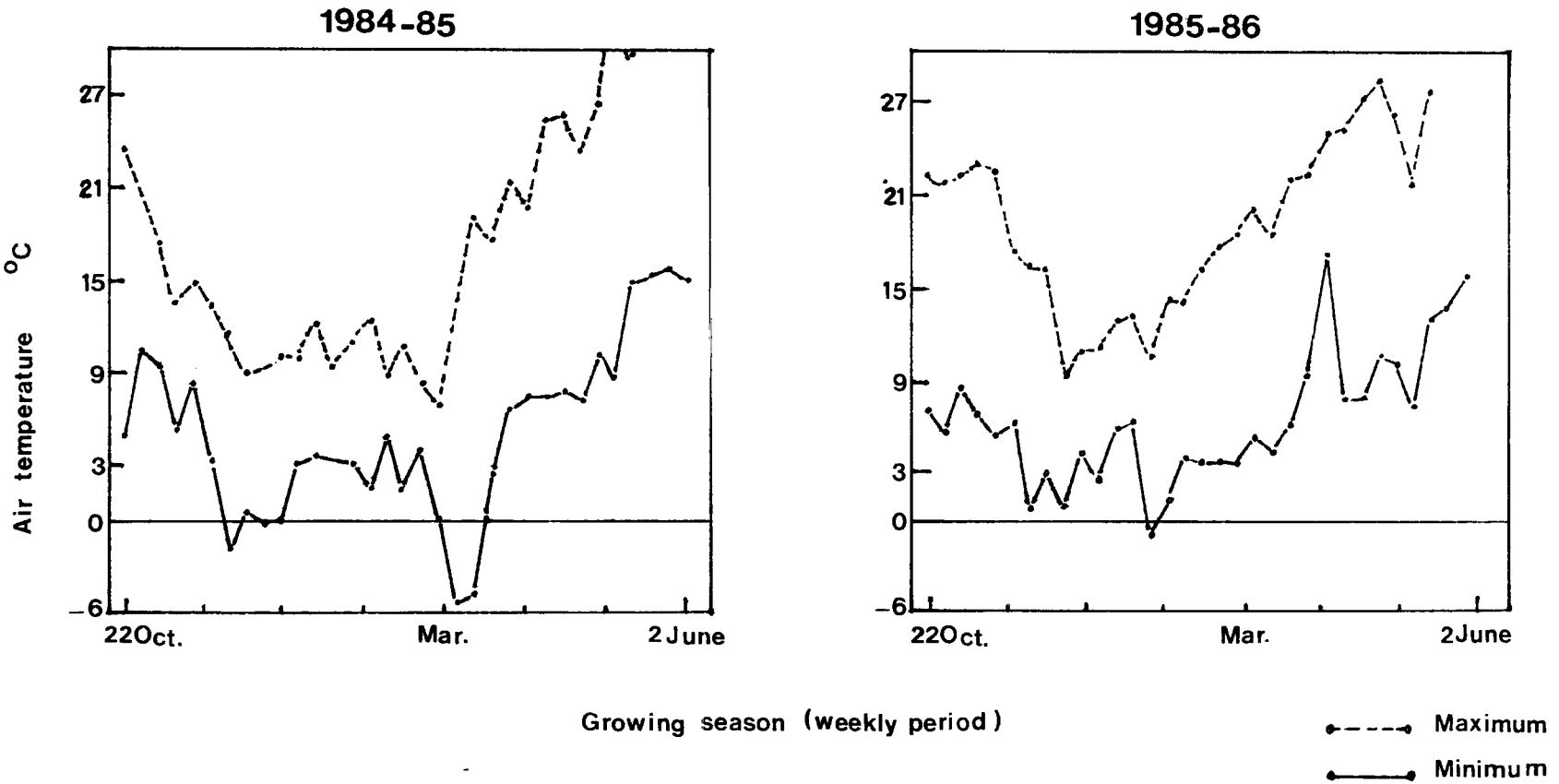


Figure 2. Variation in air temperature during growing seasons in Tel Hadya, Terbol and Breda

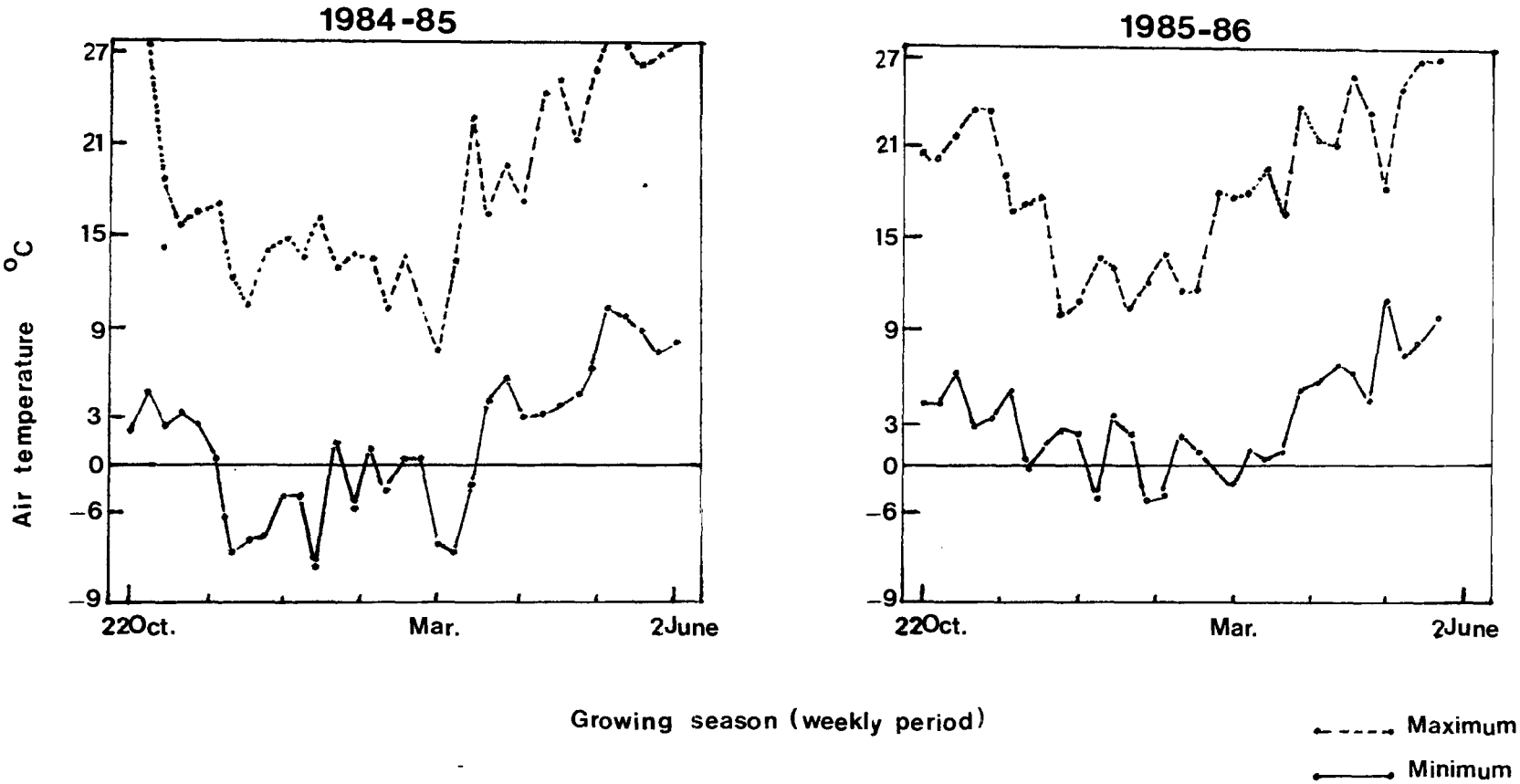


Figure 2. Continued

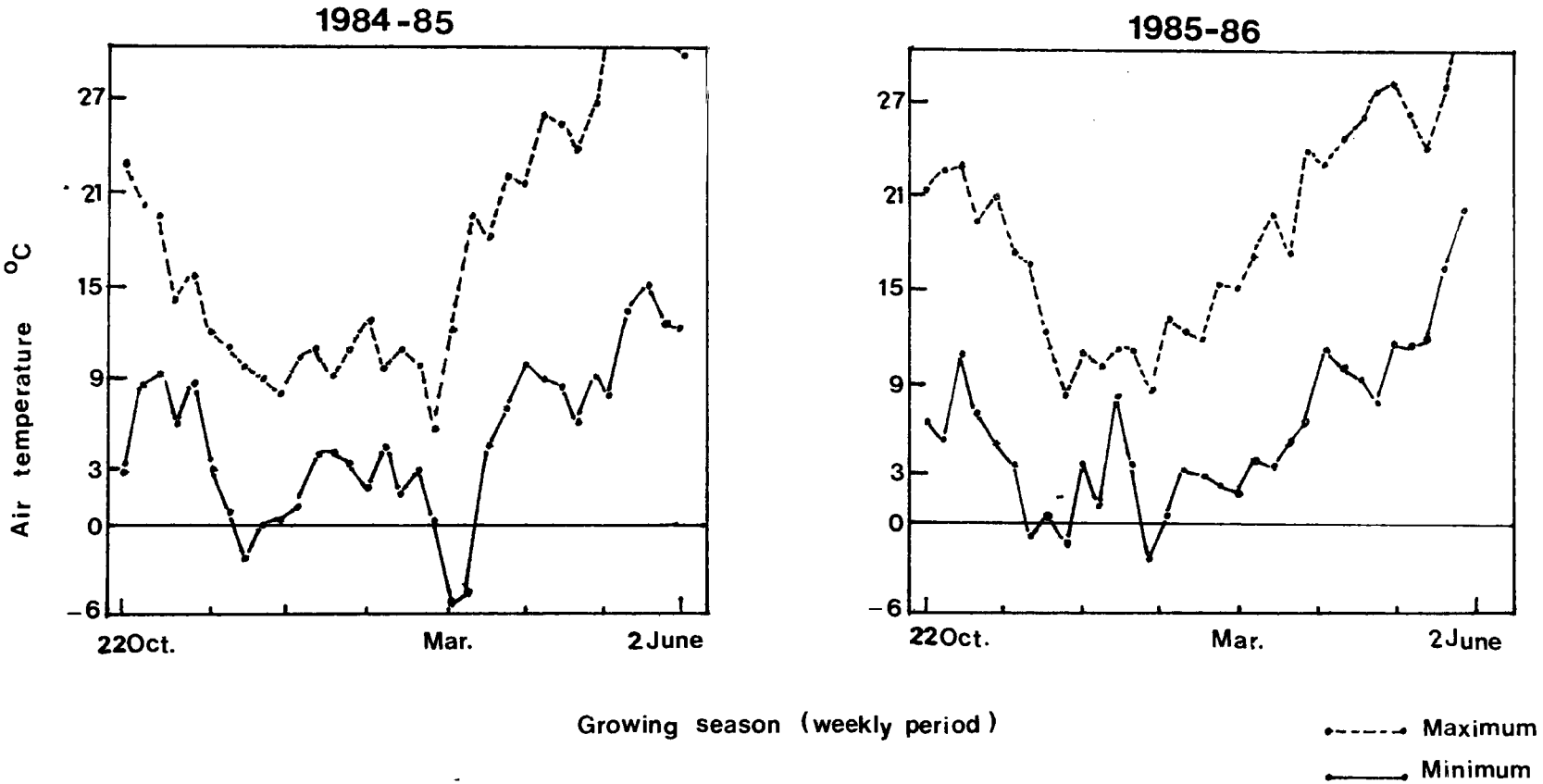


Figure 2. Continued

Table 19 Seasonal effect on the performance of 17 lentil characters over all genotypes and environments

Character	1984-85	1985-86	SE±
Seed yield kg/ha	1797.17	1615.98	109.07
Biological yield kg/ha	5018.39	5155.83	305.30
Straw yield kg/ha	3221.22	3539.85	198.38
Seed yield/plant	1.44	1.00	0.05
Biological yield/plant	4.07	3.22	0.17
Straw yield/plant	2.63	2.22	0.11
Harvest index	36	32	0.3
Number of pods/plant	26.6	18.7	0.95
Number of seeds/pod	1.43	1.47	0.01
100-seed weight	4.1	4.0	0.01
Plant height	31.5	35.0	0.21
Number of branches/plant	8.1	6.7	0.35
Time to flowering	139.2	113.3	0.07
Time to maturity	177.9	155.9	0.35
Seed protein content	25.3	24.2	0.13
Cooking time	36.7	35.6	0.10
Dehulling	76.8	37.8	0.41

Table 20 The overall means for 17 characters of lentil grown at five environments in two seasons

Character	1984 - 85 season					1985 - 86 season					Overall mean	SE± *	
	Tel Hadya			Terbol (Ter)	Breda (Br)	Tel Hadya			Terbol (Ter)	Breda (Br)		A	B
	T_1	T_2	T_3			T_1	T_2	T_3					
Seed yield kg/ha	2195	2325	2809	1057	599	1938	2011	2124	1476	532	1706.57	90.63	135.89
Biological yield kg/ha	6042	6526	7880	3051	1593	5828	6457	6744	5108	1642	5087.11	274.09	391.54
Straw yield kg/ha	3847	4202	5070	1994	993	3891	4446	4620	3632	1111	3380.54	191.66	262.18
Seed yield/plant	1.66	1.81	2.12	1.17	0.44	1.10	1.13	1.19	1.23	0.35	1.22	0.08	0.09
Biological yield/plant	4.64	5.14	5.97	3.42	1.19	3.33	3.65	3.81	4.23	1.07	3.65	0.24	0.27
Straw yield/plant	2.98	3.33	3.85	2.25	0.75	2.23	2.52	2.62	3.01	0.72	2.43	0.16	0.19
Harvest index	36.7	35.7	36.4	34.4	37.3	33.8	31.6	32.0	29.3	32.7	34.00	0.9	0.8
No. of pods/plant	30.9	32.9	37.8	23.6	7.9	19.9	20.5	20.1	26.5	6.4	22.65	1.66	1.77
No. of seeds/pod	1.43	1.47	1.45	1.43	1.37	1.51	1.53	1.50	1.40	1.43	1.45	0.01	0.02
100-seed weight	4.08	4.04	4.20	3.75	4.37	4.01	3.96	4.25	3.59	4.22	4.05	0.04	0.04
Plant height	33.8	35.5	36.9	28.4	22.8	36.5	40.6	37.2	37.6	23.5	33.22	1.20	1.09
No. of branches/plant	10.1	10.5	11.2	5.2	3.6	7.1	7.6	7.0	7.4	2.3	7.42	0.62	0.66
Time to flowering	135.1	137.2	137.1	146.9	139.7	110.6	112.8	112.3	130.1	100.7	126.25	0.18	0.18
Time to maturity	172.4	174.8	177.9	188.1	176.4	153.8	156.9	161.1	172.3	135.4	166.91	0.59	0.63
Seed protein content	26.30	26.26	25.55	22.60	25.83	24.75	24.80	23.50	24.04	23.66	24.73	0.20	0.22
Cooking time	37.17	36.74	38.94	31.36	39.01	34.76	35.81	38.62	32.03	36.73	36.12	0.29	0.28
Dehulling	80.68	78.40	75.88	65.88	83.25	36.41	34.07	29.37	36.81	52.34	57.31	1.33	1.26

* SEA, Standard error to compare environments in the same level of year.
SEB, Standard error to compare years in the same level of environment.

Interestingly, however, the rainfall distributions of the two years differed with only 14mm being received during April to May 1985 (Figure 1), in contrast to 52mm in the corresponding period in the following year at Tel Hadya, with the result that irrigation during this pod-filling period led to a response in yield of 28% in 1984-85 and a lower response of only 10% in 1985-86.

The 1984-85 season was colder than the following season at all locations (see Figure 2). This resulted, in general, in less vegetative growth as indicated by average plant height of 31.5cm in the first season comparing with 35cm in the second season (Table 19). However, at Tel Hadya and Breda, in 1984-85, the temperature was below zero for only about two weeks during the end of vegetative growth period (Figure 2). This caused little cold damage. In comparison, at Terbol the temperature decreased to below zero during vegetative growth for a period of about 13 weeks (Figure 2). This long period of low temperature at Terbol reduced the plants growth and final seed yields. In the second year the minimum temperatures were much higher than in the first year. The plant height in the first season was only 28.4cm, but it increased to 37.6cm in the second year and also number of branches/plant increased from 5.2 to 7.4. Consequently, the seed yield increased from 1057 kg/ha in the first season to 1476 kg/ha in the second season, representing an increase in yield of 40% (Table 20).

The most dramatic effect of year was on time to flowering, time to maturity and dehulling percent. The overall mean of time to flowering and maturity in the second year were earlier than in the firstl year by 26 and 22 days, respectively. These differences can be attributed to temperature differences between years, because the temperature affects not only the rates but also the duration of many processes that affect plant growth (Summerfield, 1981). The reduction of air temperature (<10°C) caused delayed flowering and extended crop duration in lentil (Wilson, 1977).

The dehulling percentage in the first year was 76.8 (over all genotypes and environments); in comparison, this percentage decreased in the second year to only 37.80%. This result revealed that the season had a major influence on seed dehulling. Cooking time decreased

in the second year, indicating the presence of a year effect on cooking time. Bhatty et al. (1983 and 1984) also reported that location and season of growth had a major effect on the cooking quality in lentil.

The significance of genotype-year interactions (Table 14) indicated that there were changes in the relative rankings or magnitudes of differences among genotypes over years. An interesting example of this interaction was for Family 370 (the Egyptian line) which was completely killed by frost damage in the 1984-85 season, but survived in the second season.

Large genotype-year interactions are common in varietal trials. As an example, Rasmussen and Lambert (1961) found the variety-year component was more than four times as large as the variety-location component in barley trials over four years at eight locations in Minnesota. This is because the year effect includes fluctuations in weather, such as amount and distribution of rainfall and temperature, which are unpredictable. In this case, Allard and Bradshaw (1964) emphasized the importance of testing a set of genotypes in a series of locations over a series of years.

3.3 Environmental effects

The environmental effects represented high proportion of variation for seed yield, biological yield and straw yield/plant, accounting for 45%, 61% and 68% of the overall variance, respectively (Table 14). These effects were also high for plant height, number of branches per plant, cooking time and number of pods per plant and ranged from 44% to 64% of the overall variance. In comparison, the environmental effect represented a small amount of the overall variance for other characters. For example, it was 12.5% for number of seeds/pod, 18.9% for 100 seed weight and 2.2% for seed dehulling (but it was also highly significant). These results indicated that there were fluctuations in the environmental conditions throughout the experiments.

In this section the comparisons between environments will be made in two ways; firstly across locations by comparing the trait performances in Tel Hadya, Terbol and Breda locations and secondly comparing the trait performances between irrigation regimes T_1, T_2 and T_3 at Tel Hadya (effect of irrigation).

3.3.1 Effects of location

The overall means for 17 characters at the three locations; Tel Hadya rainfed (unirrigated) (T_1), Terbol (Ter) and Breda (Br) are shown in Table 21.

The performances of most characters were higher in Tel Hadya than in other locations, indicating the superiority of Tel Hadya. The mean seed yield across the three locations was 1300 kg/ha. The mean seed yield at individual locations varied by an order of three from 566 kg/ha at Breda to 2066 kg/ha at Tel Hadya, emphasizing the contribution of environmental variation to total variability. The superiority of seed yield at Tel Hadya was due to a higher performance of its yield components; number of pods/plant and number of seeds/pod.

Biological yield and straw yield had a similar trend among locations to seed yield kg/ha and thus the harvest index was also higher at Tel Hadya than at other locations.

Table 21

The location mean and standard error of 17 lentil characters over years at Tel Hadya rainfed (Tl), Terbol (Ter) and Breda (Br)

Characters	Location			Mean	S.E.±
	T_1	Ter	Br		
Seed yield kg/ha	2066.31	1266.57	565.58	1299.49	64.08
Biological yield kg/ha	5935.01	4079.56	1617.51	3877.36	193.81
Straw yield kg/ha	3868.70	2812.99	1051.94	2577.88	135.52
Seed yield/plant	1.38	1.20	0.39	0.99	0.06
Biological yield/plant	3.99	3.83	1.13	2.98	0.17
Straw yield/plant	2.60	2.63	0.74	1.99	0.12
Harvest index	35.2	31.9	35.0	34.03	0.6
No. of pods/plant	25.4	25.1	7.2	19.21	1.18
No. of seeds/pod	1.47	1.41	1.40	1.43	0.01
100 seed weight	4.05	3.67	4.29	4.00	0.03
Plant height	35.1	32.7	23.2	30.33	0.85
No. of branches/plant	8.6	7.4	3.0	6.32	0.44
Time to flowering	122.9	138.5	120.2	127.19	0.13
Time to maturity	163.1	180.2	155.9	166.40	0.42
Seed protein content	25.5	23.3	24.7	24.53	0.14
Cooking time	36.0	31.7	37.9	35.18	0.20
Dehulling	58.6	51.4	67.8	59.23	0.94

Tel Hadya produced the tallest plants among locations with an average of 35.1cm, comparing with 32.7 and 23.2cm at Terbol and Breda respectively. Also the number of branches/plant was higher at Tel Hadya. These results revealed that the vegetative growth was better at Tel Hadya and reflects the presence of the appropriate growth conditions at this location. Breda (the dry site) produced the earliest plants in flowering and maturity, the brevity of the intervening period reflecting the water stress which severely reduced the length of the life cycle of plants.

Differences between locations for seed protein existed but with a narrow range of 23.3-25.5%. There was also a significant effect of location on cooking time and dehulling percent. The seeds from Terbol cooked quickly but had the lowest dehulling percent of 51.4%.

3.3.2 Effects of irrigation

A perusal of the data in Table 20 indicates that two irrigations, at pre-flowering and pod-filling stages, significantly increased most of the characters studied.

The mean seed yield across the three irrigation treatments, T_1, T_2 and T_3, over years, was 2234 kg/ha with the range of 2066 kg/ha in T_1 (unirrigated) to 2467 kg/ha in T_3 (two irrigations). Irrigation at the pre-flowering stage increased seed yield by 5% over the control (T_1), whereas irrigation twice (T_3) increased seed yield kg/ha by 14% and 19% over one irrigation and no irrigation treatments respectively. These results indicated that seed yield increased with more frequent irrigation.

Irrigation also increased the dry matter accumulated in the plants. Straw yield kg/ha increased by 12% with one irrigation and 25% with two irrigations over the no irrigation treatment. Because seed and straw yields were increased by irrigation, biological yield was also increased from 5935 kg/ha in T_1 to 7312 kg/ha in T_3 representing an irrigation response of 23%. Similarly, the mean values of seed yield, straw yield and biological yield per plant in T_3 significantly exceeded the corresponding values in T_1 and T_2. Although seed yield was increased by irrigation, harvest index decreased as shown in Table 20.

The increase in seed yield with irrigation was mainly attributed to an increase in the yield components. The mean number of pods per plant, over years, was 25 and 29 for T_1 and T_3 respectively, the last representing an irrigation response of 16%. Number of seeds per pod and 100-seed weight increased by 1% and 4%, with double irrigation, over the unirrigated treatment. Irrigation at the pre-flowering stage significantly increased plant height and number of branches per plant, while there were no significant differences between T_2 and T_3 for these characters. These results revealed that application of two irrigations enhanced reproduction growth and yield components rather than the vegetative growth of plants.

There were significant differences between irrigation treatments for time to flowering and maturity. Irrigation at pre-flowering prolonged the vegetative growth period and thus delayed the flowering and maturity by 2 and 3 days respectively. Application of two irrigations prolonged the maturity by 7 and 4 days comparing with no irrigation and pre-flowering irrigation treatments respectively.

One irrigation at the pre-flowering stage did not affect seed protein content, since protein percentages in both T_1 and T_2 were 25.53%, while double irrigation significantly decreased seed protein to 24.52%. However seed protein yield (kg/ha) increased by 15% in T_3 over T_1 due to the increase in seed yield. Irrigation at the pre-flowering stage did not influence cooking time, whereas irrigation two times increased the time required to cook the seeds from 36 minutes in T_1 to 39 minutes in T_3. Dehulling percent significantly decreased with increasing irrigation frequency. T_1 produced the highest dehulling percent of 58.6, which was reduced to 56.2% in T_2 and to 52.6% in T_3.

The results showed that seed yield increased with increase in the frequency of irrigation or increase in water supply (from location to location). Irrigation increases the availability of water in the soil profile to the plant and thereby enhances almost all physio-chemical processes in plants that ultimately contribute towards additional seed production. This is well illustrated by characters such as number of branches per plant, plant height, number of pods per plant and 100 seed weight. Though grain yield varied, Verma and Kalra (1981) observed higher uptake of nitrogen and phosphorus under irrigated lentil. They

attributed that to increased availability nutrients in the soil associated with improved absorbing and assimilation capacity of a vigorous crop as compared with a crop ill-affected by water stress.

Two irrigations, at pre-flowering and pod filling stages, were definitely superior in increasing seed yield as compared with one irrigation at the pre-flowering stage or with no irrigation. Panwar and Paliwal (1975), Singh et al. (1981) and Singh et al. (1983) also obtained higher yields of lentil with irrigation at pre-flowering and pod filling stages. However, Panwar and Paliwal (1975) reported that if only one irrigation was available, irrigation at the early pod filling stage was the most productive.

Relationship between environmental seed yield and water supply

In order to explore the relationship between seed yield and water supply at all environments studied, the linear regression and linear correlation between average seed yield (kg/ha) and the amount of water received (rainfall or rainfall + irrigation) at every environment were calculated and are shown in Figure 3.

In general, the seed yield increased with water supply as indicated by the high linearity and the high correlation coefficient of 0.94 between both factors. However, the distribution of environments around the regression line (Figure 3) indicated that the yield at Terbol was not as strongly related to water level as it was for Tel Hadya and Breda.

The accumulated results confirmed that the environmental water supply (rainfall and irrigation) was the major factor influencing seed yield at Tel Hadya (T_1, T_2 and T_3) and at Breda, while at Terbol the altitude (i.e. temperature) was more important than rainfall.

Erskine et al. (1985) also found the average seed yield kg/ha of 24 lentil genotypes was greater at Tel Hadya (in Syria) than at Terbol and Kfardan (in Lebanon). They reported that the low temperatures at Lebanese sites reduced early growth and final seed yield.

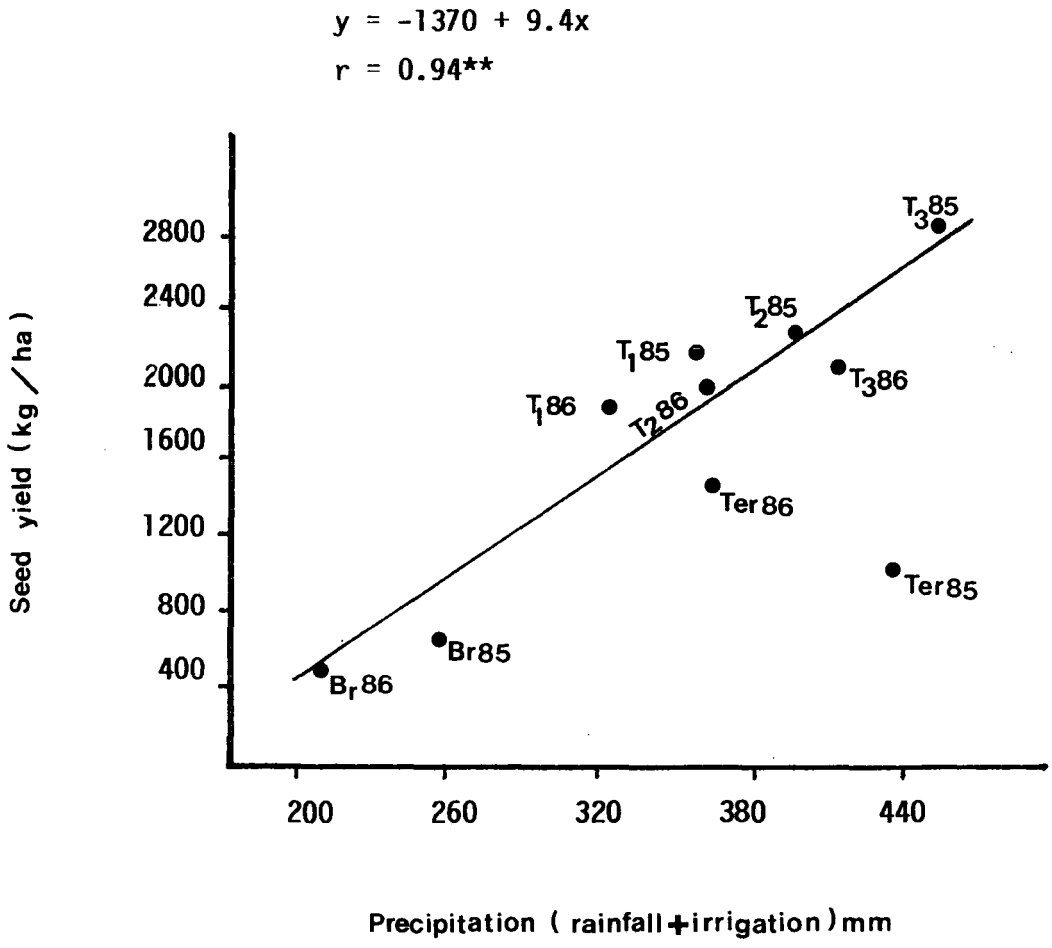


Figure 3. Linear regression between seed yield (kg/ha) and amount of water received at five environments in two growing seasons.

- Linear correlation coefficient (r) excluding Ter.

** Significant at probability level of 0.01.

3.4 Genotype and environmental variation in seed protein quality

The results of SDS-acrylamide gel electrophoresis used to investigate the differences between genotypes and the effect of environments on lentil seed storage protein are presented below. The analyses were made for 34 genotypes, one genotype per gel slab. Every slab contained five tracks representing the five environments; T_1, T_2, T_3, Br and Ter. The comparisons between genotypes and environments were made on the basis of the positions of the protein bands.

The results showed wide differences between genotypes in number and position of the bands. Number of bands ranged from 9-21. Genotype 78S26003 exhibited the largest number (21 bands), while FLIP84-67 L had the lowest number of 9 bands (Table 22). 17 bands were the most common number of bands, being found in 6 entries.

The position of bands also varied between genotypes as indicated by their Rf values presented in Table 22. The bands at Rf 0.48, 0.56, 0.72 and 0.78 were the most common bands since they exhibited the highest frequencies among all other bands, whereas the band at Rf 0.34 was present in only four genotypes.

The effect of environments was detected when band presence at positions differed from environment to environment. The results showed that nine genotypes showed differences in band position due to environment. Syrian Local Small and Jordanian Local showed the same influence, which in irrigation at pre-flowering stage in Tel Hadya (T_2) resulted in the absence of a band at Rf 0.51 (Figure 4.A). The bands at Rf 0.40 for genotype ILL 121 were absent in T_1 and T_2 environments. In ILL 857, the band at Rf 0.35 changed its position with the band at Rf 0.38 in environment T_2 (Figure 4 B). The variation in genotype 78S26003 is shown in Figure 4 C. An extra band at Rf 0.70 appeared in T_1 and T_3 environments.

Another form of variation appeared in Precoz where the bands around Rf 0.46 at T_1, T_2 and T_3 in Tel Hadya were less intense than the same bands at Breda and Terbol. These protein bands in this genotype seems to be affected quantitatively by local conditions at Tel Hadya. Its bands at Breda and Terbol showed similar variation (Figure 4 D).

Table 22

Relative frequencies of the observed bands

Genotype	Rf (0.00)																														
	.34	.36	.39	.40	.42	.44	.46	.48	.51	.54	.56	.58	.61	.62	.65	.68	.72	.74	.76	.78	.80	.82	.84	.86	.88	.90	.92	.94	.96	.98	.99
Giza 9		x				x		x	x		x	x	x	x		x	x	x		x	x	x			x	x			x	x	
Fam. 130			x				x	x	x		x		x	x		x	x	x			x	x	x	x	x	x		x	x		
Selaim		x					x	x	x		x	x	x	x	x			x			x	x		x	x	x		x	x		
ILL 1693									x		x	x		x				x		x	x				x			x	x	x	
ILL 1983						x		x	x				x	x			x		x	x	x		x		x	x		x	x	x	
ILL 40								x	x	x			x	x	x		x			x	x		x	x		x	x	x		x	
ILL 241			x		x			x	x			x	x			x		x			x			x	x		x	x			x
SLL			x	x			x	x		x	x				x		x	x	x		x	x		x		x		x		x	
SLS				x	x		x	x		x	x	x				x	x			x			x			x	x		x			
Jord. Loc.	x	x				x		x	x	x	x		x			x	x			x		x	x		x		x		x	x		
76TA66005		x	x		x		x	x		x	x		x				x			x		x		x		x		x				x
78S26003			x		x	x		x	x	x	x	x	x			x	x	x	x	x		x		x	x	x		x	x	x	x
78S26004				x	x		x	x	x	x		x	x			x		x	x	x			x	x		x	x		x			
76TA66088				x		x	x					x	x	x		x	x	x	x				x	x		x		x		x	x
ILL 857	x	x	x		x		x	x	x	x				x	x	x		x		x	x		x		x				x		x
Laird						x	x		x			x	x				x			x		x		x		x		x	x	x	
ILL 121		x		x		x	x		x	x	x		x	x		x	x			x	x		x			x		x			x
74TA161			x	x	x	x		x	x		x	x		x	x	x	x	x		x		x		x	x					x	x
Lenka	x			x	x	x	x	x	x	x	x	x			x		x	x		x		x		x		x	x		x		x
Okula		x			x	x		x			x		x	x		x			x	x	x			x	x	x		x	x		x
74TA276			x				x	x	x			x					x			x		x		x		x		x	x	x	
74TA212		x	x	x		x			x		x			x		x	x		x	x		x	x			x		x		x	
ILL 274			x	x	x		x	x			x	x	x			x	x		x	x			x	x			x	x		x	x
ILL 355		x		x	x		x			x	x		x		x		x	x		x		x	x			x	x		x	x	
ILL 358	x			x	x		x	x	x	x	x	x			x		x		x			x	x	x				x	x	x	
Precoz							x		x	x	x	x			x	x	x			x		x		x		x	x		x			x
Pant.L,406								x		x	x		x	x		x	x	x			x		x	x		x		x		x		x
ILL 2526								x	x		x		x		x	x	x	x			x	x	x				x	x		x		
ILL 2573								x	x	x		x	x		x	x	x			x		x		x		x	x	x		x		
74TA264								x	x		x	x	x			x	x			x			x			x		x	x			
FLIP 84,1-L								x	x		x	x		x		x	x			x			x			x	x		x			x
FLIP 84,27-L					x			x			x		x		x	x		x		x		x		x		x		x	x			
FLIP 84,67-L								x			x	x			x			x			x	x						x		x		
FLIP 84,78-L									x		x	x	x	x	x		x		x	x				x			x					x

Figure 4

Banding patterns of storage proteins from lentil seeds grown at five different environments in 1984-85 season.

Tracks :

T_1 : Tel-Hadya, rainfed only (346mm water)

T_2 : Tel-Hadya, rainfed + irrigation at pre-flowering stage (396mm)

T_3 : Tel-Hadya, rainfed + irrigation at pre-flowering and pod-filling stages (446mm)

Br : Breda, rainfed only (253mm)

Ter : Terbol, rainfed only (433mm)

Genotypes :

A : SLS

B : ILL857

C : 78S26003

D : Precoz

E : Lenka

Fig. 4

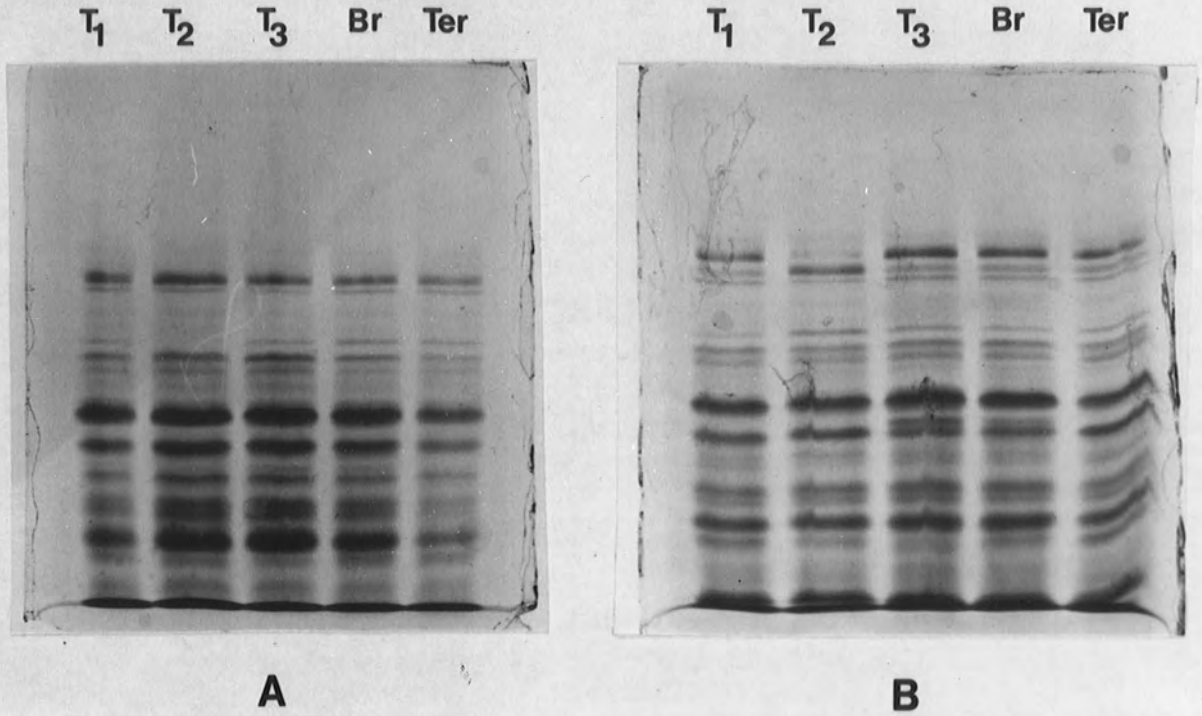
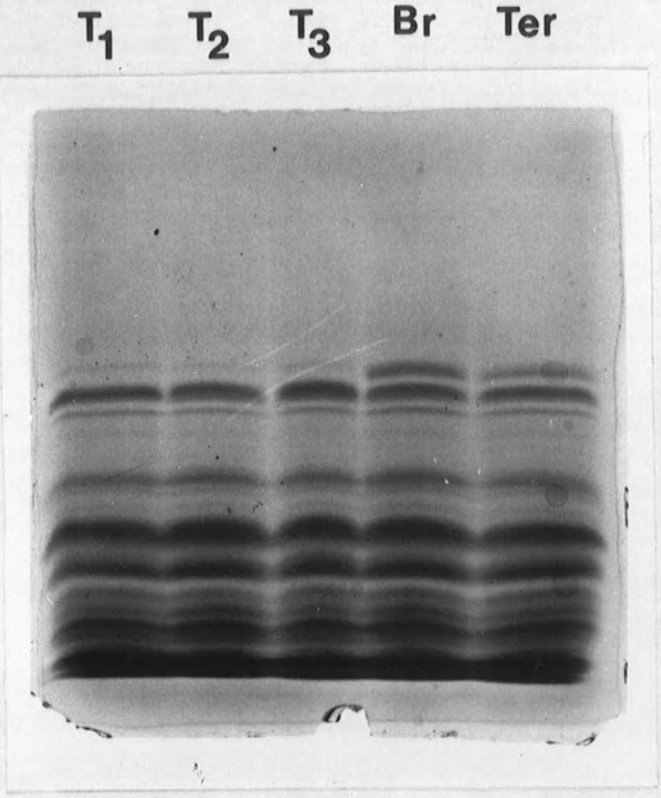
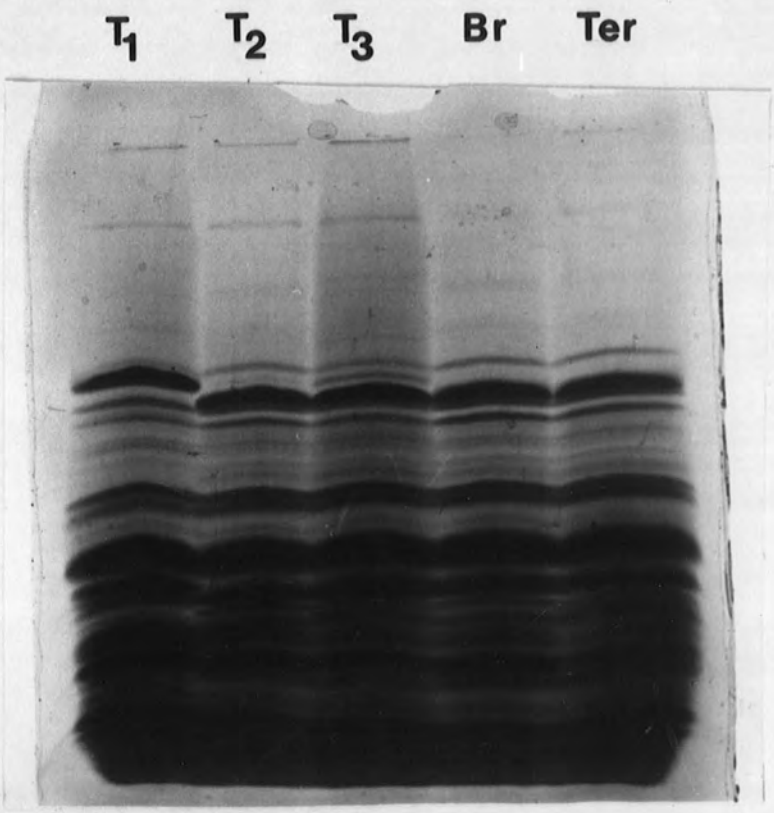


Fig.4



D



E

The genotypes; Lenka, FLIP 84-27L and FLIP 84-67L exhibited the complex influence of environments as the differences between environments, in each genotype, caused changes in more than one band. In Lenka, the protein bands were the same as in T_2, Breda and Terbol, while in T_3 an extra band appeared at Rf 0.36 and in T_1 an extra band was detected at Rf 0.68. In addition the band at Rf 0.40 changed its position to Rf 0.37 (Figure 4 E). For FLIP 84-27L, each of T_2 and Terbol showed variation in band position and similar changes were observed in other environments. FLIP 84-67L showed different bands position at T_3 and Breda, while T_1, T_2 and Terbol showed the same bands.

The results indicated that in most cases the changes occurred in high molecular weight bands at Rf 0.35-0.40. Out of nine genotypes affected by environment, six genotypes were influenced by time of irrigation. Irrigation at the pre-flowering stage (T_2) changed the band positions for three genotypes, two genotypes were affected by the non-irrigated treatment (T_1) and one genotype was affected by irrigation at the pod-filling stage (T_3). Also, protein bands were influenced by environmental effects at both Breda (Br, the dry site) and Terbol (Ter, the wet site).

The results revealed wide differences between genotypes in number and position of protein bands. Gatehouse *et al.* (1980) confirmed the presence of genetic variation in protein quantity in faba bean. They found a variation of nearly two-fold in the vicilin-legumin ratio among five varieties and also showed different patterns of legumin bands between genotypes. This difference consisted of an extra band at slightly higher molecular weight in two genotypes.

The results showed that each genotype had a different number or position of bands. Therefore, these banding patterns could be used to identify varieties especially on bands with low molecular weight (Rf>0.40).

Little information is available in the direct effect of environments on storage protein quality. However, Manteuffel *et al.* (1976) found the proportion of legumin to vicilin in faba bean, which may contain up to four times as much legumin as vicilin (Wright and

Boulter, 1972) may depend on the environment. On the other hand, Gatehouse et al. (1980) found no variation in protein quality, between four faba bean entries, due to environments, although they did not describe the prevailing environmental conditions.

The environments in this study represented a wide range of water supply regimes. They also included different timings of irrigation. Since all plant processes take place in what is effectively an aqueous medium, and since water is involved as a transporting agent or as a reactant in many of these processes, it is not surprising that water uptake can have profound effects on most plant growth processes.

In general there appears to be a reasonably clear dependence of the growth rate of developing tissues and organs on protein synthesis, and a close association between protein synthesis and RNA (ribonucleic acid) content, and between RNA and DNA levels (deoxyribonucleic acid) (Woodstock and Skoog, 1960, 1962; Williams and Rijven, 1965).

From the known effects of water on rate of plant development, it can be expected that there will be associated effects on many aspects of protein synthesis. Some researchers observed interruption of protein synthesis and proteolysis when water stress is imposed (Chen et al., 1964, Shah and Loomis, 1965). Few studies of the effects of water stress on nucleic acid metabolism have been made (Gates and Bonner, 1959; Gardner and Nieman, 1964; Shah and Loomis, 1965). However these results referred to decreasing DNA content or its increasing rate with water stress. Also, the association between RNA and protein levels was found to be closely linked in stressed leaves in wheat plants (Williams and Rijven, 1965). In faba bean, the onset of storage protein synthesis has been shown to follow a period of rapid synthesis of both DNA and RNA (Millerd and Whitfield, 1973, Manteuffel et al., 1976).

A frequently observed effect of stress is the appearance of high levels of free amino acids, especially proline and amides (Kemple and Macpherson, 1954; Chen et al., 1964). Barnett and Naylor (1966) investigated this phenomenon and found that although amino acids were

continually synthesized during water stress in Bermuda grass (Cynodon dactylon (L.) Pers.) protein synthesis was inhibited and protein levels decreased.

The accumulated information referred to above indicates that there is a relationship between water and the protein synthesis which may explain the differences in protein quality due to environments observed in the present study.

However, the present results must be considered as an initial observation of storage protein quality affected by location and irrigation in lentil. More work is needed to understand these relationships and the genetic control of the protein synthesis. From such knowledge it may be possible to advise plant breeders of a more viable strategy for breeding for improved protein quality in lentil.

3.5 Genotype-environment interaction

As shown in Table 14, the genotype-environment interaction variances were highly significant for all characters, indicating its importance as a source of phenotypic variation. Clearly there were changes in the relative rankings or magnitudes of differences among entries over environments. In this section the genotype-environmental interaction will be investigated in two parts : Firstly, genotype-irrigation interaction and secondly, the phenotypic stability in lentil.

3.5.1 Genotype-irrigation interaction

The data from irrigation treatments at Tel Hadya (T_1, T_2 and T_3) in two seasons (6 environments) were used to study the genotype-irrigation interaction effects.

The analyses of variance are presented in Table 23. The genotype and irrigation variances were highly significant for all characters. Also, the genotype-irrigation variance was highly significant for all characters. This satisfied the basic requirements for this study. The genotype-irrigation sum of squares were partitioned into two orthogonal items, the first one being genotype-irrigation interaction (linear) which is due to differences between the fitted regression lines. The second portion was the deviation from regression (pooled deviation) which measured the accumulated deviations of the observed values around these fitted lines. In Table 23, both genotype-irrigation (linear) and pooled deviation mean squares were significant for all characters, when tested against pooled error, except biological yield/plant, straw yield/plant and number of branches/plant which had non-significant pooled deviation.

When both items are significant, Hill (1975) stated that genotype-environment (linear) should be re-tested against deviation from regression to determine whether it accounts for a significant proportion of the genotype-environment interaction variance.

Consequently, the genotype-irrigation (linear) mean squares were tested against pooled deviation mean squares. The results showed that

Table 23 Pooled analysis of variance for 17 lentil characters under irrigation

Source of variation	D.F.	Mean square									
		Seed yield kg/ha	Biological yield kg/ha	Straw yield kg/ha	Seed yield/ plant	Biological yield/ plant	Straw yield/ plant	Harvest index	No.of pods/ plant	No.of seeds/ pod	100 seed weight
Genotype	33	1445620**	9017350**	5711170**	0.58**	5.77**	4.14**	0.02**	206.05**	0.37**	10.23**
Genotype-irrig. + irrig.	170	198573**	1201610**	611028**	0.27**	1.60**	0.65**	0.001**	95.05**	0.02**	0.04**
Irrigation(Linear)	1	16679500**	88029400**	36962800**	30.29**	174.53**	60.59**	0.09**	10416.2**	0.22**	2.08**
Genotype-irrigation (Linear)	33	205678**	1212080**	535665**	0.145**	1.137**	0.664**	0.0013**	51.53**	0.04**	0.05**
Pooled deviation	136	75666**	560635**	362022**	0.074*	0.438	0.210	0.0007**	29.72*	0.0116**	0.02**
Pooled error	396	53166	324766	180284	0.055	0.412	0.206	0.0005	21.57	0.0069	0.01

*,** Significant at 0.05 and 0.01 level of probability, respectively.

Table 23 (continued)

Source of variation	D.F.	Plant height	No. of branches/ plant	Time to flower-ing	Time to maturity	Seed protein	Cooking time	Dehulling
Genotype	33	100.81**	27.15**	277.76**	238.44**	5.94**	347.94**	445.36**
Genotype-irrig.+irrig.	170	10.36**	6.03**	185.72**	108.05**	1.70**	6.18**	666.94**
Irrigation (Linear)	1	874.52**	607.45**	31037.71**	17611.91**	194.74**	439.27**	104703.9**
Genotype-irrig. (Linear)	33	9.15**	7.58**	13.07**	15.07**	1.03**	2.76**	164.26**
Pooled deviation	136	4.30**	1.23	0.76**	1.91**	0.45**	3.83**	23.93**
Pooled error	396	2.91	1.36	0.26	0.94	0.16	0.60	12.72

*, ** Significant at 0.05 and 0.01 level of probability, respectively.

genotype-irrigation (linear) was significant for all characters, except straw yield (kg/ha) and cooking time (Table 23). These results indicated that the linear components were more important than non-linear components for most characters.

Another approach was used to examine the relative importance of linear and non-linear components. The overall efficiency of the regression analysis in accounting for the genotype-irrigation interaction was measured as the linear proportion of variance accounted for by regression. The results of this test are given in Table 24. In this table, the linear regression portions were high for all characters, except straw yield (kg/ha) and cooking time which showed the lowest L.P.V. values of 66.2% and 40.1% respectively. These characters also had insignificant genotype-irrigation (linear) variance. On the other hand, the three characters which showed non-significant pooled deviations, had the highest L.P.V. values. These were biological yield/plant, straw yield/plant and number of branches/plant (Table 24). These results revealed that the genotype-irrigation interaction variance could be attributed to the linear component for all characters except straw yield (kg/ha) and cooking time. These results confirmed the results mentioned above.

The importance of both linear and non-linear components were reported by Malhotra et al. (1971) and Pandey et al. (1982) in lentil and Jinks and Stevens (1959) and Bucio-Alanis (1966) in other crops. Prem Sagar and Lal (1980) found that most of the genotype-environment variation in lentil could be attributed to the linear components. However, Malhotra et al. (1971) found both linear and non-linear components of variation were significant, but the former was higher in magnitude.

In general, the above results show that the regression lines could give nearly perfect description of performances of entries for different traits in the different irrigations. Because the main objectives of this part of the study was the response to irrigation, the regression slopes are of great interest.

Table 24 The linear proportion of variance (L.P.V.%) for 17 lentil characters under irrigation

Characters	L.P.V.%
Seed yield kg/ha	87.14
Biological yield kg/ha	79.00
Straw yield kg/ha	66.16
Seed yield/plant	82.45
Biological yield/plant	96.44
Straw yield/plant	99.14
Harvest index	80.00
No. of pods/plant	78.61
No. of seeds/pod	88.07
100 seed weight	75.91
Plant height	81.75
No. of branches/plant	100.00
Time to flowering	96.19
Time to maturity	93.60
Seed protein content	74.75
Cooking time	40.06
Dehulling	93.11

The simplest approach is regression of individual entry mean trait on the mean of all entries at each irrigation level. The interpretation of the slope parameters by Finlay and Wilkinson (1963), in which the slope parameters or stability index is used as a relative comparison among entries, is straightforward and intuitively compelling. Consequently, the regression analyses were made and the linear regressions used as a measure of the response of genotypes to irrigation.

Because seed yield and seed protein are the most important traits in lentil, these characters will be demonstrated. The average performances ($\bar{x}$) of the 34 genotypes along with their regression coefficients (b), deviation from regression coefficient (S^2d) and coefficient of determination (R^2) for seed yield/plant and seed protein content are presented in Tables 25 and 26.

3.5.1.1 Seed yield response to irrigation

The mean yield of 34 genotypes across irrigation regimes ranged from 0.94 to 1.96g (1432 to 2972 kg/ha) with an overall mean of 1.5 g/plant across irrigations and years (Table 25). The highest yielding five entries were SLL, 74TA276, Jordanian local, 78S26004 and 74TA264 with differences between them non-significant. The regression coefficients (b) of individual entries ranged widely from 0.14 to 1.90. The significance of the individual regression coefficient of every genotype was examined against their standard errors using the t-test. Only two genotypes had regression coefficients significantly greater than unity; they were 74TA264 (b = 1.90) and FLIP 84-27L (b = 1.22). On the other hand, seven genotypes exhibited regression coefficients significantly below 1.0.

Conventional computation of the F-ratios for every genotype was used to test the significance of entry deviation from regression (Eberhart and Russell, 1966). The results showed that only five entries had deviations from regression values significantly different from zero (Table 25). The coefficients of determination (R^2) of individual genotypes ranged widely from 0.23 to 0.98, but most of these

Table 25 The average performances of 34 lentil genotypes for seed yield/plant

No.	Genotype	Mean seed yield/plant ($\bar{X}$)	Regression coefficient (b)	Deviation from regression (S^2d)	Coefficient of determination (R^2)
1	Giza 9	1.58	1.09		0.72
2	Fam. 130	1.41	0.73		0.76
3	Selaim	1.31	1.13		0.88
4	ILL 1693	1.14	0.62*		0.90
5	ILL 1983	0.94	0.25*		0.48
6	ILL 40	1.53	0.85		0.93
7	ILL 241	1.82	1.18		0.86
8	SLL	1.96	1.63	x	0.68
9	SLS	1.53	1.22	x	0.53
10	Jord.loc.	1.87	1.17	x	0.56
11	76TA66005	1.77	1.17		0.82
12	78S26003	1.67	1.18	x	0.66
13	78S26004	1.86	0.76	x	0.33
14	76TA66088	1.70	1.33		0.94
15	ILL 857	1.80	1.29		0.95
16	Laird	1.37	1.07		0.69
17	ILL 121	1.22	0.70		0.58
18	74TA161	1.25	1.08		0.96
19	Lenka	1.20	0.92		0.75
20	Okula	1.02	0.56*		0.77
21	74TA276	1.93	1.45		0.83
22	74TA212	1.61	1.70		0.88
23	ILL 274	1.49	1.31		0.84
24	ILL 355	1.27	0.75		0.94
25	ILL 358	1.53	0.63*		0.95
26	Precoz	1.42	0.67		0.52
27	Pant.L,406	0.99	0.42*		0.60
28	ILL 2526	1.09	0.14*		0.23
29	ILL 2573	0.91	0.45*		0.80
30	74TA264	1.84	1.90*		0.88
31	FLIP 84,1-L	1.66	1.23		0.91
32	FLIP 84,27-L	1.81	1.22*		0.98
33	FLIP 84,67-L	1.76	1.15		0.88
34	FLIP 84,78-L	1.80	1.09		0.89

Grand mean 1.50

* Denotes genotypes had a significant regression coefficient greater or less than 1.0

x Denotes genotypes had a deviation from regression significantly different from zero

values were above 0.75. The high R^2 values was another indicator that the linear component represented a high portion of genotype-environment interaction for most genotypes.

The 34 genotypes were classified into four groups according to their regression coefficients, then four genotypes were chosen to represent these groups. These genotypes were ILL 241, Laird, ILL 358 and 74TA264. The linear relationships of these individual genotypes and environmental means are shown graphically in Figure 5, where the abscissa is the environment mean yield and the ordinate is the yield of individual genotypes. The dotted line represents the population mean (the overall mean of the 34 genotypes) which has a regression coefficient of 1.0.

The first group of genotypes was represented by the genotype ILL241. This genotype had a regression coefficient of unity (b = 1.18). Its seed yield/plant was above average yields in all irrigation treatments and seasons. Consequently this genotype may be considered to be adapted to all environments, and thus it has a general adaptability (Finlay and Wilkinson, 1963).

Another group of genotypes was represented by Laird. This genotype also had a regression coefficient of unity (b = 1.07), but produced a seed yield per plant which was below average, indicating that it is poorly adapted to all environments.

The third genotype chosen was ILL 358, that exhibited little change in yield despite large changes in the environments. Its yield in T_1 in 1986 (the lowest yielding environment) was 1.38 g/plant, while in T_3 in 1985 (the highest yielding environment) it also produced a low yield of 1.96 g/plant. As shown in Figure 5, this genotype produced an above-average yield in low yielding environments, but was insensitive to environmental change. Its regression coefficient (b = 0.63) was significantly less than unity (Table 25). This genotype could be classified as specifically adapted to low moisture environments (unirrigated).

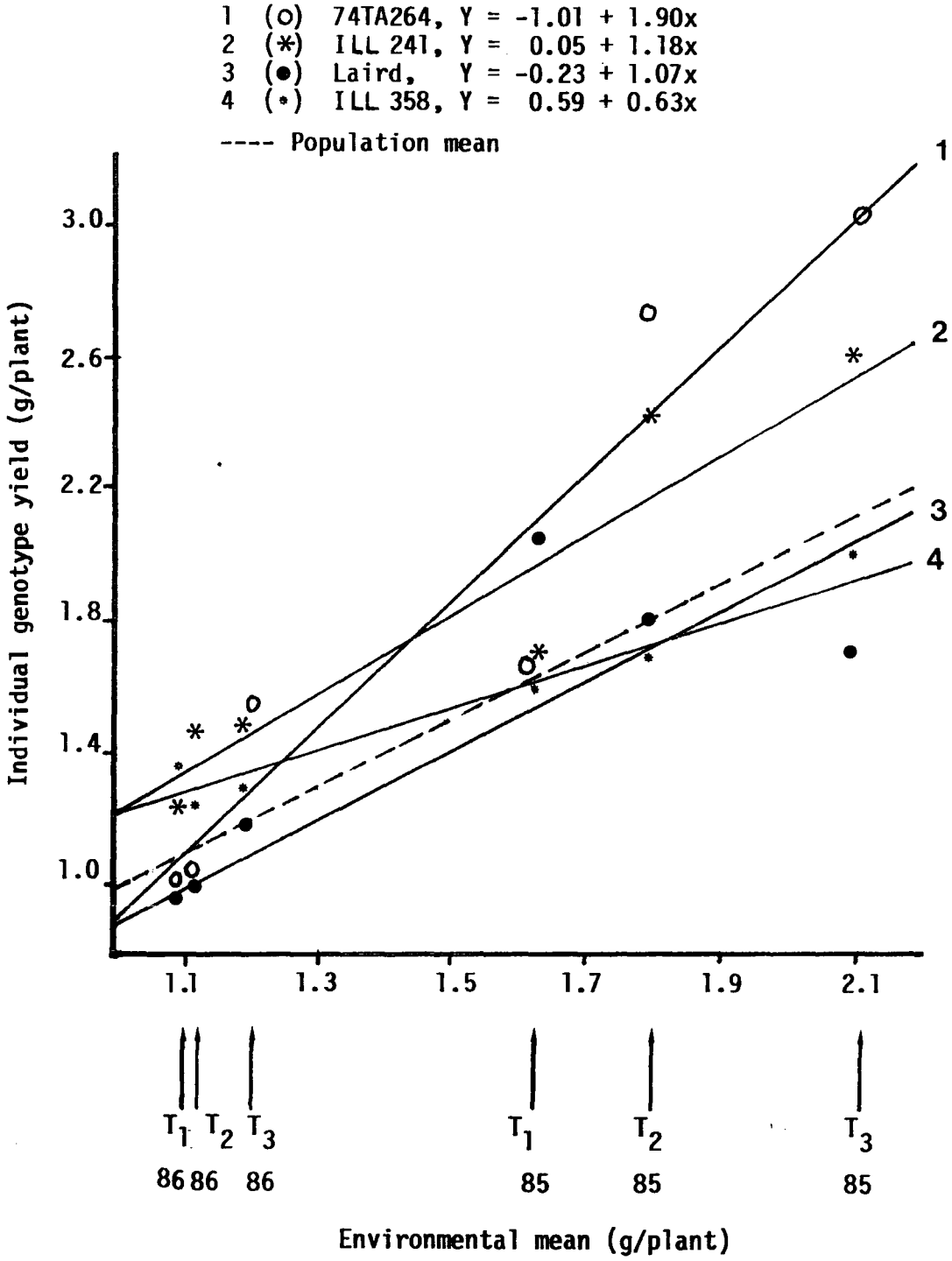


Figure 5. Regression lines, showing the relationship of individual yields of four genotypes and population mean of 34 genotypes of lentil grown at three different irrigation regimes in two years.

The genotype 74TA264 is typical of genotypes that are very sensitive to change in the irrigation level. This entry produced a seed yield per plant of only 0.98 g in the unirrigated treatment in 1986 (the low yielding environment) but with two irrigations in 1985 (the high-yielding environment) it produced a seed yield of 3.0 g/plant (Figure 5). Thus, under two irrigations conditions, it becomes one of the highest-yielding genotypes. Therefore, 74TA264 can be described as being specifically adapted to irrigation and is characterized by a regression coefficient significantly greater than unity (b = 1.90) (Table 25).

Another demonstration of the behaviour of all the genotypes can be achieved by plotting the regression coefficients and the genotype mean yields over all environments together as coordinates in a two-dimensional scatter diagram (Finlay and Wilkinson, 1963). This diagram is presented in Figure 6. Each genotype is represented by its number. The position of this number indicates the type of adaptability and the average yield performance of each genotype. The genotypes ILL 241 (no. 7), Laird (16) ILL 358 (25) and 74TA274 (30) have been labelled individually to allow direct comparisons between these genotypes in both Figures 5 and 6.

The distribution of entries (Figure 6) showed that there were distinct differences between the genotypes in their regression slopes. 16 genotypes exhibited both regression coefficients not different from unity (b = 1.0) and yields greater than the population mean. This group included 12 genotypes originating from Syria, Jordan and Lebanon, such as Syrian locals and Jordanian locals and some selections from them. This result is to be expected because they were bred under rainfed conditions which were markedly different from season to season. Thus they have wide adaptability. The Egyptian local cultivar "Giza 9" was in this group, confirming that it was unadapted to irrigation.

Nine genotypes were considered poorly adapted to all environments. Two genotypes in this group were from the Nile Valley; Family 130 (an Egyptian accession) and Selaim (the Sudanese local cultivar). This group also contained those genotypes with the highest protein content ILL 121, ILL 274 and 74TA161.

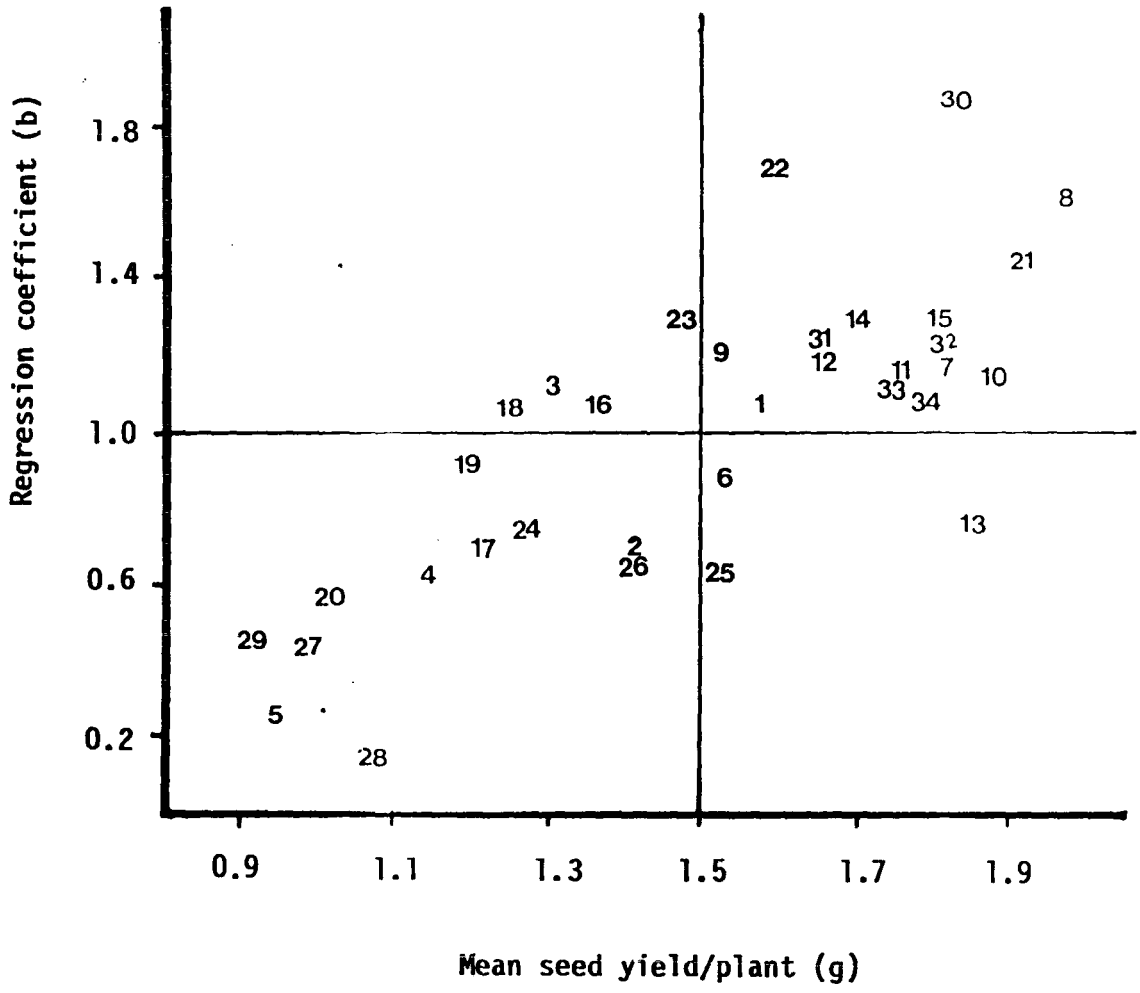


Figure 6. Adaptation of seed yield showing mean yield/plant and regression coefficients for 34 genotypes. Points on the figure are indicated by the serial number of genotypes (as presented in Table 25).

The third group of genotypes which were adapted to the unirrigated treatment (dry conditions) contained 7 genotypes. Five genotypes in this group had very small seed size (three Indian and two Ethiopian lines). In contrast, as is evident from Figures 5 and 6, genotype ILL 358 (no. 25) showed a high mean yield (above-average yield) with least response (b = 0.63) to variation in irrigation. Exploitation of this genotype would prove to be useful under dry conditions (unirrigated). It has been recently released as a cultivar for dry rainfed conditions in Ethiopia.

In contrast, as is evident from Figures 5 and 6, out of 34 genotypes only two entries exhibited a positive response to irrigation, viz 74TA264 (no. 30) and FLIP 84-27L (no. 32). Both genotypes gave high mean yields with a large response to irrigation, especially 74TA264 which had the greatest slope of 1.90. Their exploitation would prove to be very useful under irrigated conditions.

It is difficult, clearly, to identify differences between geographical groups of genotypes. However, it seems that no Egyptian or Sudanese genotypes (Nile Valley lentil genotypes) showed a specific response to high irrigation levels. On the other hand, most small seeded and very early genotypes, originating from India and Ethiopia were adapted to unirrigated environments, possibly avoiding water stress by their early flowering and maturity.

3.5.1.2 Seed protein content response to irrigation

Seed protein content ranged from 22.8 to 27.3% with an average of 25.2% for the 34 genotypes. The differences between genotypes were highly significant indicating that there was wide genetic variation in protein percentage (Table 23).

Thirty genotypes exhibited regression coefficients which did not differ significantly from unity. The genotypes Jordanian Local and FLIP 84-27L had regression coefficients below 1.0, while ILL 121 and FLIP 84-1L exhibited regression coefficients significantly greater than 1.0 (Table 26). The coefficients of determination (R^2) were high for most genotypes and only six entries showed R^2 below 0.60. This confirmed the possibility of using individual regression slopes to

Table 26 The average performances of 34 lentil genotypes for seed protein content

No.	Genotype	Mean ($\bar{X}$)	Regression coefficient (b)	Deviation from regression (S^2d)	Coefficient of determination (R^2)
1	Giza 9	24.96	0.87		0.88
2	Fam. 130	26.04	1.40	x	0.58
3	Selaim	25.51	0.88	x	0.68
4	ILL 1693	24.72	0.63		0.75
5	ILL 1983	24.06	0.74		0.92
6	ILL 40	25.03	1.26		0.96
7	ILL 241	24.71	1.70	x	0.92
8	SLL	24.71	1.12		0.98
9	SLS	25.30	0.81		0.80
10	Jord. loc.	24.78	0.52*		0.71
11	76TA66005	23.77	1.24	x	0.68
12	78S26003	24.51	0.92	x	0.75
13	78S26004	24.74	0.54	x	0.32
14	76TA66088	26.20	0.82		0.86
15	ILL 857	24.93	0.78		0.88
16	Laird	24.71	0.93		0.78
17	ILL 121	26.16	1.62*		0.95
18	74TA161	26.91	1.95	x	0.73
19	Lenka	27.33	1.20	x	0.74
20	Okula	25.48	1.12	x	0.80
21	74TA276	25.84	0.77		0.73
22	74TA212	26.64	1.25		0.93
23	ILL 274	26.60	1.71	x	0.91
24	ILL 355	25.92	0.88		0.82
25	ILL 358	25.15	0.63	x	0.54
26	Precoz	25.68	0.36	x	0.26
27	Pant.L,406	24.00	0.44		0.51
28	ILL 2526	24.55	0.64	x	0.36
29	ILL 2573	22.81	0.95		0.85
30	74TA264	24.52	1.17	x	0.74
31	FLIP 84,1-L	23.97	1.83*		0.94
32	FLIP 84,27-L	26.04	0.43*		0.72
33	FLIP 84,67-L	26.04	0.56		0.67
34	FLIP 84,78-L	24.25	1.33		0.96

Grand mean 25.19

* Denotes genotypes had a significant regression coefficient greater or less than 1.0.

x Denotes genotypes had a deviation from regression significantly different from zero.

represent the response of genotypes. However, 14 genotypes had significant non-linear components as indicated by their S^2d in Table 26.

The relationship between environment means and individual genotypes is presented graphically in Figure 7, selecting a representative of each of four groups based on mean yield and response slope. Also, the distribution of all genotypes on the basis of their regression coefficients and their means is shown in Figure 8. The order of environments in respect of their averages of protein content (environmental mean) was inversely related to their average seed yield/plant. T_3 in 1986, which showed a high environmental mean for seed yield had low average protein percent, and was named the low-protein environment. T_1 in 1985 which had low seed yield produced high average protein percent, and was named the high-protein environment.

Genotype 76TA66088 always produced above-average protein content over irrigation regimes and years, indicating that it possesses a general adaptability and average stability (Figure 7). This group included 13 genotypes, all of which produced protein levels above the overall mean (Figure 8). The genotypes Selaim and Family 130 are included in this group. Five entries in this group also showed general adaptability in seed yield/plant, these being numbers 9, 14, 21, 22 and 33.

Conversely, the genotype Laird produced below average seed protein content in all irrigation regimes and years. Furthermore, this entry showed relatively little change in protein despite changes in the irrigation level. Consequently Laird could be considered as being poorly adapted to all irrigation levels in this respect. The distribution of genotypes in Figure 8 showed that 17 entries were in this group. Most genotypes which exhibited general adaptability or response to two irrigations in seed yield showed poor adaptation to all irrigation levels with respect to protein content such as Giza9, SLL, ILL241 and 74TA264.

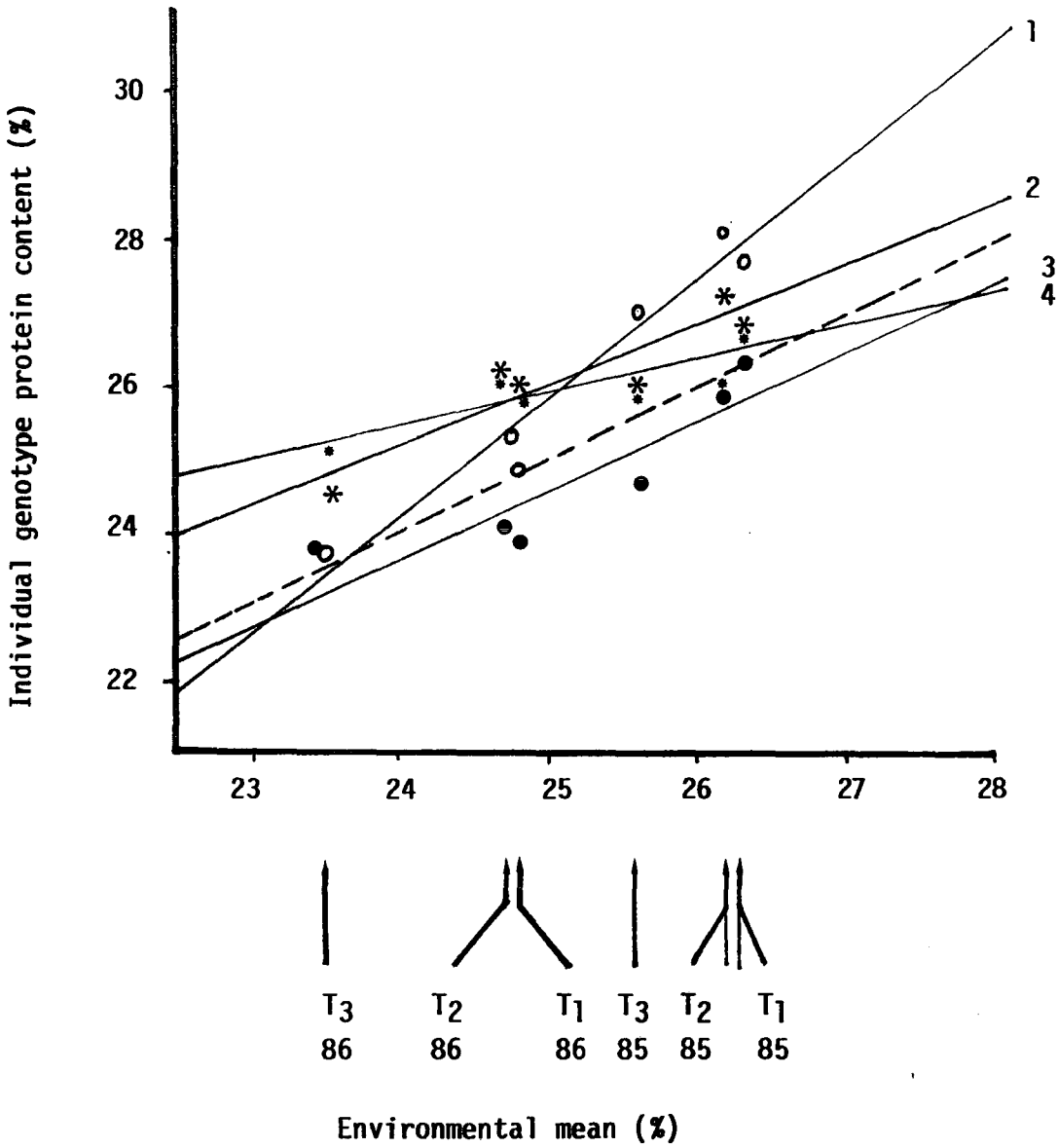


Figure 7. Regression lines, showing the relationship of individual seed protein percent of four genotypes and population mean of 34 genotypes of lentil grown at three different irrigation regimes in two years.

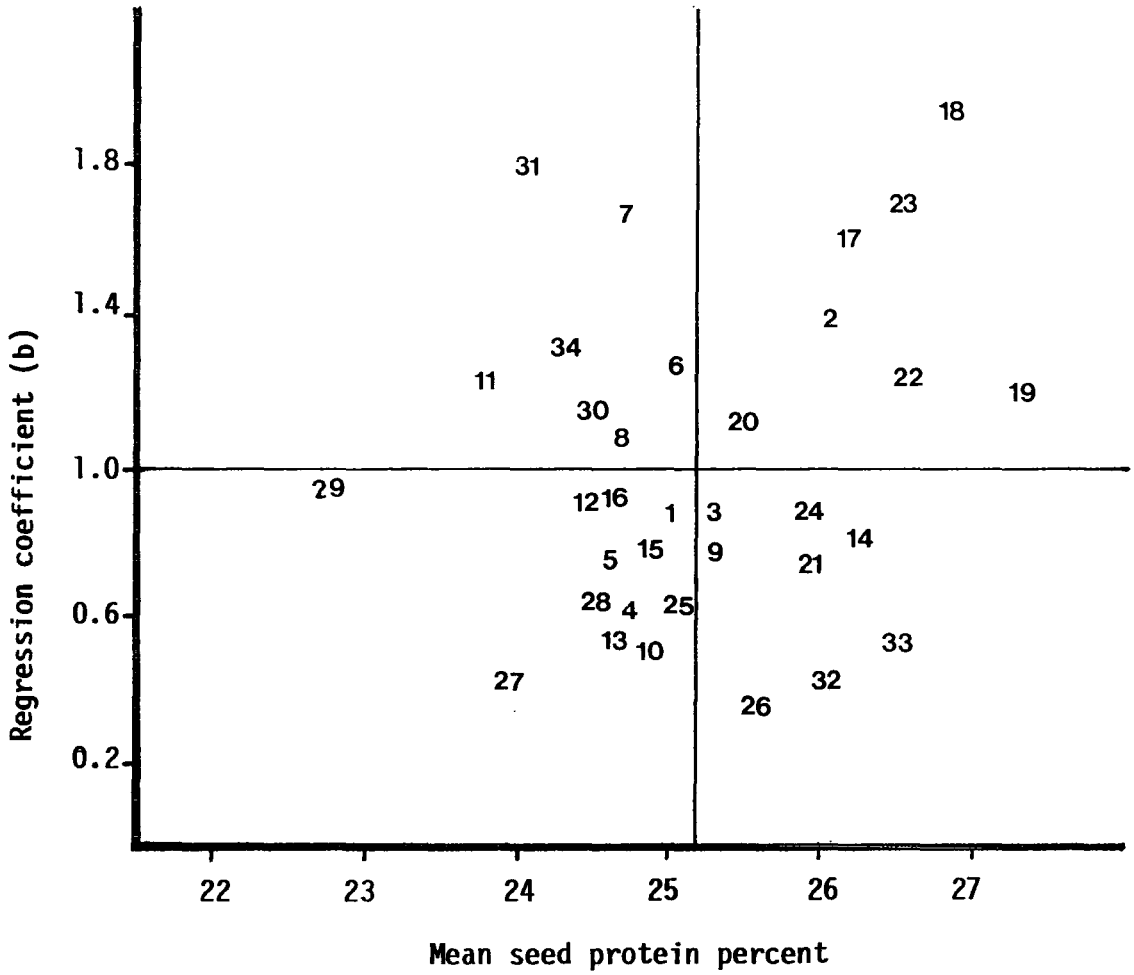


Figure 8. Adaptation of seed protein content showing mean protein percent and regression coefficients for 34 genotypes. Points on the figure are indicated by the serial number of genotypes (as presented in Table 26).

The third group of genotypes included only Jordanian Local and FLIP84-27L, both of which had low regression coefficients. As shown in Figure 7, FLIP84-27L produced a high protein content of 26.8% in the low-protein environment (T_3, 1986). However, it was insensitive to environmental change as its protein content in the high-protein environment (T_1, 1985) was only 25.2%, reflecting its small regression slope of 0.43. Although both genotypes showed the same adaptability to irrigation change with respect to their protein contents, their distribution in Figure 8 shows that FLIP84-27L is more interesting due to its high mean protein performance.

The fourth group of genotypes contained ILL121 and FLIP84-1L and is represented in Figure 7 by ILL121. This genotype had below-average stability and was very sensitive to change in irrigation level. It produced a protein content of 23.4% at T_3 in 1986 (the lowest protein environment), but its protein content increased to 28% at T_1 in 1985 (the highest protein environment). Therefore this entry was unstable and considered especially adapted to high-protein environments. The general picture of these genotypes in Figure 8 showed that FLIP84-1L (No. 31) yielded a mean protein content below the population mean, whereas ILL121 (No. 17) produced a mean protein percent greater than the population mean.

The results showed that the behaviour of genotypes with respect to seed protein was inversely related to their behaviour for seed yield/plant. Environments promoting high seed yield induced low mean protein content as expected, due to the negative relationship between seed yield/plant and seed protein content. Because we are interested in determining genotypes performing well under irrigation, FLIP84-27L and Jordanian Local, which produced a high seed protein content in two irrigation environment (T_3, 1986), probably become more important than other genotypes, with respect to protein content. Consequently, these entries could be exploited under irrigation for their high seed protein content.

Response of other characters to irrigation

As shown in Table 23, seventeen characters were measured and tested for adaptability, but only the two most important characters

have been presented. However, three other traits, viz time to flowering and maturity and 100 seed weight were also most interesting.

As would be expected, the very early genotypes tend to be specially adapted to dry (unirrigated) condition. Six out of seven entries which showed specific adaptation to the unirrigated environment were very early in flowering and maturity. These were: ILL1693, ILL1983, ILL358, Pant.L,406, ILL2526 and ILL2573, and their time to flowering and maturity ranged from 111-119 days and from 155-161 days respectively. In comparison, the genotypes adaptated to irrigation flowered at 119 to 124 days and matured at 164 to 168 days.

All genotypes that adapted to dry conditions, except Okula, had a small seed size of 2-3 g/100 seeds with an average of 2.5g/100 seeds, whereas the genotypes specifically adapted to irrigation had large seeds of 4.4-5.8 g/100 seeds with an average of 5.1g.

The adaptation of small seeded genotypes to dry conditions is predictable because short duration cultivars may by maturing rapidly avoid substantial stress. As Summerfield (1981) pointed out, such a drought avoidance strategy may explain why small-seeded lentil cultivars were considered to be more tolerant of drought than large seeded types.

It was also interesting that the genotypes which showed general adaptability for seed yield contained a wide range of maturity and seed size, some having a high mean of seed yield.

3.5.2 Root system and structure under irrigation

The two genotypes selected for this investigation, 74TA264 and ILL121 showed different responses to irrigation as indicated in adaptation analyses (see section 3.5.1.1). These different responses were confirmed by the linear regression slopes and correlation coefficients between their yields and irrigation levels (Figure 9). In addition, the genotype 74TA264 exhibited the maximum response in seed yield to irrigation, while ILL121 was the least responsive genotype to irrigation as shown in the following table.

Genotype	Season	Seed yield/plant (g)*		Increase or decrease over T_1 (%)	Average over years
		T_1	T_3		
74TA264	1984-85	1.69	3.00	77.5	68.9%
	1985-86	0.98	1.57	60.2	
ILL 121	1984-85	1.78	1.58	-11.2	-19.0%
	1985-86	1.01	0.74	-26.7	

* Average of 3 replicates

The morphology of root systems of the genotypes in both anaerobic soil (W) and in well-aerated soil (D) is shown in Plate 1. Little difference was detected in root growth of ILL121 under the two treatments employed. In both treatments the root lengths were the same, only slightly increased root branching (laterals) occurring in treatment W. The genotype 74TA264, under anaerobic conditions showed a remarkably short root length with a large number of shallow laterals compared with its root system development in well-aerated soil.

The anatomy of roots for both genotypes under W and D conditions is illustrated in Plate 2. Microscopic examination showed that there were no anatomical differences in root structures of either ILL121 or 74TA264 in well-aerated soil (D). Under anaerobic conditions (W),

ILL 121, Y = 0.37 + 0.0022
r = 0.30
74TA264, Y = -3.59 + 0.0138
r = 0.88

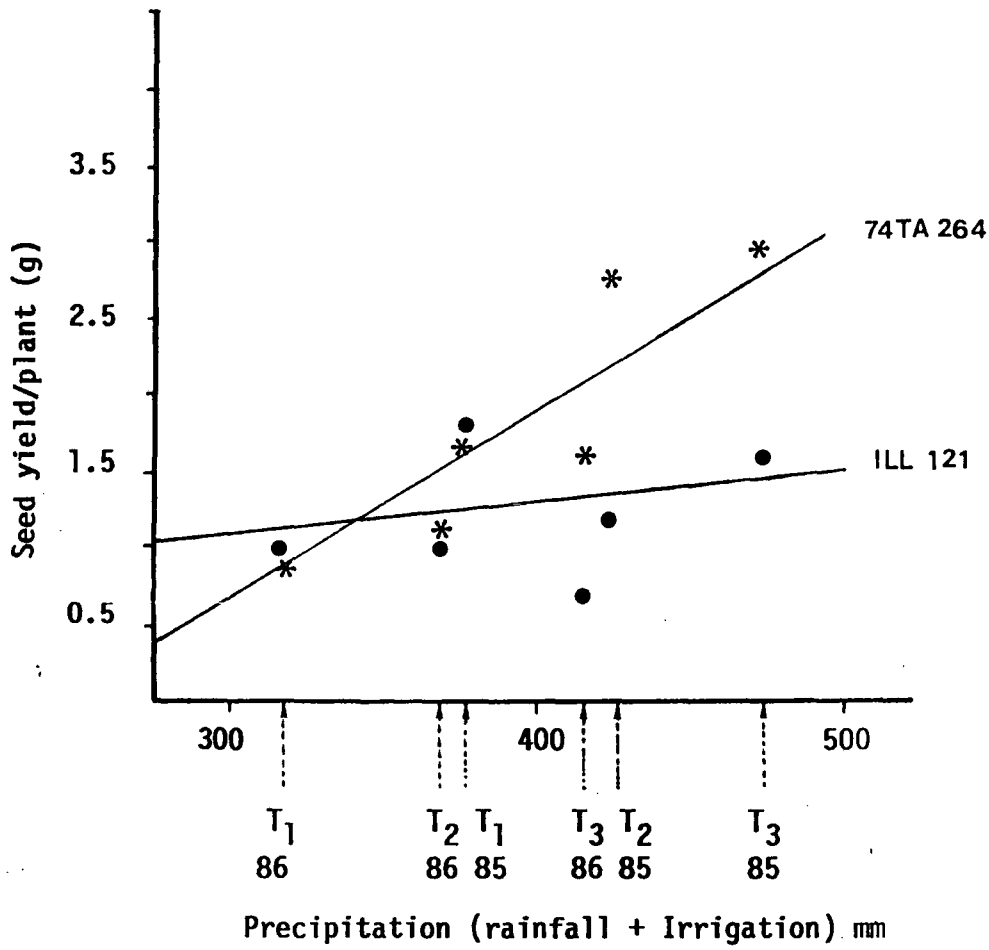


Figure 9. The relationship between seed yield and irrigation levels of 74TA264 and ILL 121 grown under irrigation at Tel Hadya in 1984-85 and 1985-86.

Plate 1

Differences in root system of two genotypes grown in a well-aerated and anaerobic soils environment

Genotypes:

- ILL 121
- 74TA264

Soil conditions:

D = well-aerated

W = Anaerobic

Plate 1

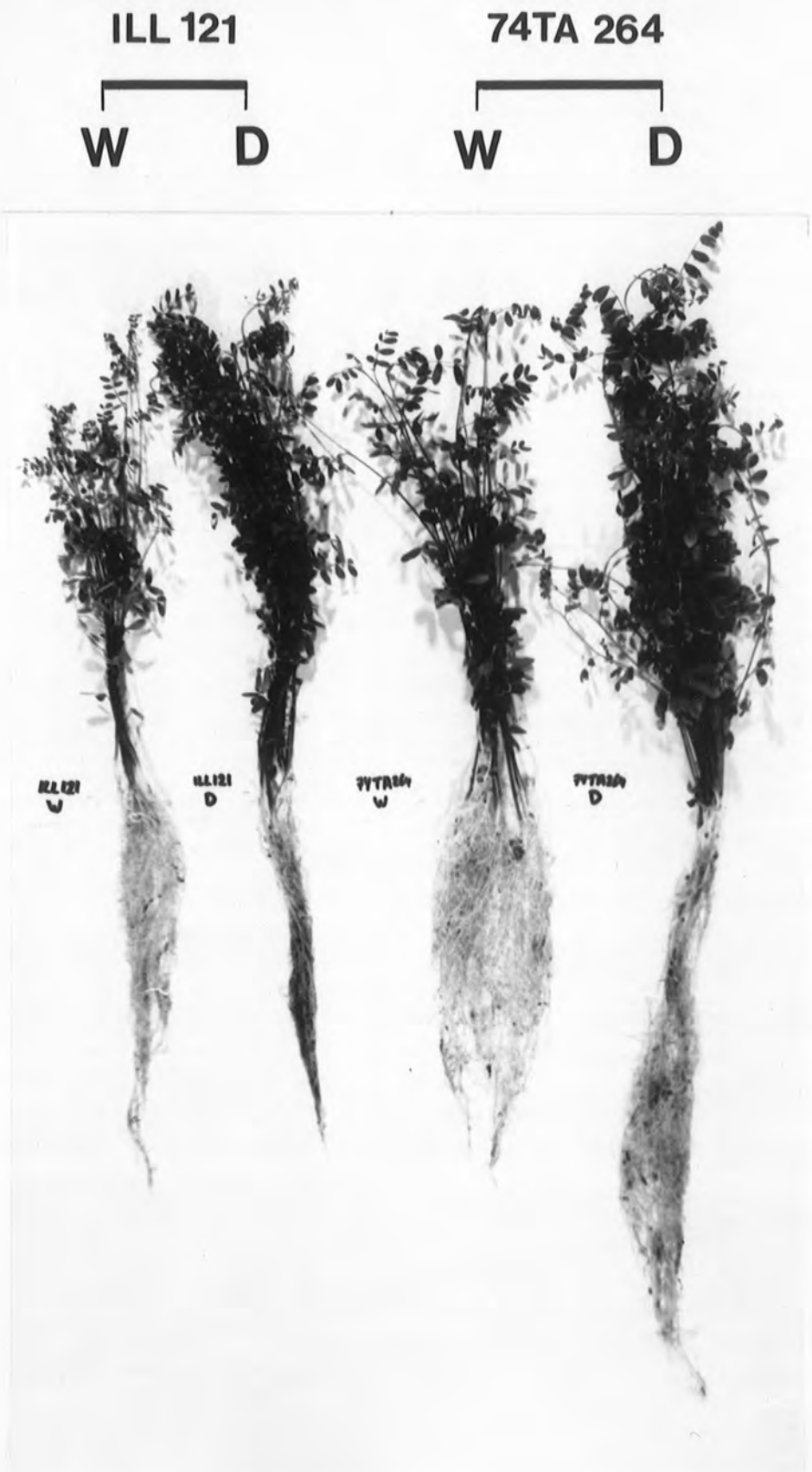


Plate 2

Fluorescence micrographs of root structures of two lentil genotypes grown in well-aerated and anaerobic soils environment.

Genotypes:

1 = ILL 121

2 = 74TA264

Soil conditions:

D = well-aerated

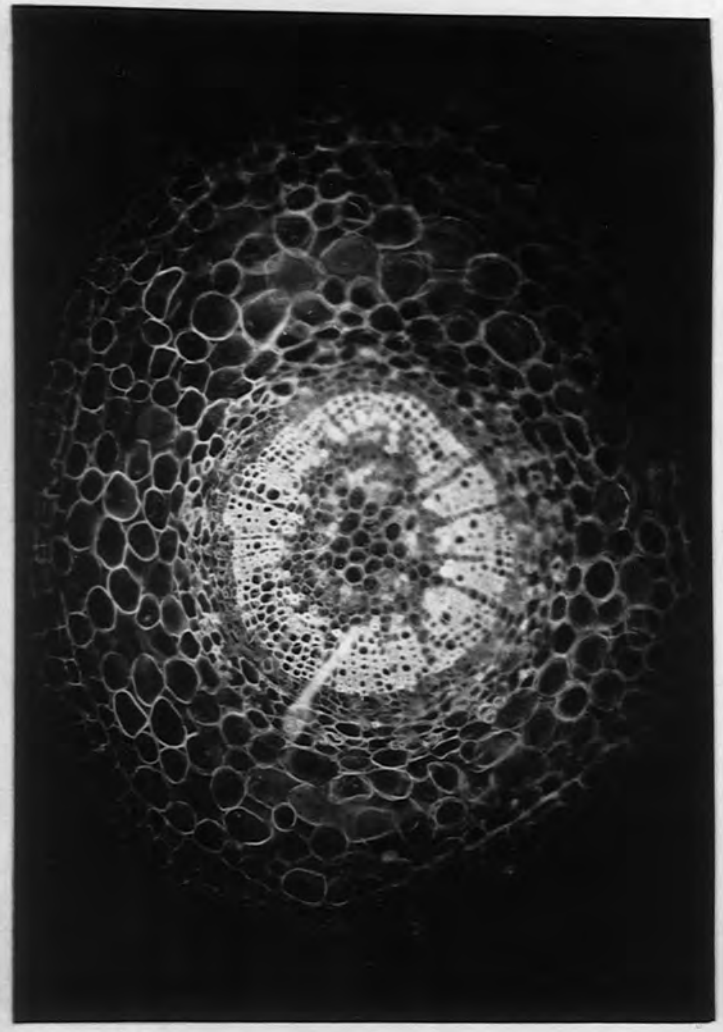
W = anaerobic

A = the air spaces formed in the root cortex of 74TA264 under oxygen deficiency (anaerobic condition).

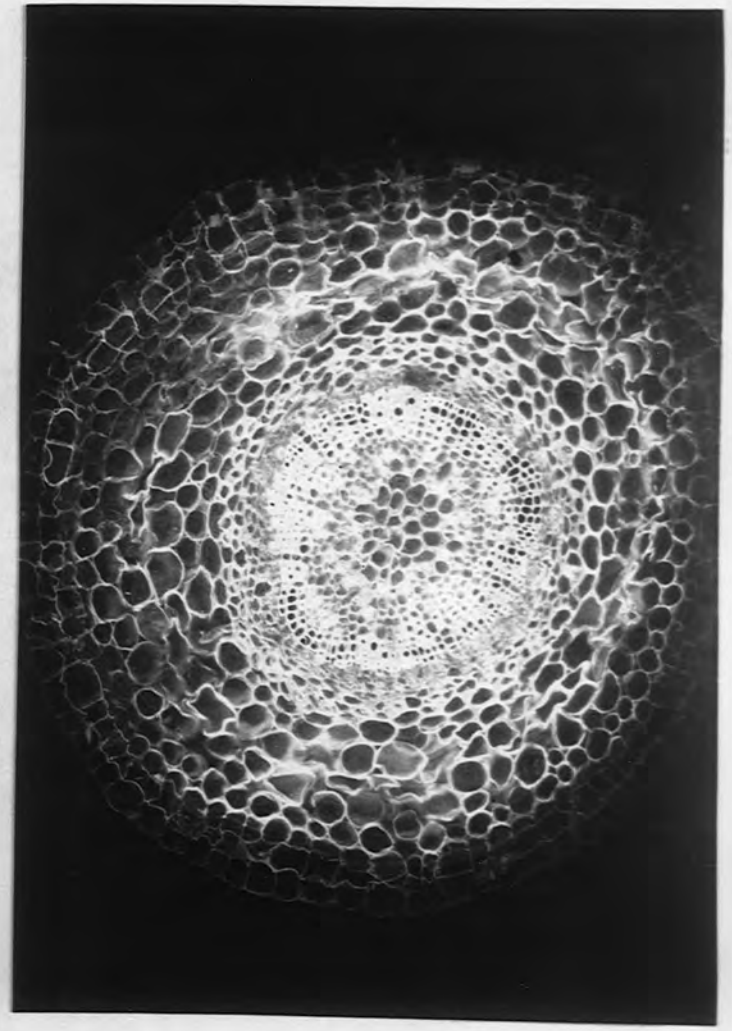
Magnifications:

D, 1 and 2 = 241

W, 1 and 2 = 386

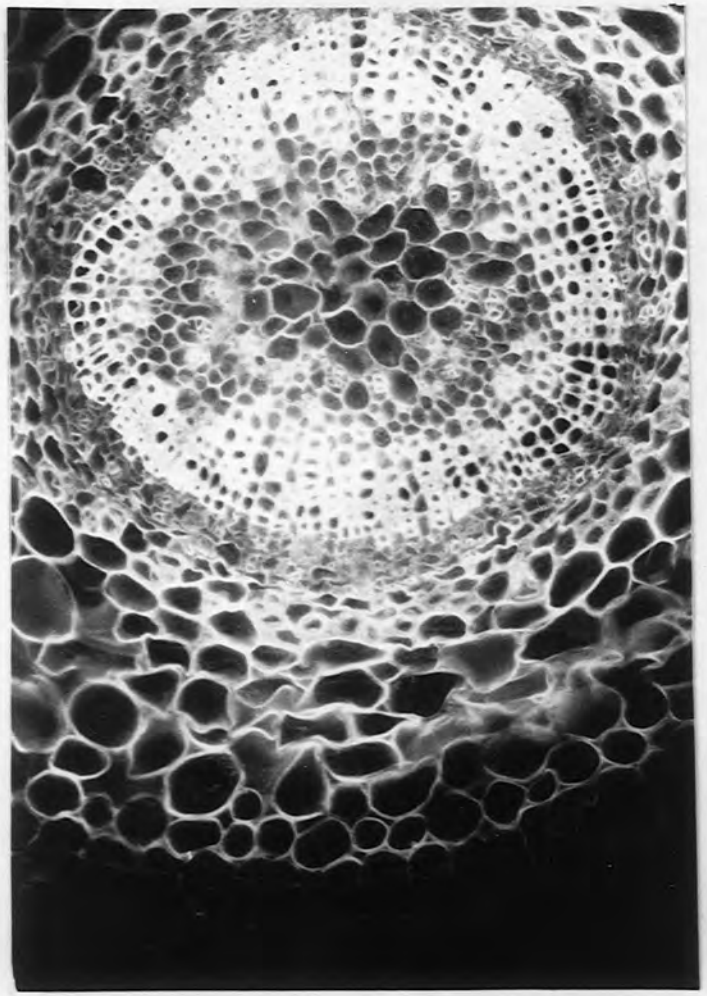


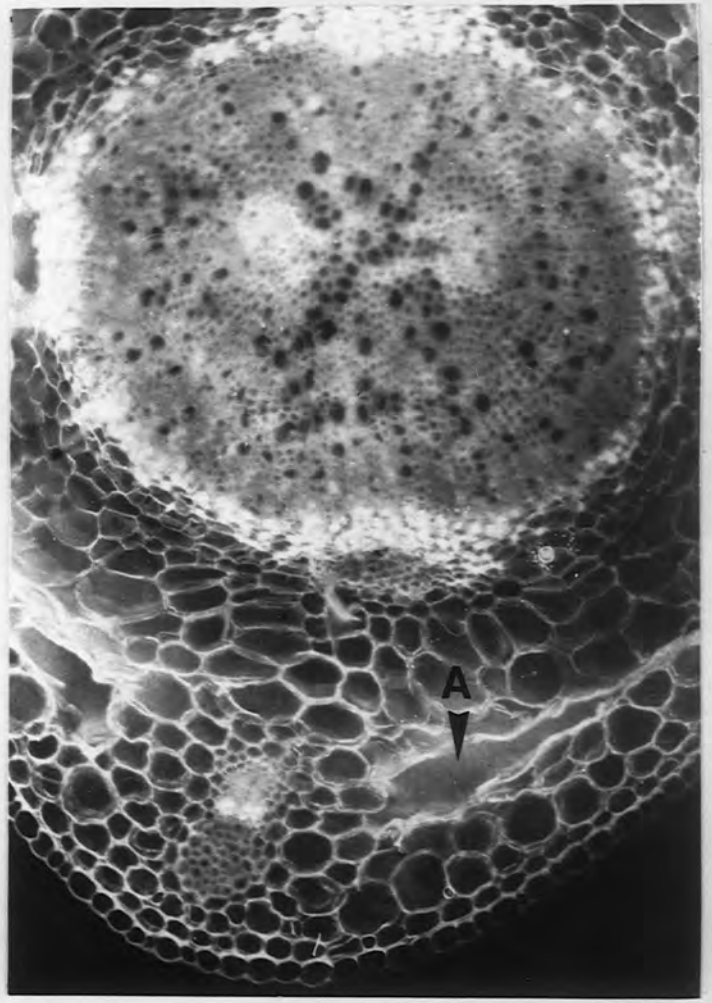
1



2

Plate 2; D





1

2

Plate 2; W

ILL121 also did not show any difference in its root structure, whereas in 74TA264 air spaces were well developed in the root cortex (Plate 2, A).

The results showed that both genotypes had a similar root anatomy and morphology under normal soil conditions, while under oxygen deficiency only 74TA264 formed cortical air spaces (aerenchyma), improving its internal aeration.

Metabolism in roots of plants grown under well-aerated conditions, unadapted to oxygen deficiency, continuously depends on supplies of oxygen from the soil. Low concentrations of dissolved oxygen at the root surface (only 0.01-0.03 atm) are often adequate for root metabolism (Greenwood and Goodman, 1971 and Armstrong and Gaynard, 1976). Under anaerobic conditions, root growth and function, for unadapted plants, are inhibited with adverse effects on shoot development (Yu et al., 1969 and Purvis and Williamson, 1972). In adapted plants adventitious roots, modified by the presence of air spaces formed by the collapse of cells in the cortex, grow from the base of the shoot (Jackson, 1955; Kramer, 1951).

This anatomical adaptation is particularly important to the continued growth or survival of plants in anaerobic conditions (Drew et al., 1980), because aerenchyma is usually regarded as an important adaptation that improves the oxygen supply to roots growing in poorly aerated soil.

The anaerobic conditions reduced the root penetration of 74TA264 as shown by its short roots compared with those in well-aerated soil. However, this genotype compensated by developing a large number of shallow laterals under anaerobic conditions, in the surface layer of soil which became drier and better aerated than the deep layer, reducing the influence of oxygen deficiency. A number of studies of pot-grow fababeans have shown that water regime can have dramatic effects on root distribution (Jones, 1963 and El-Nadi et al., 1969).

3.5.3 Phenotypic stability

In this section the seed yield data from five environments (T_1, T_2, T_3, Ter and Br) in 1984-85 and 1985-86 were used for stability analysis. The analysis of variance of seed yield per plant is presented in Table 27.

The genotype-environment mean square was highly significant indicating that genotypes differed markedly in response to environmental change. The genotype-environmental (linear) sum of squares was a large portion of genotype-environmental interaction. Although pooled deviation variance was highly significant, the genotype-environment (linear) variance was more than three times greater than pooled deviation variance. These results indicated that the linear component was the more important component of the genotype-environmental interaction.

The individual mean seed yield ($\bar{x}$) for the 34 genotypes along with their regression coefficients (b), deviation from regression coefficients (S^2d) and coefficients of determination (R^2) are given in Table 28. Seed yield per plant averaged from 0.76 to 1.61g. Nine genotypes had regression coefficients significantly different from unity, and all of these entries exhibited deviation from regression equal to zero. Seven of the same genotypes had a similar regression slope ($b \neq 1$) in the earlier analysis (Table 25). Also most of these nine genotypes had high R^2 values.

The remaining genotypes (25 entries) exhibited regression coefficients equal to unity, and out of these entries nine genotypes had significant S^2d (Table 28). These nine entries also showed relatively low R^2 estimates. Five of these nine entries had shown significant S^2d in the earlier analysis (Table 25).

The responses of these genotypes to the environmental change are shown graphically, according to Finlay and Wilkinson (1963), in Figures 10 and 11. In view of the overall similarity of these results to the analysis discussed earlier (3.5.1.1), we will discuss them briefly.

Table 27 Pooled analysis of variance for seed yield/plant of 34 lentil genotypes grown under five environments in two years

Source of variation	D.F.	Mean square
Genotype	33	0.694**
Genotype-environment + environment	306	0.376**
Environment (Linear)	1	93.042**
Genotype-environment (Linear)	33	0.182**
Pooled deviation	272	0.058**
Pooled error	660	0.036

*, ** Significant at 0.05 and 0.01 level of probability respectively.

Table 28 The average performances of 34 lentil genotypes grown at five environments in two years

No.	Genotype	Mean seed yield/plant ($\bar{X}$)	Regression coefficient (b)	Deviations from regression (S^2d)	Coefficient of determination (R^2)
1	Giza 9	1.33	0.95		0.82
2	Fam. 130	1.14	0.91		0.92
3	Selaim	1.08	0.90		0.90
4	ILL 1693	0.90	0.74*		0.90
5	ILL 1983	0.76	0.48*		0.69
6	Ill 40	1.23	0.91		0.95
7	ILL 241	1.46	1.25*		0.95
8	SLL	1.61	1.38	x	0.79
9	SLS	1.23	1.09	x	0.73
10	Jord.loc.	1.52	1.23	x	0.80
11	76TA66005	1.46	1.20		0.92
12	78S26003	1.36	1.10	x	0.80
13	78S26004	1.50	1.03	x	0.69
14	76TA66088	1.43	1.17		0.95
15	Ill 857	1.48	1.20		0.96
16	Laird	1.02	1.02	x	0.80
17	Ill 121	0.99	0.78		0.83
18	74TA161	0.97	0.93		0.93
19	Lenka	0.95	0.91		0.90
20	Okula	0.77	0.71*		0.88
21	74TA276	1.53	1.35*		0.92
22	74TA212	1.29	1.33	x	0.79
23	ILL 274	1.18	1.16	x	0.85
24	ILL 355	1.01	0.86		0.96
25	ILL 358	1.27	0.88		0.94
26	Precoz	1.22	0.85	x	0.75
27	Pant.L,406	0.82	0.56*		0.81
28	ILL 2526	0.88	0.49*		0.62
29	ILL 2573	0.77	0.54*		0.85
30	74TA264	1.51	1.46*		0.88
31	FLIP 84,1-L	1.35	1.18		0.96
32	FLIP 84,27-L	1.49	1.17		0.91
33	FLIP 84,67-L	1.50	1.12		0.91
34	FLIP 84,78-L	1.48	1.16		0.90

Grand mean 1.22

* Denotes genotypes had a significant regression coefficient greater or less than 1.0.

x Denotes genotypes had a deviation from regression significantly different from zero.

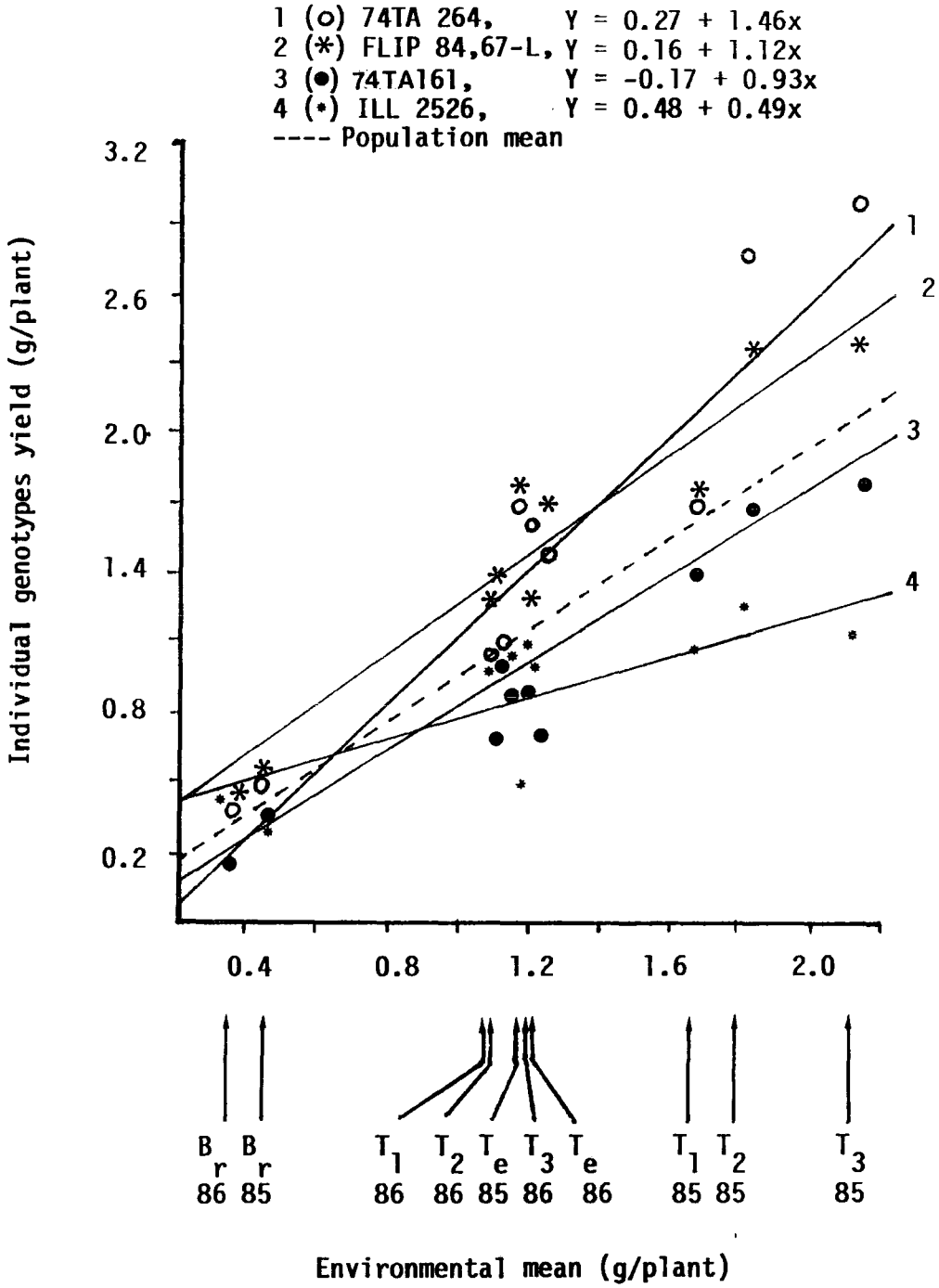


Figure 10. Regression lines, showing the relationship of individual yields of four genotypes and population mean of 34 genotypes of lentil grown at five different levels of water supply in two years.

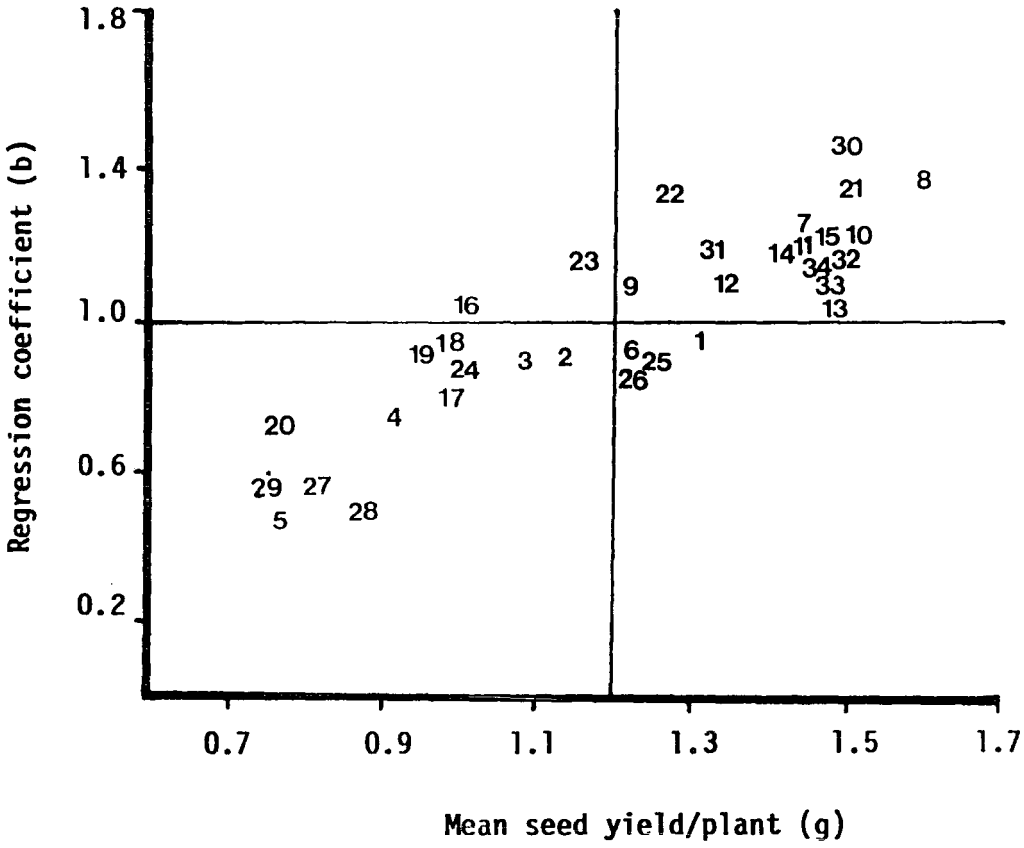


Figure 11. Adaptation of seed yield showing mean yield/plant and regression coefficients for 34 genotypes. Points on the figure are indicated by the serial number of genotypes (as presented in Table 28).

The genotype FLIP84-67L gave seed yields/plant greater than the environmental mean in all environments. The low variance estimate of this genotype of 0.418 reflected the low variability of its performance over environments. The results of this genotype indicated that it could be considered a most stable genotype. Other stable genotypes, were nos.: 1, 6, 11, 14, 15, 25, 31, 32 and 34 (Table 28 and Figure 11).

Conversely, 74TA161 gave a seed yield below average yields in all environments (Figure 10). Its variance over environments was also low (0.281). Furthermore, this genotype had a regression coefficient of unity (Table 28). Consequently this entry can be considered to be poorly adapted to all environments. This group included Family 130 (an Egyptian line), Selaim (the Sudanese local cultivar), ILL121, Lenka and ILL355.

Genotype 74TA264 showed again specific adaptation to the high yielding environments (two irrigations). Consequently this genotype showed the highest variance value of 0.732. This group included also ILL241 and 74TA276 and all these three entries had b values greater than 1 (Figure 11).

Six genotypes exhibited regression coefficients of less than unity and low average yield (Figure 11). These genotypes are represented, in Figure 10, by ILL2526. This genotype also exhibited low variance estimate of 0.118 over environments. Consequently, these genotypes can be considered specifically adapted to dry conditions (as at Breda).

Another approach to analyze adaptation was used for these genotypes which showed adaptation to dry conditions in the stability analysis. This test is the drought susceptibility index (Fischer and Maurer, 1978). This index was calculated for these six genotypes (group 1) in addition to the other four genotypes (group 2) which represented different adaptation types. The results are given in Table 29.

The rankings of susceptibility indexes (S) are exactly the reverse of those derived from relative yield (Y_d/Y_p) under drought. Values of S probably represent a precise comparison of drought susceptibilities. ILL2526 had the lowest S value, confirming its adaptability to dry

conditions, whereas 74TA264 exhibited the largest value, reflecting its lack of adaptation to dry conditions. Comparing the two groups, genotypes of group 1 had average seed yields/plant in the dry environment of 0.29g and their mean S was 0.93, while group 2 had a seed yield of 0.39g with a mean S value of 1.0.

FLIP84-78L and FLIP84-67L produced high yields in the dry site, but they showed susceptibility to this condition, reflected in their high S values (Table 29). In comparison ILL2526 had the lowest S value and the highest Y_d/Y_p ratio; also its yield, in Breda, was relatively high and ranked third. These results confirmed the adaptation of this genotype to dry conditions.

The importance of linear regression has been emphasized by many workers. Finlay and Wilkinson (1963) used simple linear regression as a measure of phenotypic stability to describe varietal adaptability to a range of environments. Eberhart and Russell (1966) emphasized the need to consider both the linear (b) and non-linear (S^2d) components of genotype-environment interactions in judging the phenotypic stability of a genotype. Breese (1969) and Paroda and Hayes (1971) emphasized that the linear regression should simply be regarded as a measure of the response of a particular genotype, whereas the deviation around the regression line should be considered as a measure of stability.

Recently, Lin *et al.* (1986) reported that the deviation from regression component does not represent the genotype's stability as stated by Eberhart and Russell (1966). They mentioned that the deviation from regression indicates no more than how good is the fit, but has no direct bearing on the genotype's stability. A poor fit, i.e., R^2 is small or S^2d is large should be taken as an indication that the use of the regression model to estimate stability is not adequate.

Accordingly, the genotypes which showed significant S^2d, most of which also had small R^2, were indicated in each character and were not used in regression analysis.

Study of genotype-environment interaction has led to identification of stable genotypes which could be used in future breeding programmes. It was possible to judge the phenotypic stability

Table 29 Seed yield/plant at the dry environment (Br, 1986) and at the wet environment (T_3, 1985) for 10 lentil genotypes with their drought susceptibility index (S) and relative yield (Y_d/Y_p).

	Genotype	Seed yield at Breda (Y_d)	Seed yield at T_3 (Y_p)	S	Y_d/Y_p
1.	ILL 1693	0.25	1.48	1.00	0.17
2.	ILL 1983	0.33	1.21	0.87	0.27
3.	Okula	0.15	1.43	1.07	0.11
4.	Pant.L406	0.32	1.40	0.93	0.23
5.	ILL 2526	0.42	1.12	0.75	0.38
6.	ILL 2573	0.25	1.20	0.95	0.21
7.	74TA264	0.37	3.00	1.05	0.12
8.	FLIP 84,67-L	0.43	2.36	0.98	0.18
9.	FLIP 84,78-L	0.53	2.25	0.92	0.23
10.	ILL 161	0.24	1.83	1.04	0.13

Group 1 = genotype 1-6

Group 2 = genotype 7-10

of the 34 genotypes of lentil included in this study using the definition of the term "stability". Consideration was also given to the mean performance and the linear response of the individual genotypes.

In contrast, genotypes FLIP84-67L, FLIP84-27L, FLIP84-78L and ILL857 were found to be the most stable and high yielding genotypes. These genotypes can be recommended for planting under the varying annual rainfall conditions of the Mediterranean area. According to Eberhart and Russell (1966), Syrian Local Large (SLL), Syrian Local Small (SLS) and Jordanian Local were considered unstable genotypes as they showed high deviation from regression.

The environments included in this study varied widely in rainfall, ranging from 203mm to 446mm, as well as in temperature and soil type, and thus produced wide variation in seed yield. This variation allowed a comparison between genotypes and allowed selection of some entries adapted to drought condition. The results showed that the absolute plant yield under water stress is a poor estimate of drought resistance. Yield under stress is affected by genotypes yield potential (Fischer and Maurer, 1978). Also, yield under stress alone is not a reliable selection criterion because the genetic component of variation relative to the environmental component of variation in yields is usually low under stress (Frey, 1964; Johnson and Frey, 1967 and Dady et al., 1973). The use of a susceptibility index circumvents the problem of disassociating the effect of drought resistance from that of potential yield on the performance of a genotype under stress. Consequently, this method in addition with stability analysis can allow reliable prediction of drought resistant genotypes.

ILL2526 showed adaptation to dry conditions and exhibited the lowest index of susceptibility. This genotype could be recommended for cultivation in dry areas and use in a hybridization programme as a source of drought tolerance.

4. Genetic analysis of variation between crosses

As a preliminary to the genetic analyses of the F_1 and F_2 data, analyses of variance were made to determine the significance of differences between the genotypes studied. The analyses of variance were performed firstly on the 8 parents, secondly on the 8 parents and their 28 F_1 crosses and finally on the 8 parents and their 28 F_2 crosses for 10 characters. Analyses of variance were also undertaken for the F_1 and F_2 crosses separately. In each case, F values were highly significant, indicating that genetic variation exists and that a genetic analysis could be appropriately undertaken for all variables.

This section will include the following sections : (1) performance of parent al lines, (2) study of the heterosis of F_1 hybrids, (3) combining ability analysis (by Griffing's method), (4) Jinks-Hayman analysis, including graphical analysis and (5) prediction of the promising genotypes and crosses for future generations.

4.1 Performance of parental lines

The mean values over replications of the eight parents are given in Table 30. The results presented show highly significant differences among parental genotypes for biological yield/plant, seed yield/plant, straw yield/plant, number of pods/plant, number of seeds/pod, 100 seed weight, plant height, time to flowering, time to maturity and seed protein.

The genotype FLIP84—1 L ranked first for seed yield/plant and second for biological yield/plant and straw yield/plant, whereas parent ILL274 had the highest values of biological yield/plant. The genotype Pant.L,406 from India gave the lowest values for most of the characters amongst the parents.

ILL274 gave the highest mean number of pods/plant, but it had a moderate 100 seed weight. FLIP84—1 L which had a moderate number of pods/plant, was ranked first for 100 seed weight. The high seed yield potential of this parent is probably due to its superiority in seed weight.

Table 30 Mean performance and standard errors of eight parents for 10 characters

Parents	Biological yield /plant (g)	Seed yield/ plant (g)	Straw yield/ plant (g)	No. of pods/ plant	No. of seeds/ pod	100-seed weight (g)	Plant height (cm)	Time to flowering (days)	Time to maturity (days)	Seed protein %
Giza 9	2.73	1.13	1.60	18.5	1.76	3.50	39.4	111.5	160.5	23.90
Family 370	2.70	0.83	1.87	17.5	1.50	3.13	37.5	101.0	157.0	24.50
78S26004	3.17	1.30	1.87	26.1	1.02	4.96	37.2	107.0	156.5	23.80
Precoz	2.90	1.27	1.63	18.0	1.62	4.52	36.0	99.5	142.5	24.70
Pant.L406	1.27	0.60	0.67	15.7	1.70	2.17	28.9	103.5	146.0	23.15
FLIP 84,1-L	4.20	1.53	2.67	20.7	1.28	5.81	42.0	109.0	162.0	23.35
ILL 274	4.33	1.23	3.10	26.1	1.37	3.48	45.5	124.0	166.0	24.20
ILL 121	2.93	0.93	2.00	21.1	1.56	2.84	44.7	125.5	164.5	25.05
Mean	3.03	1.10	1.93	20.44	1.48	3.80	38.86	110.13	156.88	23.61
SE±	0.78	0.37	0.44	6.06	0.17	0.13	2.95	1.13	3.14	0.36

The genotype Precoz ranked first for earliness in both flowering and maturity. Genotype ILL121 ranked last to flower, but ILL274 and ILL121 were latest to maturity. The two Egyptian lines Giza9 and Family 370 displayed low to moderate values for most characters, except for the number of seeds/pod, where Giza 9 ranked first. The highest level of seed protein content was found in the late-maturing genotype ILL121, which also produced a low seed yield/plant.

Although information of the kind given in Table 30 is of some help to plant breeders when choosing parents, it tells nothing about their performance in hybrid combination nor the extent to which characters highly expressed in different parents can be brought together in the offspring. For example, if attempts are made to raise seed yield by combining the large seed of "FLIP 84 - I L" and the high seeds/pod of "Giza9", it is very likely that a biological limit would be reached so that some other character, perhaps number of pods per plant would be reduced. Because of these limitations, there is little prospect of discerning which pairs of cultivars will combine advantageously without actually making the crosses. However, if information could be obtained about the genetic system controlling these characters it would be easier for the plant breeder to predict the potential performance of certain cultivars or crosses in later generations, from their performance in the F_1 and F_2 generations.

4.2 Heterosis

Heterosis in the F_1 generation was studied for 10 lentil characters viz; biological yield/plant, seed yield/plant, straw yield/plant, number of pods/plant, number of seeds/pod, 100 seed weight, plant height, time to flowering, time to maturity and seed protein. Heterosis and inbreeding depression results are summarized in Table 31.

4.2.1 Yield characters

The yield characters, i.e. biological yield/plant, seed yield/plant and straw yield/plant will be presented and discussed together.

The hybrid values, expressed as superiority of F_1 crosses over the mid-parent values, were significant for all characters. The hybrid advantage for seed yield/plant, which was 31.8% over all crosses, showed the highest value among all these traits (Table 31). Heterosis value was 24.8% and 23.7% for biological yield/plant and straw yield/plant, respectively. The useful heterosis, expressed as superiority of F_1 over the better parent in to the cross, was 13.6% for seed yield/plant. This value also exceeded that estimated for biological yield/plant (9.3%). No heterosis over the better parent was observed for straw yield/plant.

The average heterosis over crosses belies the variation between individual crosses. The heterosis for each cross was calculated on the basis of mid-parent value, higher parent involved in the cross and inbreeding depression effect. The number of crosses showing significant heterotic and inbreeding effects is presented in Table 31.

The numbers of F_1 hybrids significantly exceeding the mid-parent were 12 for each of biological yield/plant, seed yield/plant and straw yield/plant. However, out of those F_1 crosses which exhibited heterosis, 10 crosses showed significantly useful heterosis for biological yield/plant and 7 crosses for seed yield/plant and straw yield/plant. The heterosis values over the mid-parent ranged from a

Table 31. Average performance of parents (Fo), F1, F2 generation, and overall heterosis measured as deviation of F1 hybrids from mid parent ($\overline{MP}$) and better parent ($\overline{BP}$) values and inbreeding depression of 10 lentil characters

		Biological yield/ plant	Seed yield/ plant	Straw yield/ plant	No. of pods/ plant	No. of seeds/ pod	100 seed weight	Plant height	Time to flowering	Time to maturity	Seed protein
Generation mean	F_o	3.03	1.10	1.93	20.4	1.476	3.80	39.9	110.13	156.88	23.61
	F_1	3.77	1.46	2.31	28.7	1.496	3.52	39.5	110.04	158.62	23.45
	F_2	3.63	1.36	2.27	28.0	1.495	3.40	39.8	109.14	158.52	23.62
Heterosis %	(1)	24.8**±8.35	31.8**±10.66	23.7**±7.68	40.3**±10.66	1.3±1.56	---	1.6±1.76	-0.1±0.67	---	---
	(2)	9.3±5.99	13.6±7.04	----	26.3**±8.11	---	---	---	---	---	---
Inbreeding depression	(3)	3.7±7.53	6.9±7.91	1.7±7.70	2.4±8.99	0.1±2.76	3.4±1.80	-0.76±2.06	0.8±0.82	0.1±0.27	-0.7±0.72
No.of F_1's significantly exceeded	$\overline{MP}$	12	12	12	11	1	2	6	8	4	0
	$\overline{BP}$	10	7	7	10	0	0	2	1	1	0
No.of crosses significantly exhibited inbreeding depression		1	1	1	1	0	0	0	2	0	0

*,** Significant at 0.05 and 0.01 level of probability, respectively.
(1) $(\bar{F}1 - \overline{MP})/\overline{MP} \times 100$ (2) $(\bar{F}1 - \overline{BP})/\overline{BP} \times 100$ (3) $\bar{F}1 - \bar{F}2/\bar{F}1 \times 100$
--- Not calculated since F1 value was less than $\overline{MP}$ and/or $\overline{BP}$ values.

lowest negative value of -34.1% up to 107.2% for biological yield/plant, from -30.7% to 110.5% for seed yield/plant and from -31.6% to 104.7% for straw yield/plant. In comparison, the ranges of useful heterosis were (-44.3% to 86.1%), (-36.6% to 78.9%) and (-35.5% to 78.5%) for those characters, respectively.

Of the seven F_1 crosses which showed useful heterosis for seed/yield plant, three involved the parent 78S26004; these being 78S26004 x Precoz, 78S26004 x Pant.L,406 and 78S26004 x ILL121 (Table 33). In three other crosses, ILL121 was involved as a common parent; these were: Giza9 x ILL121, 78S26004 x ILL121 and ILL274 x ILL121. Data presented in Table 33 show that parents 78S26004 and ILL121 had the highest F_1 array means among all the parents. The same trend occurred for the other two yield characters. ILL121 which was involved in four crosses and 78S26004, involved in three crosses, showed significant useful heterosis for biological yield/plant. In straw yield/plant, each of 78S26004 and ILL121 involved in three crosses showed significantly useful heterosis. The data in Tables 32 and 34 show that the array means of ILL121 and 78S26004 were ranked second and third respectively in both biological and straw yield/plant. The four F_1 crosses, which showed significant useful heterosis for seed yield/plant, also showed heterosis for biological and straw yield per plant.

Inbreeding depression, estimated as the average percent decreases of the F_2 from the F_1 were 3.7%, 6.9% and 1.7% for biological yield/plant, seed yield/plant and straw yield/plant, respectively. However these estimates were not significant. Although the numbers of individual F_2 crosses showing inbreeding depression were 12, 14 and 13 for these three characters respectively, in only one F_2 cross for each character did inbreeding depression reach the level of statistical significance. Comparing the three yield traits seed yield/plant, which exhibited the greatest amount of heterosis, showed the most inbreeding depression. A similar observation was reported by El-Hosary (1981) and Nassib (1982) in faba bean crosses. They found significant heterotic effects and highly significant inbreeding depression for seed yield/plant. Nassib (1982) pointed out that the significant inbreeding depression indicated that observed heterosis in F_1's is real.

Table 32 Mean performance, over replicates, of parents and their arrays of 8 x 8 diallel crosses for biological yield/plant in F_1 and F_2 generations

Parent	Giza 9	Fam.370	78S26004	Precoz	Pant.L,406	FLIP84,1-L	ILL 274	ILL 121	Array mean (F_1)
Giza 9	2.73	4.03**	2.30	3.97**	3.73**	3.17	3.70	4.60**	3.53
Fam. 370	2.77	2.70	4.13*	4.23**	2.30	2.73	4.90*	3.27	3.54
78S26004	2.37	3.37	3.17	4.63**	4.60**	4.40	3.67	5.90**	4.10
Precoz	3.83	4.37	5.27	2.90	2.33	2.34	4.27	4.50**	3.65
Pant.L,406	2.00	2.50	3.20	3.07	1.27	2.43	3.17	2.57	2.80
FLIP84, 1-L	2.87	3.57	4.73	5.57	3.07	4.20	4.33	3.73	3.42
ILL 274	4.27	4.07	4.00,	3.47	6.10	4.33	4.33	5.63**	4.25
ILL 121	3.63	2.10	2.40	2.70	2.70	3.73	5.63	2.93	4.14
Array mean (F_2)	3.06	3.18	3.56	3.90	2.74	4.01	4.28	3.23	

- The diagonal values (underlined) represent the parent means.
- F_1 means are above diagonal values and F_2 means below diagonal values.
- Array means include parental means.

*,** F_1 crosses exhibited significant heterosis over $\overline{MP}$ and $\overline{BP}$, respectively.

Table 33 Mean performance, over replicates, of parents and their arrays of 8 x 8 diallel crosses for seed yield/ plant in F_1 and F_2 generations

Parent	Giza 9	Fam. 370	78S26004	Precoz	Pant.L406	FLIP 84, 1-L	ILL 274	ILL 121	Array mean (F_1)
Giza 9	1.13	1.60*	0.87	1.37	1.73**	1.10	1.17	1.83**	1.35
Fam. 370	1.03	0.83	1.67*	1.80*	0.93	1.07	2.14**	1.23	1.41
78S26004	0.90	1.17	1.30	2.00**	2.00**	1.03	1.37	2.33**	1.57
Precoz	1.57	1.77	1.87	1.27	1.03	0.97	1.57	1.57*	1.45
Pant.L406	0.83	0.97	1.30	1.13	0.60	0.97	1.17	1.10*	1.19
FLIP 84,1-L	1.00	1.50	1.70	1.80	1.37	1.53	1.63	1.30	1.20
ILL 274	1.63	1.50	1.47	1.37	2.50	1.63	1.23	2.20**	1.56
ILL 121	1.27	0.73	0.87	0.60	1.07	1.30	2.20	0.93	1.56
Array mean (F_2)	1.17	1.19	1.32	1.42	1.22	1.48	1.69	1.12	

- The diagonal values (underlined) represent the parent means.
- F_1 means are above diagonal values and F_2 means below diagonal values.
- Array means include parental means.

*,** F_1 crosses exhibited significant heterosis over $\overline{MP}$ and $\overline{BP}$, respectively.

Table 3 4 Mean performance,over replicates, of parents and their arrays of 8 x 8 diallel crosses for straw yield /plant in F_1 and F_2 generations

Parent	Giza 9	Fam. 370	78S26004	Precoz	Pant.L406	FLIP 84, 1-L	ILL 274	ILL 121	Array Mean (F_1)
Giza 9	1.60	2.37*	1.43	2.60**	2.00*	2.07	2.53	2.77**	2.17
Fam. 370	1.73	1.87	2.47**	2.43*	1.37	1.67	2.76	2.03	2.12
78S26004	1.47	2.20	1.87	2.63**	2.60**	3.37*	2.30	3.57**	2.53
Precoz	2.27	2.60	3.40	1.63	1.30	1.47	2.70	2.93**	2.21
Pant.L406	1.17	1.53	1.90	1.93	0.67	1.47	2.00	1.47	1.61
FLIP 84,1-L	1.87	2.07	3.03	3.77	1.70	2.67	2.70	2.43	2.23
ILL 274	2.63	2.57	2.53	2.10	3.60	2.70	3.10	3.43**	2.69
ILL 121	2.37	1.37	1.53	2.10	1.63	2.43	3.43	2.00	2.58
Array mean (F_2)	1.89	1.99	2.24	2.48	1.77	2.53	2.83	2.11	

- The diagonal values (underlined) represent the parent means.
- F_1 means are above diagonal values and F_2 means below diagonal values.
- Array means include parental means.

*,** F_1 crosses exhibited significant heterosis over $\overline{MP}$ and $\overline{BP}$, respectively.

Variable inbreeding depression can be observed when comparing F_1 array means with their respective F_2 values for all of those three characters (Tables 32-34). For example, the ILL121 F_1 array mean for seed yield/plant was 1.56 (Table 33), this decreased to 1.12 in the F_2 generation accounting for approximately 28% inbreeding depression on average. In comparison, the array mean of Precoz was 1.45 in the F_1 and 1.42 in the F_2, indicating about 2% inbreeding depression only.

Variable degrees of heterosis have been found for seed yield in lentil. Goyal et al. (1976) found that heterosis over the better parent was 146%, while Singh et al. (1975) found values ranging from 42% to 267%, and El-Hady (1983) reported values between 20% to 257%. Conversely, Singh and Jain (1971) did not find heterosis over better parent and El-Hady (1983) found negative heterosis of -9.72% in one cross (Giza9 x Family 370).

4.2.2 Seed yield components

The heterosis of the characters, the number of pods/plant, the number of seeds/pod and 100-seed weight will be presented and discussed together as yield component characters.

Highly significant average heterotic effects expressed as percent increase of the F_1 hybrids over the average of the parents were found for number of pods/plant (40.3%) (Table 31). Useful heterosis was also exhibited for number of pods/plant, the value of 26.3% being highly significant. Low percentage heterosis was found for number of seeds/pod (1.3 ± 1.56) and no heterosis was shown for the 100-seed weight trait.

With respect to the heterosis of individual crosses, out of 28 F_1 hybrids, 11 cross combinations exhibited significant heterosis over the mid-parent for number of pods/plant. Only one cross showed significant heterosis over the mid-parent for number of seeds/pod and two crosses for 100 seed weight. Amongst yield components, useful heterosis was seen only in the number of pods/plant where in 10 F_1 crosses it significantly exceeded the better parent.

Table 35 Mean performance, over replicates, of parents and their arrays of 8 x 8 diallel crosses for number of pods/plant in F_1 and F_2 generations

Parent	Giza 9	Fam. 370	78S26004	Precoz	Pant.L406	FLIP 84, 1-L	ILL 274	ILL 121	Array Mean (F_1)
Giza 9	18.45	28.64**	14.20	22.69	32.56**	19.96	22.49	33.60**	24.07
Fam. 370	19.78	17.47	30.81	29.72**	19.78	20.17	39.19**	29.56*	26.92
78S26004	18.15	20.14	26.05	37.57**	48.30**	21.15	28.77	49.02**	31.98
Precoz	40.77	32.15	35.46	17.98	24.97	15.77	30.08	32.47**	26.41
Pant.L406	14.90	20.32	25.15	25.14	15.71	22.06	27.44	24.38	26.90
FLIP 84,1-L	19.25	26.46	31.53	32.93	38.25	20.71	29.39	22.91	21.52
ILL 274	32.07	33.70	21.17	26.42	63.86	35.18	26.07	45.52**	31.12
ILL 121	27.60	17.41	17.87	12.43	23.07	28.23	44.35	21.11	32.32
Array mean (F_2)	23.87	23.43	24.44	27.91	28.30	29.08	35.35	24.01	

- The diagonal values (underlined) represent the parent means.
- F_1 means are above diagonal values and F_2 means below diagonal values.
- Array means include parental means.

*,** F_1 crosses exhibited significant heterosis over $\overline{MP}$ and $\overline{BP}$, respectively.

Table 36 Mean performance, over replicates, of parents and their arrays of 8 x 8 diallel crosses for number of seeds/pod in F_1 and F_2 generations

Parent	Giza 9	Fam. 370	78S26004	Precoz	Pant.L406	FLIP 84, 1-L	ILL 274	ILL 121	Array mean (F_1)
Giza 9	1.76	1.72	1.68*	1.63	1.67	1.59	1.60	1.61	1.66
Fam. 370	1.72	1.50	1.48	1.70	1.57	1.58	1.64	1.47	1.58
78S26004	1.48	1.45	1.02	1.12	1.10	1.15	1.09	1.17	1.23
Precoz	1.54	1.45	1.19	1.62	1.52	1.49	1.27	1.52	1.48
Pant.L406	1.86	1.65	1.59	1.62	1.70	1.57	1.59	1.82	1.57
FLIP 84,1-L	1.45	1.68	1.20	1.35	1.49	1.28	1.41	1.65	1.47
ILL 274	1.57	1.35	1.52	1.43	1.40	1.23	1.37	1.47	1.43
ILL 121	1.53	1.50	1.33	1.64	1.80	1.45	1.39	1.56	1.53
Array mean (F_2)	1.61	1.54	1.35	1.48	1.64	1.39	1.41	1.53	

- The diagonal values (underlined) represent the parent means.
- F_1 means are above diagonal values and F_2 means below diagonal values.
- Array means include parental means.
* F_1 crosses exhibited significant heterosis.

Table 37 Mean performance, over replicates, of parents and their arrays of 8 x 8 diallel crosses for 100-seed weight in F_1 and F_2 generations

Parent	Giza 9	Fam. 370	78S26004	Precoz	Pant L406	FLIP 84, 1-L	ILL 274	ILL 121	Array mean (F_1)
Giza 9	3.50	3.36	3.68	3.67	3.21*	3.48	3.45	3.39	3.47
Fam. 370	3.05	3.13	3.70	3.58	3.01*	3.35	3.34	2.86	3.29
78S26004	3.37	3.88	4.96	4.78	3.77	4.28	4.44	4.10	4.21
Precoz	2.53	3.90	4.43	4.52	2.81	4.10	4.19	3.20	3.86
Pant.L406	3.02	2.88	3.25	2.78	2.17	2.84	2.75	2.49	2.88
FLIP 84,1-L	3.67	3.39	4.44	4.08	2.49	5.81	3.99	3.44	3.91
ILL 274	3.30	3.32	4.75	3.67	3.08	3.80	3.48	3.32	3.62
ILL 121	3.05	2.84	3.75	2.96	2.60	3.30	3.59	2.84	3.21
Array mean (F_2)	3.19	3.30	4.10	3.61	2.78	3.87	3.62	3.12	

- The diagonal values (underlined) represent the parent means.
- F_1 means are above diagonal values and F_2 means below diagonal values.
- Array means include parental means.

* F_1 crosses exhibited significant heterosis.

Those hybrids with significant useful heterosis for seed yield also showed significant heterosis for number of pods/plant. However, three crosses exhibited useful heterosis for number of pods/plant and did not reach the level of significance for useful heterosis of seed yield/plant (Giza 9 x Family 370, Family 370 x Precoz and Precoz x ILL 121) (see Table 35). These results indicate that heterosis for other characters does not always allow prediction of the degree of heterosis for yield. This is perhaps due to the inconsistent contribution of yield components to overall yield in different crosses as reported by Singh and Singh (1973) in green gram.

The average values of inbreeding depression were 2.4%, 0.1% and 3.4% for no. of pods/plant, no. of seeds/pod and 100 seed weight, respectively. Only one F_2 cross showed significant inbreeding depression for number of pods/plant.

Variable degrees of heterosis for yield component characters were also reported in lentil (Singh et al., 1975 and Goyal et al., 1976). Singh and Jain (1971) found that heterosis for seed yield was associated with heterosis in the yield components.

4.2.3 Plant height

The average heterotic effect expressed as percent increase of the F_1 hybrids over the parents was 1.6%, but this was not significantly greater than zero. The inbreeding depression value was negative (-0.8%) (Table 31) but not significantly less than zero, reflecting the negligible heterotic effect in this character.

With respect to individual heterosis, out of 28 F_1 crosses, 6 crosses showed significant heterosis expressed as percent increase above the mid-parent. In comparison, only two crosses exhibited significant useful heterosis; these hybrids were Family 370 x Precoz and 78S26004 x Precoz. The plant heights of those crosses were 41.7 cm and 42.3 cm, respectively (Table 38).

Out of eight crosses exhibiting no heterosis only one cross showed significant negative inbreeding depression, which means that the F_2 value exceeded that for its respective F_1 cross.

Table 38 Mean performance, over replicates, of parents and their arrays of 8 x 8 diallel crosses for plant height in F_1 and F_2 generations

Parent	Giza 9	Fam.370	78S26004	Precoz	Pant.L406	FLIP 84, 1-L	ILL 274	ILL 121	Array mean (F_1)
Giza 9	39.4	35.6	33.6	42.4*	37.1	35.3	40.0	42.0	38.2
Fam. 370	40.8	37.5	40.0	41.7**	34.0	39.9	42.1	43.8	39.3
78S26004	37.7	36.3	37.2	42.3**	35.5	40.1	35.6	40.5	38.1
Precoz	34.0	41.1	43.8	36.0	37.4*	32.7	42.2	47.4*	40.3
Pant.L406	35.2	36.5	38.6	40.7	28.9	37.7	41.4*	40.4	36.6
FLIP 84,1-L	42.2	38.6	41.7	42.6	36.6	42.0	42.5	38.6	38.6
ILL 274	35.7	40.9	39.2	40.7	39.5	42.5	45.5	44.2	41.7
ILL 121	43.8	34.5	41.9	44.4	40.9	38.6	44.2	44.7	42.7
Array mean (F_2)	38.6	38.3	39.6	40.4	37.1	40.6	41.0	41.6	

- The diagonal values (underlined) represent the parent means.
- F_1 means are above diagonal values and F_2 means below diagonal values.
- Array means include parental means.

*,** F_1 crosses exhibited significant heterosis over $\overline{MP}$ and $\overline{DP}$, respectively.

Negative heterosis of plant height was reported by El-Hady (1983) and Goyal et al. (1976), who noticed no significant heterosis for plant height in ten lentil hybrids.

4.2.4 Phenological characters

Time to 50% flowering and time to 90% maturity were used as criterion for earliness in this study, and will be discussed together.

The average of time to flowering of the F_1 hybrids was 110.0 days compared with 110.1 days for time to flowering in the parents (Table 31). The heterosis value was not significantly different from zero (-0.1%), but was negative in sign. No heterotic effect was detected in time to maturity.

Eight crosses showed significant heterosis over the mid-parent (negative values) for time to flowering and four crosses for time to maturity. In comparison, only one hybrid (Giza 9 x 78S26004) exhibited significant useful heterosis for both characters. This cross flowered at 103.7 days (Table 39) and matured at 152.8 days (Table 40), being 3.3 and 3.7 days earlier in flowering and maturity respectively than the earlier parent, 78S26004 (better parent).

Inbreeding depression was positive but not significant, being 0.8% and 0.1% for time to flowering and time to maturity, respectively. These values reflected the low heterotic effect for flowering and complete absence of heterotic effect for maturity. However, in the F_2 generations two crosses (78S26004 x Precoz and Precoz x Pant.L,406) flowered earlier than their F_1's (Table 39), showing significant inbreeding depression.

El-Hady (1983) also found a negative heterosis value of -6% for time to flowering in lentil. Mak and Yap (1977) reported no heterosis for time to flowering in long bean (Vigna sesquipedalis Fraw).

4.2.5 Seed protein

No overall heterotic effects were observed for this character on the basis of either mid-parent or better parent. The inbreeding

Table 39 Mean performance, over replicates, of parents and their arrays of 8 x 8 diallel crosses for time to flowering in F_1 and F_2 generations

Parent	Giza 9	Fam-370	78S26004	Precoz	Pant.L,406	FLIP84,1-L	ILL 274	ILL 121	Array mean (F_1)
Giza 9	111.5	103.3*	103.7**	108	114	114.5	114*	116.5	110.7
Fam. 370	104.5	101	104	104	104.5	105.5	103.7*	105*	103.9
78S26004	103.5	101	107	110	111	111.5	115	113.5*	109.5
Precoz	106	103	103.5	99.5	113	103.5	101.5*	111	106.3
Pant.L 406	110	108	110.5	102	103.5	111.5	115.5	104*	109.6
FLIP 84,1-L	110.5	110	112	102.5	104	109	116	121	111.6
ILL 274	114	111	111	103.5	113	116	124	122.5	114
ILL 121	117.5	107	113.5	101.5	115	121	121	125.5	114.9
Array mean (F_2)	109.7	105.7	107.8	102.7	108.3	110.6	114.2	115.3	

- The diagonal values (underlined) represented the parent means.
- F_1 means are above diagonal values and F_2 means below diagonal values.
- Array means include parental means.

*,**F_1 crosses exhibited significant heterosis over $\overline{MP}$ and $\overline{BP}$, respectively.

Table 4.0 Mean performance, over replicates, of parents and their arrays of 8 x 8 diallel crosses for time to maturity in F_1 and F_2 generations

Parent	Giza 9	Fam.370	78S26004	Precoz	Pant.L,406	FLIP84,1-L	ILL 274	ILL 121	Array mean (F_1)
Giza 9	160.5	155.2*	152.8**	159.5	157	160	159.5*	161.5	158.3
Fam. 370	158.5	157	155.5	155	153	156.5	160.8	158	156.4
78S26004	154	154.5	156.5	155.5	154.5	161	160	160.5	157
Precoz	156	155.5	156.5	142.5	158.5	161	163.5	163.5	157.4
Pant.L,406	153.5	152.5	156	156.5	146	157.5	158	156.5	155.1
FLIP 84,1-L	160	157	156.5	161	156.5	162	162.5	163	160.4
ILL 274	163	158	159.5	160.5	162	161.5	166	161.5*	161.5
ILL 121	163	157	158	164	158.5	164	165	164.5	161.1
Array mean (F_2)	158.6	156.3	156.4	156.6	155.2	159.8	161.9	161.8	

- The diagonal values (underlined) represent the parent means.
- F_1 means are above diagonal values and F_2 means below diagonal values.
- Array means include parental means.

*,** F_1 crosses exhibited significant heterosis over $\overline{MP}$ and $\overline{BP}$, respectively.

Table 41 Mean performance, over replicates, of parents and their array of 8 x 8 diallel crosses for seed protein in F_1 and F_2 generations

Parent	Giza 9	Fam.370	78S26004	Precoz	Pant. L,406	FLIP 84,1-L	ILL 274	ILL 121	Array mean (F_1)
Giza 9	23.90	24.32	23.58	24.15	23.25	23.05	22.90	23.80	23.62
Fam. 370	24.70	24.50	24.20	24.95	23.80	22.90	23.58	24.35	24.08
78S26004	24.25	24.60	23.80	22.70	22.95	23.55	22.50	23.58	23.36
Precoz	22.90	24.25	23.20	24.70	21.65	23.40	24.90	25.20	23.96
Pant. L, 406	23.95	25.50	23.40	22.90	23.15	21.05	22.90	22.50	22.66
FLIP 84, 1-L	25.10	22.45	22.30	23.50	22.95	23.35	22.55	23.95	22.98
ILL 274	23.15	23.30	23.30	23.70	22.90	22.60	24.20	24.35	23.49
ILL 121	23.20	24.60	23.60	25.10	21.80	24.00	24.10	25.05	24.10
Array mean (F_2)	23.89	24.24	23.56	23.78	23.32	23.28	23.41	23.93	

- The diagonal values (underlined) represent the parent means.
- F_1 means are above diagonal values and F_2 means below diagonal values.
- Array means include parental means.

depression value was negative (-0.7%), but not significantly different from zero (Table 31).

Mak and Yap (1977), in long bean, found no significant heterosis for seed protein on the basis of the average of F_1's over the mean of the higher parent, but heterosis in individual crosses varied considerably from -51% to +48%.

4.3 Combining ability analysis (Griffing's diallel analysis)

The analyses of general combining ability (GCA) and specific combining ability (SCA) were made by the method of Griffing (1956) as method 2, model I. The results of these are presented in Table 42.

The mean squares of GCA were significant for all characters in both F_1 and F_2 generations, except for number of pods/plant in the F_2 generation. The mean squares of SCA were also significant for all characters in both generations, except for plant height and number of seeds/pod, which had a non-significant effect of SCA in both F_1 and F_2 generations. These results indicate the importance of both GCA and SCA mean square for all characters except number of seeds/pod and plant height.

It is useful to examine the relative importance of specific combining ability because significant variation due to SCA may indicate the need to isolate certain parents and perform a more thorough comparison of their performance and that of their hybrid progenies. In the comparison of relative importance of specific combining ability, Griffing (1956b) recommended that the average of the squares of SCA effects should be compared with the average of the squares of GCA effects. Many researchers have used comparisons of mean squares as a method of assessing the importance of different types of combining ability. However, this practise always results in an under-estimatation of the importance of SCA. In this regard, Baker (1977) recommended the use of components of the mean squares, not the mean squares themselves, when comparing GCA and SCA. Also, Sokol and Baker (1977) suggested the use of the ratio of SCA to GCA sums of squares (SCA(SS)/GCA(SS)) as an indicator of their relative importance.

It should be remembered that, in inbred lines, the variance of general combining ability is equal to the additive variance in the base population and the variance of specific combining ability is equal to the non-additive variance. Gilbert (1958) suggested that the GCA of the parents may provide a good prediction of how hybrids will perform, because the GCA effects may be less subject to environmental influence, and thus provide a better indicator of a hybrid's long-term performance than the performance of that hybrid itself. An estimate of how well

Table 42 Mean squares for combining ability analysis, general (σ^2gca) and specific (σ^2sca) combining ability variance components, the ratio of SCA and GCA sum of squares and the coefficient of determination (R^2) for lentil characters in an 8-parent diallel cross

	D.F	Biological yield per plant		Seed yield per plant		Straw yield per plant		Number of pods per plant		Number of seeds per pod	
		F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
GCA	7	2.03**	2.69**	0.17*	0.31**	1.11**	1.25**	112.10**	115.33	0.161**	0.12**
SCA	28	0.80**	0.81*	0.18**	0.15*	0.28**	0.32*	68.66**	98.78*	0.016	0.013
Error	35	0.30	0.43	0.07	0.08	0.11	0.17	27.38	53.61	0.0214	0.015
σ^2gca		0.12	0.19	0.0	0.016	0.08	0.093	4.34	0.0	0.0145	0.010
σ^2sca		0.50	0.39	0.12	0.073	0.17	0.15	41.28	45.17	0.0	0.0
$\frac{SCA(SS)}{GCA(SS)}$		1.58	1.21	4.27	1.94	1.02	1.02	2.45	-	-	-
R^2		0.54	0.71	0.31	0.58	0.66	0.74	0.45	0.48	1.00	1.00

*, ** Significant at 0.05 and 0.01 level of probability, respectively.

Table 42 (continued)

	DF	100-seed weight		Plant height		Time to flowering		Time to maturity		Seed protein	
		F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
GCA	7	2.09**	2.09**	43.36**	29.23**	148.49**	183.28**	67.67**	78.31**	2.1.75**	1.0418**
SCA	28	0.15**	0.21**	7.34	8.95	19.96**	11.25**	11.25**	10.35**	0.5441*	0.7023**
Error	35	0.03	0.01	5.18	5.94	2.22	1.44	2.09	2.61	0.2799	0.2303
σ^2gca		0.20	0.188	3.60	2.03	12.85	17.14	5.64	6.80	0.1895	0.0812
σ^2sca		0.12	0.195	0.0	0.0	17.75	10.41	9.16	7.74	0.264	0.472
$\frac{SCA(SS)}{GCA(SS)}$		0.28	0.40	-	-	0.54	0.26	0.67	0.53	1.001	2.696
R^2		0.82	0.73	0.93	0.83	0.68	0.82	0.66	0.73	0.74	0.39

GCA estimates will predict hybrid performance is given by taking the GCA sum of squares as a per cent of the total sum of squares for genetic variation (additive and non-additive variation) among the progeny in a diallel cross (Baker, 1977). This ratio is equivalent to a coefficient of determination (R^2) corresponding to the correlation of hybrid performance with the average of parental GCA's. The ratio of SCA (SS)/GCA (SS) and the values of (R^2) were calculated to determine the relative importance of both GCA and SCA (Table 42).

Two other tests can be used to compare the importance of both GCA and SCA. The first, the relative importance of general and specific combining abilities in determining performance in hybrid combinations, can be assessed by the ratio $2\sigma^2gca/(2\sigma^2gca + \sigma^2sca)$ (Baker, 1978). The estimates of the GCA variance component (σ^2gca) and the SCA variance component (σ^2sca) are given in Table 42. The closer the ratio is to unity, the greater the predictability based on general combining ability alone. The second test is the correlation coefficient between the general combining ability values of individual parents, which are presented in Table 43, and the parental mean demonstrated in Table 30. The results of those two tests are presented in Table 44.

The estimates of general combining ability component of variance (σ^2gca) and specific combining ability component of variance (σ^2sca) are presented in Table 42. They were used to estimate the additive (σ^2A) and non-additive (σ^2NA) components of variance, phenotypic (σ^2ph) and genotypic (σ^2g) variance components as described by Griffing (1956b). These estimates together with environmental variance (σ^2E) are given in Table 45.

The results showed that the parameters varied from character to character. Relatively low value of SCA (SS)/GCA (SS) and the high values of R^2 occurred with the following characters; 100 seed weight, number of seeds/pod, plant height, time to flowering and time to maturity (Table 42). These traits also had a higher additive component of variance (σ^2A) than non-additive component of variance (σ^2NA) (Table 45). These results indicated that additive gene action plays the predominant role in the genetic control of these characters,

Table 43 Estimates of GCA effect of 8 parents for 10 lentil characters measured in F_1 and F_2 generations (ranks in parenthesis) and their standard error*

Parent	Biological yield per plant	Seed yield per plant	Straw yield per plant	Pods per plant	No. of seeds per pod	100 seed weight	Plant height	Time to flowering	Time to maturity	Seed protein
Giza 9	-0.15 (6)	-0.04 (6)	-0.11 (6)	-3.07 (7)	0.16 (1)	-0.10 (5)	-1.08 (6)	0.64 (5)	0.24 (5)	0.11 (4)
	-0.43 (7)	-0.12 (5)	-0.31 (7)	-2.74 (7)	0.13 (2)	-0.24 (6)	-0.80 (6)	0.48 (5)	0.54 (5)	0.16 (3)
F.370	-0.15 (6)	-0.02 (5)	-0.12 (7)	-0.89 (4)	0.08 (2)	-0.28 (6)	-0.35 (5)	-5.86 (1)	-1.61 (3)	0.46 (2)
	-0.33 (6)	-0.14 (6)	-0.2o (6)	-3.19 (8)	0.04 (3)	-0.19 (5)	-1.23 (7)	-3.78 (2)	-1.66 (3)	0.49 (1)
78S26004	0.35 (3)	0.15 (1)	0.20 (3)	4.02 (1)	-0.26 (8)	0.64 (1)	-1.35 (7)	-0.78 (4)	-1.13 (4)	-0.18 (6)
	0.02 (4)	0.02 (4)	0.00 (4)	-1.53 (5)	-0.16 (8)	0.64 (1)	-0.26 (5)	-1.53 (3)	-1.56 (4)	-0.12 (5)
Precoz	-0.03 (4)	0.04 (4)	-0.07 (5)	-1.24 (6)	0.01 (5)	0.31 (3)	0.75 (3)	-4.06 (2)	-2.26 (2)	0.39 (3)
	0.26 (3)	0.09 (3)	0.17 (3)	0.44 (4)	0.00 (5)	0.20 (3)	0.33 (4)	-6.33 (1)	-2.76 (2)	0.15 (4)
Pant.L406	-0.88 (8)	-0.23 (8)	-0.65 (8)	-1.08 (5)	0.08 (2)	-0.70 (8)	-3.42 (8)	-1.01 (3)	-3.71 (1)	-0.74 (8)
	-0.63 (8)	-0.14 (6)	-0.50 (8)	0.53 (3)	0.14 (1)	-0.70 (8)	-3.04 (8)	-1.48 (4)	-3.51 (1)	-0.38 (7)
FLIP 84,1-L	-0.08 (5)	-0.13 (7)	0.04 (4)	-4.89 (8)	-0.04 (6)	0.49 (2)	0.02 (4)	1.09 (6)	2.14 (6)	-0.53 (7)
	0.48 (2)	0.17 (2)	0.31 (2)	1.64 (2)	-0.10 (7)	0.54 (2)	1.08 (3)	0.98 (6)	1.69 (6)	-0.39 (8)
ILL 274	0.59 (1)	0.13 (2)	0.46 (1)	3.34 (3)	-0.06 (7)	0.02 (4)	2.35 (2)	4.57 (7)	3.37 (8)	-0.04 (5)
	0.91 (1)	0.31 (1)	0.60 (1)	7.21 (1)	-0.08 (6)	0.11 (4)	1.76 (2)	5.33 (7)	3.79 (8)	-0.20 (6)
ILL 121	0.36 (2)	0.10 (3)	0.26 (2)	3.80 (2)	0.04 (4)	-0.38 (7)	3.07 (1)	5.39 (8)	2.94 (7)	0.53 (1)
	-0.27 (5)	-0.18 (8)	-0.09 (5)	-2.37 (6)	0.03 (4)	-0.36 (7)	2.16 (1)	6.33 (8)	3.49 (7)	0.30 (2)
S.E. F_1	0.16	0.08	0.10	1.55	0.07	0.07	1.01	0.67	0.65	0.16
S.E. F_2	0.19	0.08	0.12	2.17	0.04	0.03	0.72	0.36	0.48	0.14

* F_1 estimates are above the F_2 estimates in each cell in the table.

Table 44 The ratio $2\sigma^2gca/(2\sigma^2gca+\sigma^2sca)$ and the correlation coefficient (r) between general combining ability values and the parental means in the F_1 and F_2 generations for 10 lentil characters

Characters	$2\sigma^2gca/(2\sigma^2gca+\sigma^2sca)$		r	
	F_1	F_2	F_1	F_2
Biological yield/plant	0.32	0.49	0.77*	0.89**
Seed yield/plant	0.00	0.31	0.36	0.72
Straw yield/plant	0.49	0.55	1.00**	0.89**
No. of pods/plant	0.17	0.07	0.66	0.46
100 seed weight	0.77	0.66	0.94**	0.95**
No. of seeds/pod	1.0	1.0	0.52	0.54
Plant height	0.77	0.57	0.87**	0.97**
Time to flowering	0.59	0.77	0.95**	0.97**
Time to maturity	0.55	0.64	0.89**	0.90**
Seed protein	0.59	0.25	0.96**	0.81**

*, ** Significant at 0.05 and 0.01 level of probability, respectively.

Table 45 Estimates of the variance components for 10 lentil characters calculated from Griffing's diallel analysis method in the F_1 and F_2 generations

		Biological yield/ plant	Seed yield/ plant	Straw yield/ plant	No. of pods/ plant	No. of seeds/ pod	100 seed weight	Plant height	Time to flower-ing	Time to matur-ity	Seed protein
σ^2A	F_1	0.24	0.0	0.16	8.68	0.03	0.40	7.20	25.70	11.28	0.38
	F_2	0.38	0.04	0.19	3.32	0.02	0.38	4.06	34.28	13.60	0.16
σ^2NA	F_1	0.50	0.12	0.17	41.28	0.0	0.12	2.16	17.75	9.16	0.26
	F_2	0.39	0.07	0.15	45.17	0.0	0.20	3.01	10.41	7.74	0.47
σ^2G	F_1	0.74	0.12	0.33	49.96	0.03	0.52	9.36	43.45	20.44	0.64
	F_2	0.77	0.11	0.34	48.49	0.02	0.58	7.07	44.69	21.34	0.63
σ^2E	F_1	0.30	0.07	0.11	27.38	0.02	0.03	5.18	2.22	2.09	0.28
	F_2	0.43	0.08	0.17	53.61	0.02	0.01	5.94	1.44	2.61	0.23
σ^2ph	F_1	1.04	0.19	0.44	77.34	0.05	0.55	14.54	45.67	22.53	0.92
	F_2	1.20	0.19	0.51	102.10	0.04	0.59	13.01	46.13	23.95	0.87

σ^2A : Additive variance, σ^2NA : non-additive variance, σ^2G : genetic variance, σ^2E : environmental variance, σ^2ph: Phenotypic variance.

providing confidence that the GCA's of the parents will give a fairly reliable prediction of hybrid performance. The high ratio of $2\sigma^2gca/(2\sigma^2gca + \sigma^2sca)$ for these traits (Table 44) also confirmed the above results.

Biological yield/plant, straw yield/plant and seed protein exhibited higher values of SCA (SS)/GCA (SS) than the characters mentioned above (Table 42). However, for these last three characters, the ratios of SCA(SS)/GCA(SS) were, in most cases, near unity. In addition, R^2 values were not low, and in some cases were high (0.71 for biological yield/plant in F_2 and 0.74 for straw yield/plant in the F_2 and protein in the F_1 generation). The results suggest that for those traits additive and non-additive effects have equal importance.

On the other hand, seed yield/plant and number of pods/plant showed different results. Both characters exhibited the highest values of SCA (SS)/GCA (SS) among all characters coupled with low estimates of R^2, that indicates the predominant role of non-additive gene action in the genetic control of these two traits. The ratio $2\sigma^2gca/(2\sigma^2gca + \sigma^2sca)$ (Table 44) confirmed the earlier results for all characters.

The correlation coefficient estimates (Table 44) showed a strong correlation between general combining ability effects and parental means for most characters, indicating that parental means provided a good prediction of general combining ability and hence hybrid performance. Number of pods/plant did not exhibit high values in both generations and seed yield/plant showed high correlation in the F_2 generation (0.72), but was not significant. Also, number of seeds/pod did not show significant correlation between general combining ability effects and parental means in both generations.

The additive component of variance was higher in magnitude than the non-additive component for 100 seed weight, number of seeds/pod, plant height, time to flowering and time to maturity in both F_1 and F_2 generations and straw yield/plant in the F_2 and seed protein in the F_1 generations (Table 45). The traits biological yield/plant and seed yield/plant in both generations and straw yield/plant in the F_1

generation had higher non-additive component values than additive component estimates. In general, these results also agreed with those mentioned above.

A predominant role of additive component gene action has been found in lentil for number of seeds/pod and seed size (Goyal et al., 1977) and time to flowering (Malhotra et al., 1973).

The different values of additive and non-additive component of variances affected the estimates of heritabilities among characters. Table 46 presents the estimates of broad sense ($h^2_{b.s.}$) and narrow sense ($h^2_{n.s.}$) heritabilities in the F_1 and F_2 generations for all the characters studied.

The traits which had highly additive component values gave high estimates of broad and narrow sense heritabilities. These were: 100 seed weight, plant height, time to flowering and time to maturity in the F_1 and F_2 generations and seed protein in the F_1 generation. The estimates of heritabilities for number of seeds/pod were less than the expected values due to the high environmental variance (error variance) for this trait (Table 45).

In comparison, the traits which had high non-additive component values showed lower estimates of broad and narrow sense heritabilities than other characters. 100 seed weight gave the highest narrow sense heritability in the F_1 generation ($b^2_{n.s.}$ = 72.7%), whereas seed yield/plant gave the lowest value of ($b^2_{n.s.}$ = 0.0) among all characters. 100 seed weight character was also less influenced by environment, environmental variance for this trait representing only 5.5% and 1.7% from phenotypic variance in the F_1 and F_2 generations, respectively. For comparison, these ratio was 36.8% and 42.1% for seed yield/plant in the F_1 and F_2 generations, respectively (Table 45).

It should be emphasized here that, since the parents of this diallel cross were not randomly selected, the above conclusions must be confined to the eight parental lines and their crosses used in the present investigation.

Table 46 Estimates of broad ($h^2_{b.s}$) and narrow ($h^2_{n.s}$) sense heritabilities calculated from Griffing's diallel analysis method for 10 lentil characters in the F_1 and F_2 generations

	Biological yield/ plant	Seed yield/ plant	Straw yield/ plant	No. of pods/ plant	No. of seeds/ pod	100 seed weight	Plant height	Time to flower-ing	Time to maturity	Seed protein
$h^2_{b.s.}$ F_1	71.2	63.2	75.0	64.6	60.0	94.6	64.4	95.1	90.7	69.6
F_2	64.2	57.9	66.7	47.5	50.0	98.3	54.8	96.9	89.1	25.4
$h^2_{n.s}$ F_1	23.1	0.0	36.4	11.2	60.0	72.7	49.5	56.3	50.1	41.3
F_2	31.7	21.1	37.3	3.3	50.0	64.4	31.2	74.3	56.8	18.4

4.4 Jinks-Hayman analysis method

The use of another type of diallel analysis, that described by Jinks and Hayman (1953) in addition to the Griffing's analysis, would give additional genetic information. Therefore, it has also been used in the present study.

In order to determine the validity of the genetical parameters and interpretations, tests of the hypothesis were made according to the method of Hayman (1954).

Testing the validity of hypotheses

Several assumptions are made when the diallel analysis of Jinks and Hayman is used. These are : (1) homozygous parents; (2) diploid segregation; (3) absence of reciprocal differences; (4) gene frequencies equal to 0.5 at all segregating loci; (5) genes independently distributed between the parents (no linkage); (6) no epistasis (absence of non allelic gene interaction) and (7) no multiple alleles.

Failure of one or more of these assumptions invalidates the genetic analysis.

In this study, assumptions 1 and 2 were valid since lentil is a diploid, self-pollinated crop. Other assumptions were tested together in two tests conducted on two generations (the F_1 and the F_2) in this study.

The first test was the analysis of variance for W_r-V_r (parent-offspring covariances - array variances). In this test, the values of W_r-V_r over arrays are expected to be consistent and the F value over arrays of the analysis of variance of W_r-V_r is expected to be non-significant for an additive-dominance model with independent gene distribution.

The second test of the assumptions was the regression coefficient (b W_r/V_r) of the parent-offspring covariances (W_r) on the array variances (V_r). The linear regression coefficient should be

significantly different from zero but not significantly different from unity if all the assumptions are to be met (Jinks and Hayman, 1953).

F values of the analysis of W_r-V_r and the regression coefficients (bW_r/V_r) for the ten characters involved in the present study in both F_1 and F_2 generations are shown in Table 47. As mentioned earlier, the non-significance of the F values and a non-significant deviation of regression coefficient from b=1 indicates the adequacy of the additive-dominance model with independent gene distributions.

The results in Table 47 showed that only the traits 100-seed weight, no. of pods/plant and time to maturity in both F_1 and F_2 generations, and time to flowering in the F_1 generation completely fulfilled the assumptions of the two analyses.

On the other hand, other traits failed to meet the assumptions due to either the significance of F values and/or insignificant differences of the regression coefficient (b Wr/Vr) from zero and/or their significant differences from unity. These traits were biological yield/plant, seed yield/plant, straw yield/plant, no. of pods/plant, seed protein content and plant height in both F_1 and F_2 generations and time to flowering in the F_2 generation. These characters appeared to suffer from failure of one or more of the basic assumptions required for an additive-dominance model.

For such failures, Hayman (1957, 1963) recommended that it is desirable to eliminate separately the epistatic parent(s) (the parent(s) corresponding to the maximum and minimum Wr-Vr value), then re-analyze the data. He pointed out that this will restore the rectilinearity of the Wr/Vr graph. This suggestion was implemented for the characters which showed failure of the assumptions outlined above. However, it only worked successfully for the character time to flowering. For time to flowering, it was clear that array parent Precoz was an epistatic parent; it had the minimum Wr-Vr value (Appendix Table 4) and its array ranked first in earliness (Table 39). The removal of the array of Precoz in the F_2 generation improved b Wr/Vr from 0.213 to 1.34 and it became close to unity and highly

Table 47 F value of the analysis of variance of W_r-V_r and regression coefficient (b) of W_r on V_r in the F_1 and F_2 generations

Character	F_1		F_2	
	F value	bW_r,V_r	F value	bW_r,V_r
Biological yield/plant	5.03+	0.04**	0.54	0.31*
Seed yield/plant	0.0003	0.08*	12.81+	0.65^o
Straw yield/plant	0.10	0.14*	0.06	0.62^o
No. of pods/plant	1.32	0.09*	19.4+	0.08**
100-seed weight	2.04	1.12	1.51	1.09
No. of seeds/pod	1.50	0.67	0.26	1.11
Plant height	0.56	0.67^o	0.30	0.75^o
Time to flowering:				
(1) All parents	1.47	1.11	0.07	0.21^o
(2) Parent 4 excluded	0.06	0.96	4.18	1.34
Time to maturity	0.12	0.92	0.04	0.97
Seed protein	6.01+	0.42**	0.05	0.07**

*,** Significant different from unity at the 0.05 and 0.01 probability levels, respectively.

\+ Any significant F value indicates failure of one or more of the assumptions underlying the analysis for a particular character.

^{o} Not significantly different from unity and from zero.

significantly different from zero and thus fulfilled the required assumptions for this character. Also, this parent was eliminated in the F_1 generation (see Appendix Table 3).

For other characters showing failure of the assumptions required for the genetic analysis, the removal of a parent(s) which showed epistasis was attempted but it was unsuccessful in correcting such failure in most cases. These results indicated that the failure of the genetic assumptions in these characters may not be due only the presence of epistasis but could be due to one or more other factors, such as gene interaction or unequal distribution of positive and negative alleles at the loci under consideration. The tests which have been used in this study, especially the regression of Wr on Vr, will only be able to detect epistasis in the absence of any correlation of gene frequences in the parents of the diallel, and it is not possible to differentiate between the effects of epistasis and gene interaction (Nassar, 1965).

Therefore,.the genetic analysis was continued forward only for the characters 100-seed weight, number of seeds/pod, time to flowering and time to maturity. As other characters did not fit the assumption of an additive-dominance model with independent gene distribution, further genetic analysis of these traits would not be reliably performed. Most of those characters which showed failure of the assumptions also demonstrated the importance of specific combining ability. These demonstrated the presence of non-allelic interaction (epistasis) on the genetic systems of those traits, because the specific combining ability is associated with non-allelic interaction (Jinks, 1954).

It should be emphasized here that the genetic components estimated by the Griffing method and presented in Table 45 were calculated assuming no epistatic effects. In the presence of epistasis, the expectation for σ^2gca would be = $\frac{1}{2}\sigma^2 A + \frac{1}{4}\sigma^2 AA + \frac{1}{8}\sigma^2 AAA \ldots$. (Matzinger and Kempthorne, 1956). Such a situation would result in different variance component estimates from those mentioned in Table 11 (see materials and methods).

Since the method of analysis was described in detail by Jinks and Hayman (1953), a summary with a brief interpretation of the estimates of genetic and environmental parameters and ratios is given in Table 48. The use of second-degree statistics allowed estimates of the genetic and environmental variance components to be made of the four characters mentioned above (Table 49).

100 seed weight

The additive genetic component D was highly significantly different from zero (Table 49) in the F_1 and F_2 generations. The dominance components of variation (H_1 and H_2) were also highly significant in both generations. These results indicated that both additive and dominance effects were important; however, the D values were relatively larger than those of H_1 and H_2, indicating that the additive effect was more important than the dominance effect for the genetic control of seed weight in this study. These results were in agreement with results obtained by Griffing's method, where the additive components were higher than non-additive components in both generations.

The H_2 value was smaller than the H_1 value in both generations, indicating that the positive and negative alleles at the loci were not equal in proportion in the parents. $H_2/4H_1$ value was less than 0.25, being 0.16 in both generations, supporting the view that for seed weight, in this study, there were unequal proportions of genes with positive and negative effects distributed among the parents. The significant and positive values of F supported these results and suggested that the frequencies of dominant genes exceeded the frequencies of recessive genes in the parents. Estimates of F, H_1 and H_2 were larger in the F_2 than in the F_1 generation. This is to be expected because the F_2, unlike the F_1, is a segregating generation.

Another parameter that gives a good indication of the equality of distribution among the parental lines of dominant versus recessive alleles is the ratio $[(4DH_1)^{\frac{1}{2}} + F/(4DH_1)^{\frac{1}{2}} - F]$. If this value exceeds 1, it is an indication of more dominant than recessive genes among the parents. This value was 2.92 for the F_1 and 2.56 for the F_2 generation in this character.

Table 48 Jinks-Hayman's (1953) diallel analysis parameters and ratios and their interpretation

Parameters	Interpretation
D	The component attributable to additive gene actions.
H_1	The component attributable to dominance effects (in the absence of dominance $H_1 = 0$).
H_2	This value should be the same as H_1 when $\mu = v = 0.5$ and the interpretation is the same as H_1
h^2	This estimate indicates the square difference of mean performance between hybrids and parents (if it is large and significant it indicates the existence of differences between hybrids and parents).
F	The sign and magnitude of F is an indicator of the relative frequencies of dominant and recessive alleles in the parents. A positive value indicates an excess of dominant alleles and a negative value indicates an excess of recessive alleles.
E	The conventional experimental error from the analysis of variance.
$(H_1/D)^{1/2}$	An estimate of the mean degree of dominance over all loci.
$H_2/4\ H_1$	This ratio measures average value of μv over all loci. It has a maximum of 0.25 when $\mu = v = 0.5$. An unequal distribution of positive and negative alleles causes this ratio to be less than 0.25.
$\frac{(4DH_1)^{1/2}+F}{(4DH_1)^{1/2}-F}$	The ratio of the total number of dominance to recessive genes at all parents. This ratio gave good indication of the equality of distribution of dominance versus recessive genes among the parents.
h^2/H_2	This ratio provides an approximate number of genes or groups of genes controlling the character.

Table 49 Estimates of components of variance, their ratios and standard errors (SE) for 4 lentil characters in the F_1 and F_2 generations from an 8-parental diallel cross in lentil

	No.of seeds/pod		100 seed weight		Days to flowering		Days to maturity	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
D	0.038**	0.044**	1.419**	1.433**	89.93**	90.70**	70.18**	69.66**
SE±	0.007	0.004	0.054	0.054	6.84	4.23	3.00	3.05
H_1	0.011	0.013	0.614**	0.934**	66.86**	38.59**	57.21**	47.82**
SE±	0.015	0.009	0.126	0.125	16.60	10.19	6.92	7.05
H_2	0.014	0.019*	0.381**	0.610**	51.24**	31.43**	26.90**	23.07**
SE±	0.013	0.008	0.109	0.109	14.62	8.98	6.02	6.13
h^2	0.021	0.006	0.229**	0.490**	0.278	0.028	8.39*	7.13
SE±	0.009	0.005	0.073	0.073	9.88	6.07	4.04	4.11
F	-0.027	-0.001	0.914**	1.011**	37.81	34.05**	78.92**	67.79**
SE±	0.016	0.091	0.129	0.128	24.32	10.15	7.12	7.25
E	0.021**	0.015**	0.028	0.014	2.215	1.442	2.035*	2.606*
SE±	0.002	0.001	0.018	0.018	2.44	1.50	1.00	1.02
$(H_1/D)^{1/2}$	0.53	0.55	0.66	0.81	0.86	0.65	0.90	0.83
$H_2/4H_1$	0.32	0.35	0.16	0.16	0.19	0.20	0.12	0.12
K_D/K_R+	0.21	0.97	2.92	2.56	1.65	1.81	4.30	3.85
$h^2/H_2(K)$	0.60	0.30	0.38	0.80	0.005	0.001	0.31	0.31

+ $K_D/K_R = \dfrac{(4DH_1)^{1/2} + F}{(4DH_1)^{1/2} - F}$

*,** Significant at 0.05 and 0.01 level of probability, respectively.

The overall dominance effects of heterozygous loci (h^2) were positive and highly significant in both F_1 and F_2 generations, indicating that dominance due to heterozygosity was prominent in this trait.

The value of $(H_1/D)^{\frac{1}{2}}$ is an estimate of the mean degree of dominance over all loci. With no dominance this value is expected to equal zero; with average partial dominance the value is expected to fall within the range of 0-< 1, with complete dominance this value should equal 1 and with over-dominance it should be >1. For 100 seed weight, these values were 0.66 and 0.81 in the F_1 and F_2 generations respectively, indicating partial dominance.

The ratio h^2/H_2 estimates the number of genes (K) or groups of linked genes showing some degree of dominance. In this study, 100 seed weight involved one gene or group of linked genes. It should emphasize here that this estimate will be under-estimated if the dominance effects of the genes affecting the character are not equal in size and direction, or if the distribution of the genes is correlated.

The estimates of the environmental variance (E) were not significant in both F_1 and F_2 generations, indicating that seed weight in this study was not influenced by environmental factors.

Narrow sense heritability was estimated following the method used by Mather and Jinks (1971). For 100 seed weight this heritability was 75% and 70% in the F_1 and F_2 generations, respectively. These high values were due to the high estimates of D and the low values of E. These heritability values were approximately equal to those estimated by the Griffing method (Table 46). This indicates that 100 seed weight was a highly heritable character in the present study.

The relative values of $(W_r + V_r)$ over arrays indicate the relative number of dominant to recessive alleles in the parents of the arrays. By comparing the $(W_r + V_r)$ value for each array with the mean of the common parent (comparing $W_{ri} + V_{ri}$ with P_i) we can see whether the distribution of dominant to recessive alleles is correlated with the phenotypes of the common parents. This correlation will be negative if

the parents with a high performance have the lowest values of $W_{ri} + V_{ri}$ i.e. contain most dominant genes, and positive if the reverse is true. Hence, we can deduce whether or not the increasing or decreasing alleles are dominant alleles. Therefore the order of dominance of the parents determined by the value of $W_r + V_r$ (arranged in descending order from most dominant to most recessive alleles) and descending order of parental means were calculated and presented in Table 50 together with the correlation coefficient between parental mean performance and the values of $W_r + V_r$.

For 100 seed weight, the order of parental means showed that parents 3 (78S26004) and 6 (FLIP84-1 L) had the highest array values, whereas parents 5 (Pant.L,406) and 8 (ILL121) gave the lowest array values in both F_1 and F_2 generations. The parental arrays which possessed the most dominant alleles were for parent 1 (Giza9) and 2 (Family 370) in the F_1 generation and parent 1 and 5 in the F_2 generation. On the other hand parents 4 (Precoz) and 6 (FLIP84-1 L) had the most recessive alleles in both generations. The correlation coefficient between parental means and their order of dominance were 0.64 and 0.90 in the F_1 and F_2 generations respectively. Because these correlation values were positive, the dominant genes act to decrease seed weight and accumulation of recessive genes in the parents produced increased seed weight.

The graphical analysis provides information on some important points (Mather and Jinks, 1971). Firstly, it supplies a test of adequacy of the genetical model, as previously discussed. In the absence of non-allelic interaction and with independent distribution of the genes among the parental inbreds, W_r is related to V_r by a straight regression line of unit slope ($bW_r/V_r = 1$). If the model is adequate, a measure of the average degree of dominance is provided by the departure from the origin of the point where the regression line cuts the W_r axis. With complete dominance, the regression line with $b = 1$ would pass through the origin. In the case of over-dominance, the regression line would cut the W_r axis below the origin, and with partial (incomplete) dominance the line would cut the W_r axis above the origin. If dominance is absent, the points would cluster about the position where the slope of the parabola is +1 (Hayman, 1954; Jinks, 1954 and 1955).

Table 50 Parental order of means (OR_1) and parental order of dominance (OR_2) and correlation coefficient (r) between Vr + Wr and observed parental mean for F_1 and F_2 generations

Character		OR_1	OR_2	r
No. of seeds/pod	F_1	12584673	12867435	0.19
	F_2	51284763	72561843	-0.27
100 seed weight	F_1	36471285	12385746	0.64
	F_2	36742185	51827346	0.90**
Time to flowering	F_1	87613542	25431687	0.96**
	F_2	87615324	42351678	0.90**
Time to maturity	F_1	78614325	76812354	-0.83**
	F_2	78614325	32768514	-0.65

*, ** Significant at 0.05 and 0.01 probability level, respectively.

- The order of mean of time to flowering and time to maturity characters are in order of earliness.

Secondly, the relative order of points along the regression line indicates the distribution of dominant and recessive genes among the parents. The points nearest the origin stem from the arrays of the parents with the most dominant genes and the points furthest from the origin stem from arrays derived from parents with most recessive genes.

The regression coefficients for the 100 seed weight character are summarized in Table 47, and W_r/V_r graphs are presented in Figure 12. The V_r/W_r regression coefficient was equal to unity; b = 1.12 ± 0.11 in the F_1 and b = 1.09 ± 0.10 in the F_2 generation. In both generations the regression coefficients were significantly different from zero, indicating the adequacy of the additive-dominance model. In both generations the regression lines intercepted the W_r axis above the origin indicating partial dominance and thus confirmed the ratio of $(H_1/D)^{\frac{1}{2}}$ obtained in genetical analysis. The position of the array points on the regression line indicated that parents 6 (FLIP84-1L) and 4 (Precoz) possess the most recessive alleles, whereas parent 1 (Giza9) seems to carry most of the dominant alleles in both generations. Parent 6 occupied the far end of the regression line in both generations, while the change in positions of parents 2, 3 and 5 from the F_1 to F_2 generation indicates that those parents seem to have dominant and recessive genes more or less in equal proportion in the two generations.

The order of dominance for this character confirmed that parent FLIP 84-1 L carried the most recessive genes in both generations. The correlation between parental order of means and order of dominance was positive (Table 50), indicating that recessive genes act towards increasing seed weight.

Number of seeds per pod

The results presented in Table 49 show highly significant differences for the estimates of the additive component of variation (D values) in the F_1 and F_2 generations, indicating that genetic differences exist among parents. The dominance components of variation (H_1 and H_2) were not significantly different from zero in both generations (except H_2 in the F_2 generation). These results confirmed the evidence that the genetic system controlling number of seeds per

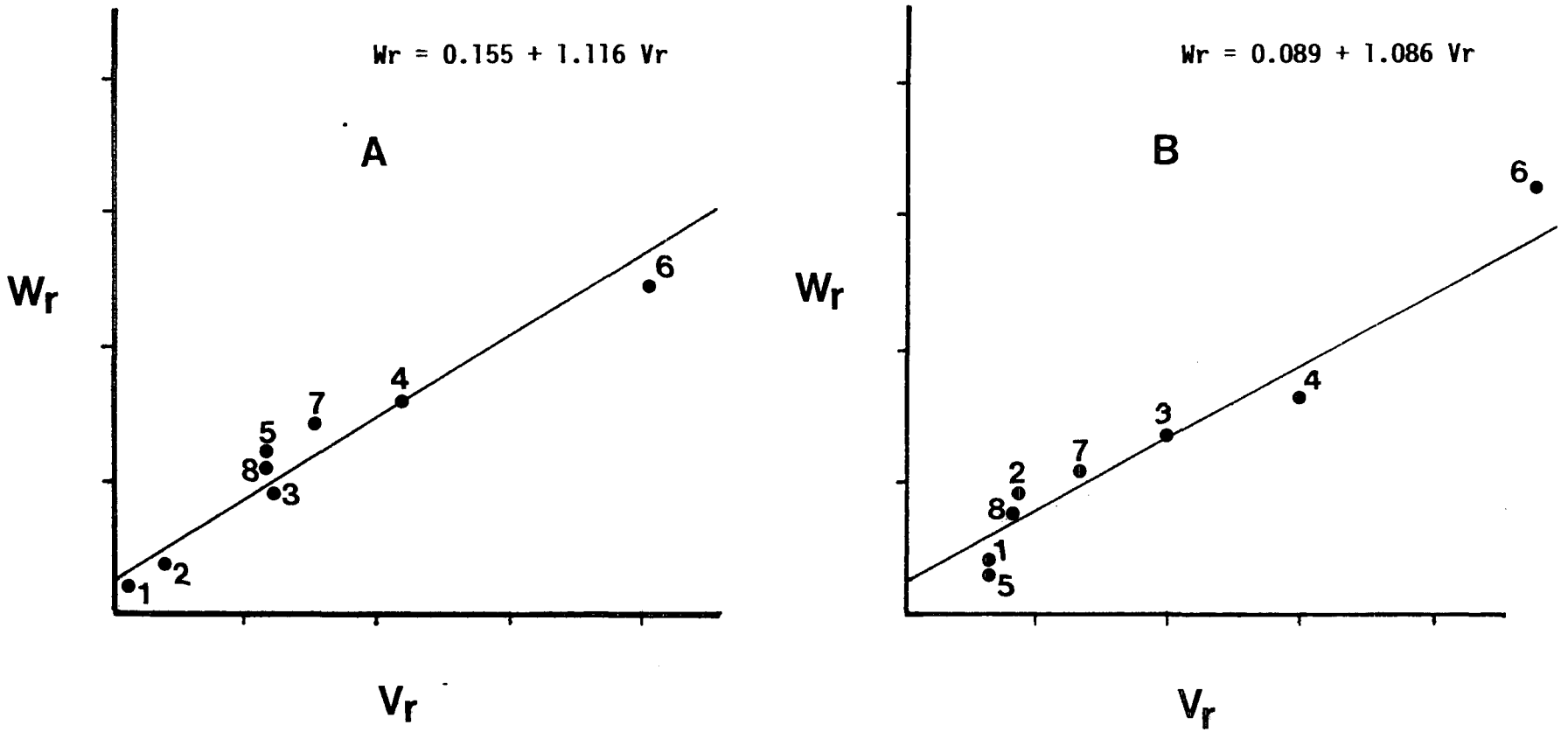


Figure 12. Vr, Wr graphs for 100 seed weight in the F_1(A) and F_2(B) generations from a diallel cross in lentil.

pod was largely additive. These results agreed with the results obtained from the Griffing analysis (Table 42), where the estimates of non-additive components were zero in both F_1 and F_2 generations and confirmed the evidence that additive effects predominantly control this character.

The crude estimate of frequencies at non-additive loci (Crumpacker and Allard, 1962) can be obtained from the ratio of $H_2/4H_1$. In this character equal distribution of positive and negative alleles occurred among the parents. An insignificant F value supported this result.

Narrow sense heritability was 56% and 50% for this character in the F_1 and the F_2 generations, respectively. These values were approximately equal to those estimated by the Griffing method (Table 46). The narrow sense heritability was not very high because of the relatively high estimate of error variance in this trait. However, these heritability values were above 50% in both generations.

Time to flowering

The results presented in Table 49 (excluding parent Precoz) show that both additive (D) and dominant (H_1, H_2) components of variation were highly significantly different from zero in both the F_1 and F_2 generations, indicating the importance of both additive and dominant gene action in controlling earliness in lentil. However, the D values were higher in magnitude than the H_1 and H_2 values, suggesting greater importance of additive effects than dominance effects. These results agreed with the results obtained by the Griffing analysis.

The values of F were highly significant and positive in both generations, indicating a preponderance of dominant alleles controlling this character. The value of K_D/D_R being >1 supported the results mentioned above, i.e. that more dominant than recessive alleles were present in the parents. This finding caused the estimate of $H_2/4H_1$ to be less than 0.25.

The estimate of number of gene groups (K) was very low in both generations. These underestimated values occur because the dominance effects of the genes affecting this character were not equal. The

average degree of dominance $(H_1/D)^{\frac{1}{2}}$ was less than one in both generations, revealed partial dominance. Days to flowering was not influenced by environmental factors due to insignificant (E) estimates in both generations (Table 49).

The order of parental means of the F_1 and F_2 generations for time to flowering were similar (Table 50). Those were 87613542 in the F_1 generation and 87615324 in the F_2. These are arranged in descending order, meaning that parents 8 and 7 were latest and parents 2 and 4 were the earliest. On the other hand, the orders of dominance of those parents were also almost similar in both generations (Table 50) and showed that the arrays of parents 2 (Family 370) and 4 (Precoz) had the most dominant alleles, whereas parent arrays 7 (ILL274) and 8 (ILL121) carried the most recessive alleles.

Because the correlation coefficients between the parental order of dominance and parental means were positively highly significant, the recessive genes were mostly positive, i.e. acting towards delaying flowering. Conversely, the dominant genes caused increased earliness. The narrow sense heritability for this character was 69% in the F_1 and 77% in the F_2 generation, indicating that this trait is highly heritable. The high narrow sense heritabilities were obtained also by the Griffing method and therefore supported these results.

The graphical analysis for time to flowering was presented by two graphs in each generation. The first graph (A) included all the parents, whereas the graph (B) excluded parent 4 (Precoz) which showed epistasis.

In the F_1 generation (Figure 13), although the two tests of the hypothesis (Table 47) were acceptable, parent 4 was removed to keep the same population in the F_1 as in the F_2 and make interpretation comparable for both generations.

In Figure 13 (A), the regression line cut the W_r axis below the origin and the intercept was negative (-2.28), indicating overdominance. Removal of parent 4 (Figure 13 (B)) changed the position of regression line which was relocated above the origin, indicating partial dominance. This is explained by the particular

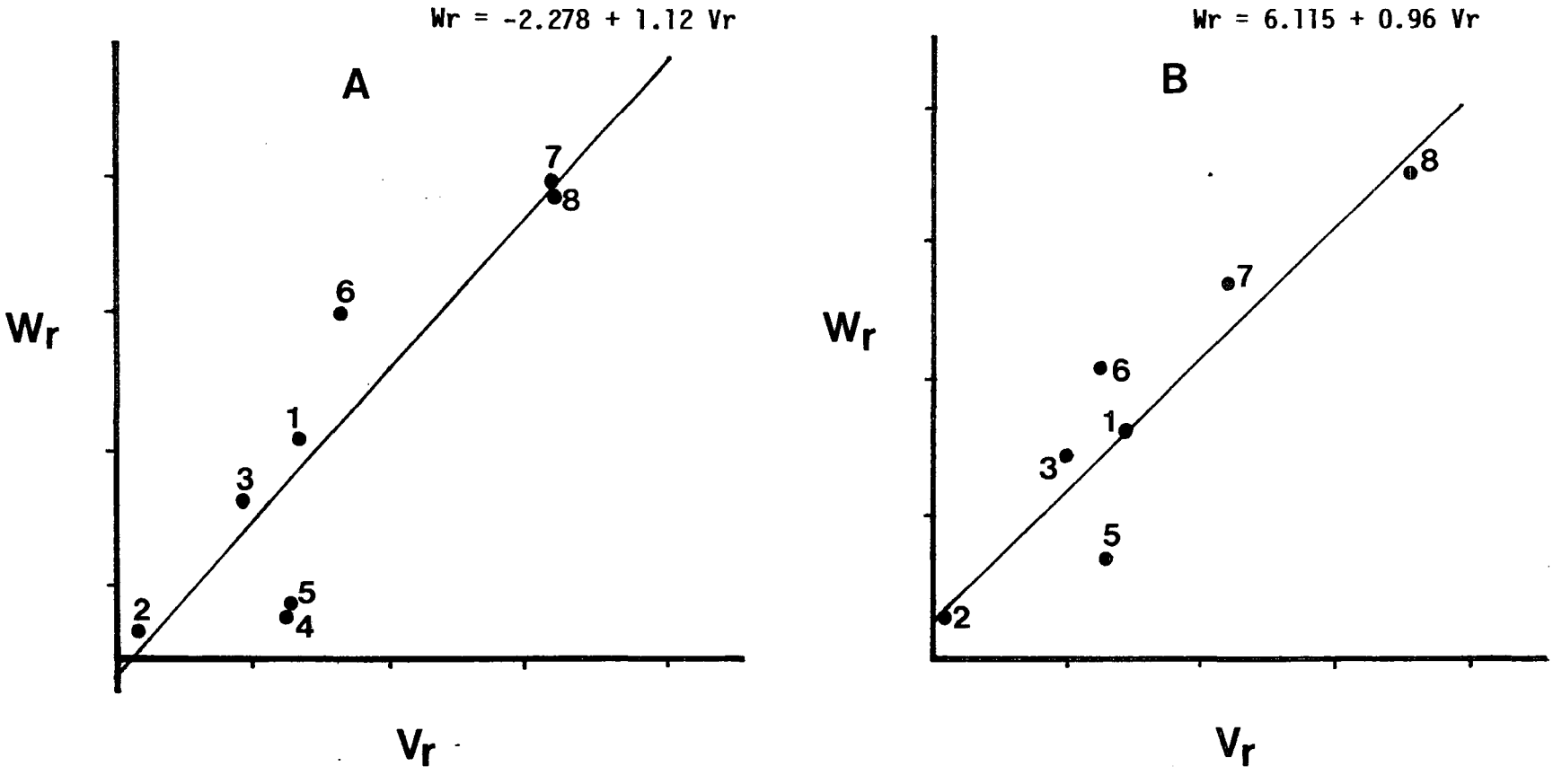


Figure 13. Vr, Wr graphs for days to flowering in the F_1 generation from a diallel cross in lentil. (A) all parents included. (B) epistatic parent 4 is excluded.

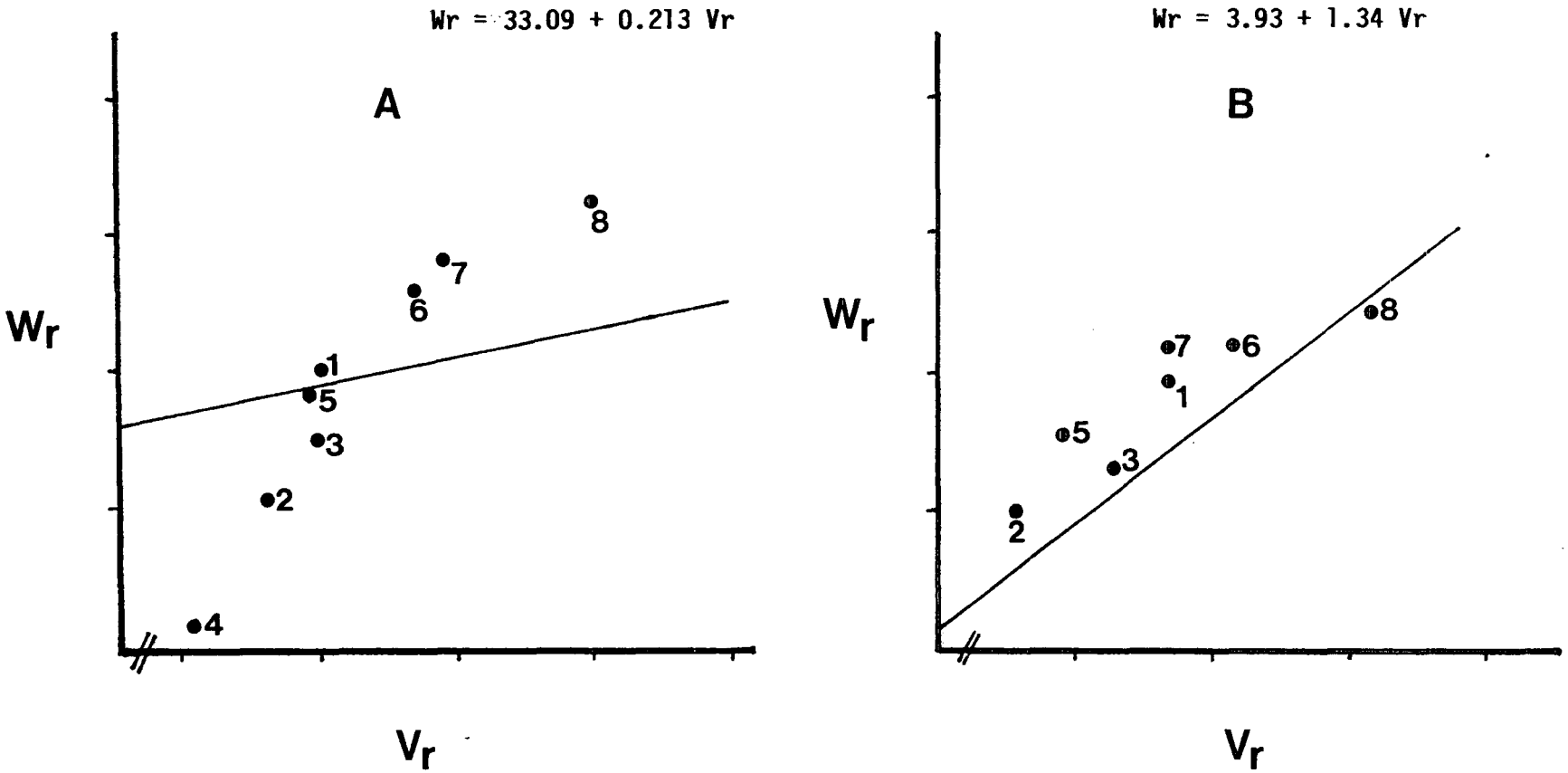


Figure 14. Vr, Wr graphs for days to flowering in the F_2 generation from a diallel cross in lentil. (A) all parents included. (B) epistatic parent 4 is excluded.

combination of dispersion and unidirectional dominance as well as the existence of epistatic effects which inflates $(H_1/D)^{\frac{1}{2}}$ seriously and may easily turn partial dominance into apparent over-dominance (Hayman 1957). The intercept in Figure 13 (B) is positive indicating partial dominance and the regression coefficient (0.96) significantly differed from zero, but not from unity, indicating the adequacy of the model.

In the F_2 generation (Figure 14 (A)) the regression line (b=0.21) differed significantly from unity, indicating the presence of epistasis. Exclusion of array 4, which had the lowest value of W_r-V_r (Appendix Table 4) removed the epistatic effect and the regression line (Figure 14 (B)) became equal to unity (1.3). The intercept was positive and the regression line cut the W_r axis above the origin, indicating partial dominance.

In both generations, the distributions of array points along the regression line were similar and parents Family 370 (2) and Precoz (4) carried the most dominant genes as mentioned before. These parents, Family 370 and Precoz, were also good combiners and they ranked first and second for GCA as shown in Table 43.

Time to maturity

The additive component (D) was highly significantly different from zero (Table 49). The dominance components (H_1 and H_2) were also highly significant, but lower in magnitude than the additive component values in the F_1 and F_2 generations. These results indicate the importance of both additive and dominance effects, with greater importance of additive effects in controlling time to maturity.

H_1 values were higher than H_2 values in both generations causing the ratio of $H_2/4H_1$ to be less than 0.25, indicating unequal gene frequences over all loci. The significance of F values supported this finding. As the sign of F was positive, dominant alleles were more frequent than recessive alleles. The ratios of K_D/K_R were 4.30 and 3.85 in the F_1 and F_2 generations, indicating that they were more dominant than recessive alleles among the parental lines. The degree of dominance estimated by $(H_1/D)^{\frac{1}{2}}$ revealed partial dominance. h^2 value

was significant only in the F_1, suggesting that dominance due to heterozygosity was more prominent in the F_1 generation. The ratio of h^2/H_2 suggested that at least one factor (K) controlled this character. Time to maturity in this study was influenced by environmental effects, as shown by the significant (E) value in both generations. The narrow sense heritability for this trait was 55% and 61% in the F_1 and F_2 generations, respectively. All these results were in complete agreement with the results obtained by the Griffing analysis.

The order of parental means was exactly the same in both generations, being 78614325 (Table 50). However, the order of dominance was different in the F_1 and F_2 generations. The sign of correlation between order of dominance and order of parental means was negative in both generations, but only significant in the F_1 generation. The negative correlation indicated that the dominant genes act toward increasing days to maturity and recessive genes in the parents act in decreasing days to maturity, i.e. inducing earliness.

The graphical analyses are given in Figure 15. The regression coefficients (bW_r/V_r) were not different from unity in both generations indicating the adequacy of the genetical model. In both (A) and (B) it was clear from the position of array points that array parent 4 (Precoz) was extremely recessive compared with other parents; Parent 5 (Pant.L,406) was the second most recessive one. The array means of those parents for time to maturity were, 157 and 155 days in the F_1 and 157 and 155 days in the F_2 (Table 40) indicating little difference between them. In addition, both parents had the highest values of general combining ability amongst parents for this trait (Table 43).

These results suggested that Precoz and Pant.L,406 could be used as sources of earliness in maturity in a lentil breeding program.

Here it should be emphasized again that throughout this study a given (fixed) set of genotypes was investigated. The estimates of genetic components of variation (D, H_1, H_2,...) from this experiment characterized those genotypes involved in the present study only.

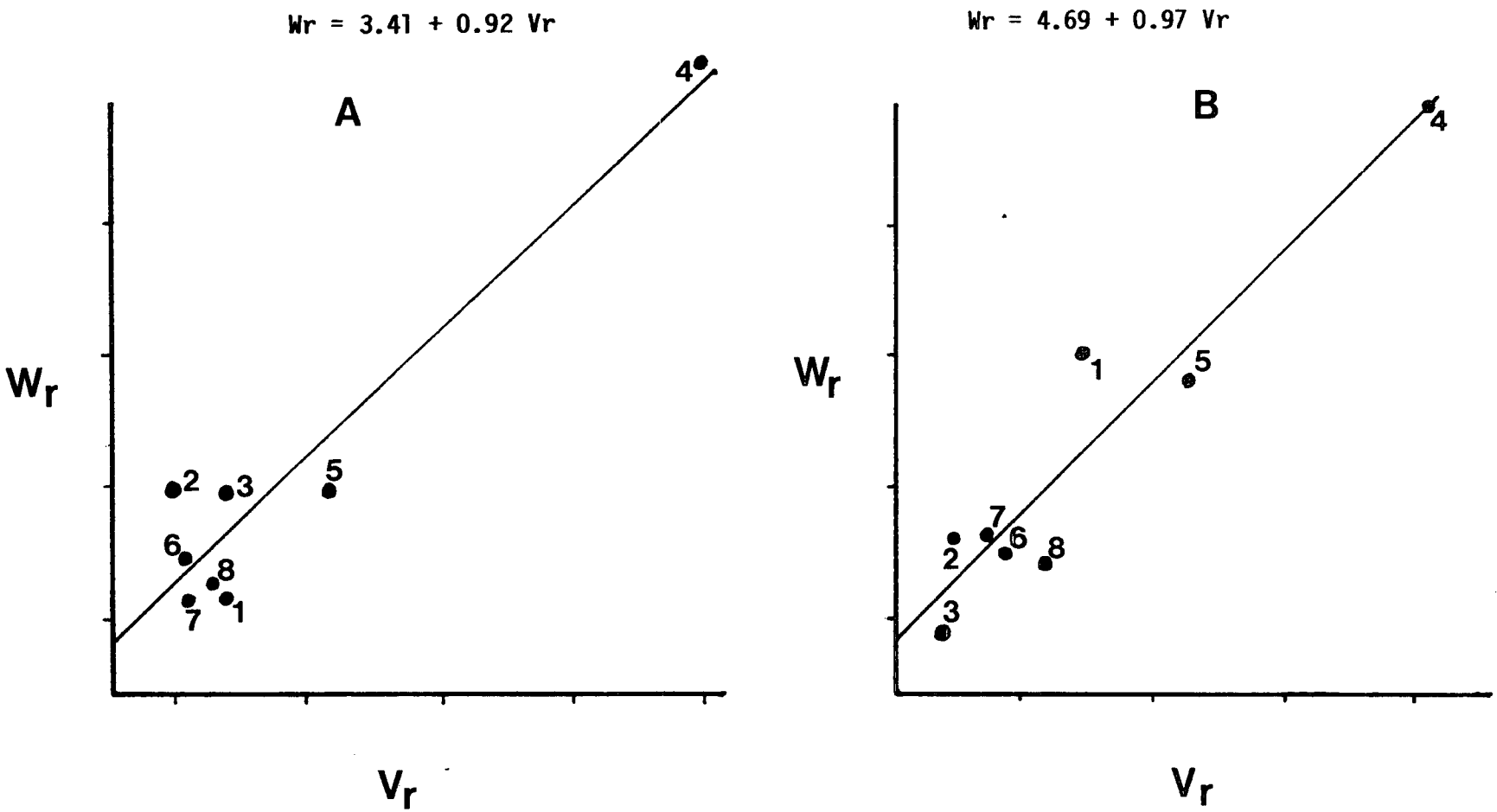


Figure 15. Vr, Wr graphs for days to maturity in the F_1(A) and F_2(B) generations from a diallel cross in lentil.

4.5 Prediction of promising genotypes and crosses for future generations

Prediction of the potential of crosses for producing superior progenies can be made on the basis of the genetic information provided by the various analyses presented earlier in this chapter, in conjunction with the estimates of the specific combining ability effects involving each F_1 and F_2 mean performance for all characters in Tables 51 to 60.

For seed yield per plant, the results indicated that the largest portion of genetic variability for this character was due to non-additive variance. Also, the poor correlation between general combining ability effects and parental mean indicated that we can not use the performance of parental means to predict their general combining ability. In addition, narrow sense heritability of this trait was low. Therefore, selection for seed yield may be difficult in the present sample of the parents and their intercrosses.

Because the specific combining ability was a major effect, in addition to the presence of overdominance (as indicated by the negative intercept values, not tabulated), this character was affected by non-allelic interaction, which is always associated with the presence of SCA and over-dominance (Jinks, 1954). It is thus possible that estimates of non-additive components include a substantial proportion of epistatic effects, besides dominance effects. Therefore, the superior F_1's are expected to throw out desirable transgressive segregants, provided that the desirable complementary genes and epistatic effects are coupled in the same direction to maximize seed yield.

The seven crosses which exhibited useful heterosis, also had high SCA effects (Table 51). Most of these crosses maintained their superiority in the F_2 generation. In addition to those crosses, hybrid Pant.L,406 x ILL274 produced the highest seed yield in the F_2 generation (Table 33), and it also had the highest SCA effect value (Table 51). These crosses are an immediate source of transgressive segregants.

Table 51 Estimates of specific combining ability (SCA) effects for seed yield per plant in the F_1 and F_2 generations from an 8-parent diallel cross in lentil*

Parents	Fam. 370	78S26004	Precoz	Pant.L406	FLIP 84,1-L	ILL 274	ILL 121
Giza 9	0.35	-0.61	-0.01	0.62	-0.11	-0.30	0.39
	-0.01	-0.30	0.30	-0.21	-0.35	0.15	0.29
Fam. 370		0.17	0.40	-0.19	-0.16	0.66	-0.22
		0.01	0.51	-0.06	0.17	0.03	-0.25
78S26004			0.43	0.70	-0.36	-0.29	0.71
			0.46	0.12	0.22	-0.16	-0.27
Precoz				-0.16	-0.33	0.02	0.04
				-0.13	0.24	-0.33	-0.61
Pant.L406					-0.06	-0.11	-0.15
					0.04	1.03	0.08
FLIP 84,1-L						0.25	-0.05
						-0.14	0.02
ILL 274							0.59
							0.78

* F_1 and F_2 data are in the first and the second row, respectively.
S.E. of the difference between effects of two crosses having one parent line in common is 0.35 for F_1's and 0.37 for F_2's.
S.E. of the difference between effects of two crosses having no parent line in common is 0.33 for F_1's and 0.35 for F_2's.

Table 52 Estimates of specific combining ability (SCA) effects for biological yield per plant in the F_1 and F_2 generations from an 8-parent diallel cross in lentil*

Parent	Fam. 370	78S26004	Precoz	Pant.L406	FLIP 84,1-L	ILL 274	ILL 121
Giza 9	0.72	-1.50	0.54	1.16	-0.21	-0.34	0.78
	0.03	-0.72	0.50	-0.44	-0.68	0.29	0.83
Fam. 370		0.32	0.80	-0.28	-0.64	0.86	-0.55
		0.18	0.94	-0.03	-0.08	0.00	-0.79
78S26004			0.71	1.52	0.53	-0.88	1.58
			1.49	0.31	0.74	-0.42	-0.85
Precoz				0.36	-1.06	0.10	0.56
				-0.06	1.33	-1.20	-0.79
Pant.L406					-0.21	-0.15	-0.52
					-0.28	2.33	0.10
FLIP 84,1-L						0.22	-0.15
						-0.55	0.03
ILL 274							1.08
							1.05

* F_1 and F_2 data are in the first and the second row, respectively.
S.E. of the difference between effects of two crosses having one parent line in common is 0.74 for F_1's and 0.88 for F_2's.
S.E. of the difference between effects of two crosses having no parent line in common is 0.69 for F_1's and 0.83 for F_2's.

Table 53 Estimates of specific combining ability (SCA) effects for straw yield per plant in the F_1 and F_2 generations from an 8-parent diallel cross in lentil*

Parents	Fam. 370	78S26004	Precoz	Pant.L406	FLIP 84,1-L	ILL 274	ILL 121
Giza 9	0.37	-0.89	0.55	0.53	-0.10	-0.04	0.39
	0.04	-0.43	0.21	-0.23	-0.34	0.14	0.59
Fam. 370		0.16	0.40	-0.09	-0.48	0.20	-0.33
		0.20	0.43	0.03	-0.25	-0.03	-0.54
78S26004			0.27	0.82	0.89	-0.59	0.88
			1.03	0.20	0.52	-0.27	-0.58
Precoz				-0.20	-0.73	0.09	0.52
				0.07	1.09	-0.86	-0.17
Pant.L406					-0.15	-0.03	-0.37
					-0.31	1.30	0.02
FLIP 84,1-L						-0.03	-0.10
						-0.41	0.01
ILL 274							0.49
							0.73

* F_1 and F_2 data are in the first and the second row, respectively.
S.E. of the difference between effects of two crosses having one parent line in common is 0.45 for F_1's and 0.55 for F_2's.
S.E. of the difference between effects of two crosses having no parent line in common is 0.42 for F_1's and 0.52 for F_2's.

In view of this it may be desirable to treat the advanced generation of these seven crosses as separate populations.

The genetic analysis of biological yield per plant showed the importance of both GCA and SCA. The additive genetic component represented 32% and 49% of the genetic variance in the F_1 and F_2 generations respectively and the correlation between GCA effects and parental mean were high in both generations. That indicates the possibility of using the general combining ability effect and parental means to predict promising crosses. This trait also exhibited significant heterosis. Parent ILL274 was ranked first in both F_1 and F_2 generations as the best general combiner (Table 43), and also produced the highest array means (Table 32). These results may provide evidence that the parent ILL274 may be involved as a common parent in any breeding program to improve biological yield/plant.

The F_1 crosses which exhibited useful heterosis also showed high SCA effect values. Three of these crosses showed high estimates of SCA effect in both generations. These were: Giza9 x ILL121, 78S26004 x Precoz and ILL274 x ILL121 (Table 52). Cross Pant.L,406 x ILL274 gave the highest value of SCA effect in the F_2 generation. These four crosses appeared to be the best ones in terms of their future potential for producing transgressive segregants. However, we cannot expect great genetic advance in this character due to the moderate narrow sense heritability of 32% between crosses.

The results of straw yield per plant showed that parents Giza9 and Family 370 gave low straw yield in both generations, while parent ILL274 gave the highest straw yield in both generations (Table 34). Also, this parent maintained its superiority in GCA effect in both generations (Table 43). The genetic analysis and correlation coefficient between parental order of means and order of GCA effect of parents indicated that the importance of both additive and non-additive effects of this trait and the performance of the parents give a good prediction of their GCA effects. Therefore using the parent ILL274 as a common parent in the cross combinations will be useful in improving straw yield.

Because some crosses exhibited useful heterosis in this character, accordingly some of these crosses had high SCA effects and can be selected as being promising. These are: Giza9 x Precoz, 78S26004 x Pant.L,406, 78S26004 x FLIP84 – 1 L, 78S26004 x ILL121 and ILL274 x ILL121 in the F_1 generation. Other promissing crosses are those of Pant.L,406 x ILL274, Precoz x FLIP84 – 1 L and 78S26004 x Precoz and ILL274 x ILL121. These crosses had the highest SCA effect in the F_2 generation. These crosses could provide the potential in a hybridization program to improve straw yield. Also, in this character, as in biological yield/plant, the expected genetic advance will not be great due to the moderate narrow sense heritability for straw yield.

Number of pods per plant is a yield component character, along with 100 seed weight and number of seeds/pod. The phenotypic correlation between seed yield/plant and number of pods/plant was 0.91, while it was -0.31 with number of seeds/pod and 0.34 with 100 seed weight. This indicates that number of pods/plant is the most important yield component character in this study and causes the major effect on seed yield/plant.

The results accumulated for number of pods/plant showed that gene action was mainly non-additive as indicated by the value of the ratio $2\ \sigma^2gca/(2\ \sigma^2gca + \sigma^2sca)$ and the non-significant correlation coefficient between parental mean and GCA effect of the parents (Table 44).

The regression V_r/W_r was very low and did not significantly differ from zero and was significantly different from unity in both F_1 and F_2 generations (Table 47). These results gave confidence that gene interaction played a significant part in determining the control of this character. As a result transgressive segregation can occur and selection for maximization of this trait in an early generation should be made. However, because of the low heritability estimates for this trait ($b_{n.s.}$ = 11% in the F_1 and 3% in the F_2 generation), selections must be evaluated in a progeny test.

The following combinations exhibited heterosis and high SCA (Table 54) and therefore may be recommended for improving number of pods/plant. They are: 78S26004 x Pant.L,406, 78S26004 x ILL121 and

Table 54 Estimates of specific combining ability (SCA) effects for number of pods per plant in the F_1 and F_2 generations from an 8-parent diallel cross in lentil*

Parents	Fam. 370	78S26004	Precoz	Pant.L406	FLIP 84,1-L	ILL 274	ILL 121
Giza 9	5.74	-13.61	0.15	9.84	1.06	-4.64	6.01
	-0.60	- 3.90	16.75	-9.20	-5.96	1.29	6.39
Fam. 370		0.82	5.0	-5.11	-0.91	9.89	-0.21
		-1.45	8.58	-3.33	1.70	3.37	-3.35
78S26004			7.94	18.50	-4.85	-5.44	14.34
			10.23	-0.17	5.10	-10.83	-4.56
Precoz				0.44	-4.96	1.14	3.06
				-2.14	4.53	-7.54	-11.96
Pant.L406					1.17	-1.67	-5.19
					9.76	29.81	-1.40
FLIP 84,1-L						4.09	-2.86
						0.02	2.64
ILL 274							11.53
							13.19

* F_1 and F_2 data are in the first and the second row, respectively.
S.E. of the difference between effects of two crosses having one parent line in common is 7.02 for F_1's and 9.82 for F_2's
S.E. of the difference between effects of two crosses having no parent line in common is 6.62 for F_1's and 9.26 for F_2's.

Table 55 Estimates of specific combining ability (SCA) effects for 100 seed weight in the F_1 and F_2 generations from an 8-parent diallel cross in lentil*

Parents	Fam. 370	78S26004	Precoz	Pant.L406	FLIP 84,1-L	ILL 274	ILL 121
Giza 9	0.16	-0.45	-0.12	0.43	-0.49	-0.06	0.28
	-0.01	-0.52	-0.92	0.47	-0.12	-0.06	0.17
Fam. 370		-0.25	-0.04	0.41	-0.44	0.01	-0.07
		-0.06	0.40	0.27	-0.45	-0.08	-0.10
78S26004			0.24	0.25	-0.43	0.20	0.25
			0.11	-0.18	-0.23	0.51	-0.02
Precoz				-0.39	-0.28	0.28	-0.32
				-0.22	-0.15	-0.12	-0.36
Pant.L406					-0.53	-0.15	-0.01
					-0.84	0.18	0.17
FLIP 84,1-L						-0.10	-0.26
						-0.34	-0.37
ILL 274							0.10
							0.36

* F_1 and F_2 data are in the first and the second row, respectively
S.E. of the difference between effects of two crosses having one parent line in common is 0.22 for F_1's and 0.16 for F_2's.
S.E. of the difference between effects of two crosses having no parent line in common is 0.21 for F_1's and 0.15 for F_2's.

Table 56 Estimates of specific combining ability (SCA) effects for number of seeds/pod in the F_1 and F_2 generations from an 8-parent diallel cross in lentil*

Parents	Fam. 370	78S26004	Precoz	Pant L406	FLIP 84,1-L	ILL 274	ILL 121
Giza 9	0.00	0.29	-0.03	-0.06	-0.02	0.01	-0.08
	0.06	0.03	-0.08	0.11	-0.06	0.04	-0.12
Fam. 370		0.18	0.13	-0.08	0.06	0.14	-0.14
		0.08	-0.08	-0.02	0.25	-0.10	-0.06
78S26004			-0.12	-0.21	-0.04	-0.08	-0.10
			-0.14	0.12	-0.03	0.27	-0.04
Precoz				-0.06	0.03	-0.17	-0.02
				-0.02	-0.04	0.01	0.11
Pant L406					0.04	0.08	0.20
					-0.04	-0.15	0.14
FLIP 84,1-L						0.03	0.16
						-0.08	0.02
ILL 274							0.00
							-0.06

* F_1 and F_2 data are in the first and the second row, respectively.
S.E. of the difference between effects of two crosses having one parent line in common is 0.20 for F_1's and 0.17 for F_2's.
S.E. of the difference between effects of two crosses having no parent line in common is 0.19 for F_1's and 0.16 for F_2's.

ILL274 x ILL121 in the F_1 generation and Giza9 x Precoz and Pant.L,406 x ILL274 in the F_2 generation.

The results of genetic analysis for 100 seed weight indicated a simple additive gene action system with partial dominance. The graphical analysis and the order of dominance indicated that parent FLIP84 - 1 L contained most recessive genes. This parent was also the second highest general combiner (Table 43). The correlation coefficient between parental order of means and order of dominance revealed that the recessive genes act towards increasing seed weight.

The accumulated results coupled with the high estimates of narrow sense heritability for this trait, suggest that parental means for 100 seed weight are a good guide to their potential in hybrid combination. Breeding by classical methods, such as pedigree method, can be advocated to fix the additive variation for 100 seed weight.

The results of genetic analysis for number of seeds/pod showed the importance of GCA and the relatively high D values compared with the insignificant H_1 and H_2 values. These results, in addition to the ratio $2\sigma^2 gca/2\sigma^2 gca + \sigma^2 sca = 1$, indicated the predominance of additive genetic components of variance for this character.

The array means (Table 36) indicate that when improving number of seeds/pod the parents Giza9 and Pant.L,406 should be involved in the cross combination as a common parent. These parents also had the highest GCA effects in both generations (Table 43). Their crosses; Giza9 x Pant.L,406 and Pant.L,406 x ILL121 in the F_2 generation yielded the highest number of seeds/pod (means of 1.86 and 1.80 respectively) and also had high SCA effects (Table 56).

The genetic control of plant height was mainly additive, as indicated by the ratio of $2\sigma^2 gca/2\sigma^2 gca + \sigma^2 sca$, but exhibited some non-additive effects (dominance). The existence of non-additive effects, specially in the F_2 generation, resulted in a moderate narrow sense heritability estimate of 31.2% in the F_2. The results also showed strong positive correlation between GCA effects and parental means (Table 44), suggesting that we can confidently select the parents having the highest GCA according to their performance.

Parents ILL121 and ILL274 had the highest array means (Table 38) and also exhibited the highest GCA effect values (Table 43) in both generations. Therefore, these two parents (ILL121 and ILL274) could be usefully involved in any cross combinations as a parent to increase plant height.

This character showed negative inbreeding depression (Table 31), since the average of the F_2 was higher than the F_1 mean. In fact the F_2 mean value should be intermediate between the mid-parent and F_1 mean values. However, epistasis could be the cause of this F_2 deviation from the expected value. The presence of non-additive genetic effect in the F_2 may be seen as supporting this assumption. An alternative cause of inbreeding depression could be that maternal effects are involved (Falconer, 1981). This assumption cannot be tested here because only a half of diallel set was used and reciprocal crosses were not made in this study.

The hybrid crosses which showed high performance in the F_2 should be exploited. The tallest crosses in the F_2 generation were Giza9 x ILL121, 78S26004 x Precoz, Precoz x FLIP84-1 L, Precoz x ILL121, FLIP84-1 L x ILL274 and ILL274 x ILL121 (Table 38). These crosses also showed high SCA effects (Table 57). Four crosses in which they were involved produced the highest seed yield and also the highest straw yield per plant; they were 78S26004 x Precoz, Precoz x FLIP84-1 L, FLIP84-1 L x ILL274 and ILL274 x ILL121.

Results for time to flowering showed that Family 370 and Precoz were the earliest arrays in the F_1 and F_2 generations (Table 39). These arrays carry the most dominant alleles for this character, as shown in Table 50 and Figure 13, 14, and occupied the first and second positions as general combiners in both generations (Table 43). The hybrid cross between both parents should have been the earliest cross. However, this did not occur and the cross between these two parents had an undesirable SCA effect (+3.85, Table 58). Such effects could be due, in part, to the existence of non-allelic interaction correlated with the epistatic parent Precoz. However, these two parents resulted in the earliest F_1 and F_2 hybrids with other parents. Of the six F_1

Table 57 Estimates of specific combining ability (SCA) effects for plant height in the F_1 and F_2 generations from an 8-parent diallel cross in lentil*

Parents	Fam. 370	78S26004	Precoz	Pant.L406	FLIP 84,1-L	ILL 274	ILL 121
Giza 9	-2.49	-3.42	3.19	2.07	-3.18	-0.76	0.52
	3.29	-0.83	-5.07	-0.55	2.33	-4.85	2.85
Fam. 370		2.17	1.77	-1.71	0.70	0.66	1.55
		-1.79	2.47	1.18	-0.78	0.84	-5.96
78S26004			3.37	0.79	1.95	-4.88	-0.71
			4.15	2.31	1.30	-1.88	0.47
Precoz				0.59	-2.61	-0.44	4.09
				3.82	1.61	-0.97	2.38
Pant.L406					1.57	2.99	1.27
					-0.98	1.24	2.19
FLIP 84,1-L						0.65	-4.03
						0.13	-4.22
ILL 274							-0.76
							0.70

* F_1 and F_2 data are in the first and the second row, respectively.
S.E. of the difference between effects of two crosses having one parent line in common is 3.05 for F_1's and 3.27 for F_2's.
S.E. of the difference between effects of two crosses having no parent line in common is 2.88 for F_1's and 3.08 for F_2's.

Table 58 Estimates of specific combining ability (SCA) effects for time to flowering+ in the F_1 and F_2 generations from an 8-parent diallel cross in lentil*

Parents	Fam. 370	78S26004	Precoz	Pant.L406	FLIP 84,1-L	ILL 274	ILL 121
Giza 9	-1.59	-6.18	1.35	4.30	2.70	-1.27	0.40
	-1.56	-4.81	2.49	1.64	-0.31	-1.16	1.34
Fam. 370		0.58	3.85	1.30	0.20	-5.03	-4.60
		-3.06	3.74	3.89	3.44	0.09	4.91
78S26004			4.78	2.73	1.13	1.15	-1.17
			1.99	4.14	3.19	-2.16	-0.66
Precoz				8.0	-3.60	-9.07	-0.40
				0.44	-1.51	-4.86	-7.86
Pant.L406					1.35	1.88	-10.45
					-4.86	-0.21	0.79
FLIP 84,1-L						0.28	4.45
						0.34	4.34
ILL 274							2.48
							-0.01

* F_1 and F_2 data are in the first and the second row, respectively.
S.E. of the difference between effects of two crosses having one parent line in common is 2.00 for F_1's and 1.61 for F_2's.
S.E. of the difference between effects of two crosses having no parent line in common is 1.88 for F_1's and 1.52 for F_2's.
+ Negative values desirable.

crosses and four F_2 crosses which exhibited the highest SCA, four F_1 and three F_2 crosses had Precoz and Family 370 as common parents (Table 58).

Because the genetic system controlling this character was mainly additive with minor, but significant, dominance effects, one would expect that the good arrays will maintain their supermacy in later generations. Therefore Family 370 could be used in building up breeding materials responsive to selection for earlines, while crosses such as Family 370 x ILL121, Precoz x ILL274 and Giza9 x 78S26004 could provide great potential in a hybridzation program for earliness.

The results of time to maturity in Table 40 showed that arrays Pant.L,406, Family 370, Precoz and 78S26004 were the earliest. The rankings of GCA of these parents were Pant.L,406 followed by Precoz, Family 370 and 78S6004 with the same order in both F_1 and F_2 generations (Table 43). The order of dominance (Table 50) and graphical analysis revealed that parent Precoz was the most recessive followed by Pant.L,406. Because the genetic correlation between order of dominance and order of means was negative, both Precoz and Pant.L,406 are superior parents in selection for earliness.

Genotypic correlations between time to flowering and time to maturity were positive and high (rg = 0.66 in both F_1 and F_2 generations), suggesting that selection for earliness in maturity can be made indirectly through selection for earliness in flowering.

The genetic analysis showed the importance of both additive and non-additive variance for seed protein content. However, the additive component of variance was higher in magnitude than the non-additive component of variance in the F_1 generation, while the reverse prevailed in the F_2 generation (Table 45). This result was confirmed by the estimates of ($2\sigma^2gca/2\sigma^2gca + \sigma^2sca$) and narrow sense heritability, which were higher in the F_1 than in the F_2 generation.

This character showed negative inbreeding depression in the F_2 generation (Table 31). The inbreeding depression may be due to epistasis effects or maternal effects, as discussed in plant height.

Table 59 Estimates of specific combining ability (SCA) effects for time to maturity+ in the F_1 and F_2 generations from an 8-parent diallel cross in lentil*

Parents	Fam. 370 .	78S26004	Precoz	Pant.L406	FLIP 84,1-L	ILL 274	ILL 121
Giza 9	-1.64	-4.57	3.28	2.23	-0.62	-2.34	0.08
	1.44	-3.16	0.04	-1.71	-0.41	0.49	0.79
Fam. 370		0.01	0.63	0.08	-2.27	0.78	-1.57
		-0.46	1.74	-0.51	-1.21	-2.31	-3.01
78S26004			0.66	1.11	1.76	-0.47	0.46
			2.64	2.89	-1.81	-0.91	-2.11
Precoz				6.23	2.88	4.61	4.58
				5.59	3.89	1.29	5.09
Pant.L406					0.83	0.11	-0.97
					0.14	3.54	0.34
FLIP 84,1-L						-1.24	-0.32
						-2.16	0.64
ILL 274							-3.04
							-0.46

* F_1 and F_2 data are in the first and the second row, respectively.

S.E. of the difference between effects of two crosses having one parent line in common is 1.94 for F_1's and 2.17 for F_2's.

S.E. of the difference between effects of two crosses having no parent line in common is 1.83 for F_1's and 2.04 for F_2's.

+ Negative values desirable.

Transgressive segregation may occur because of presence of epistasis and selection for maximization of this variable in early generations should be made. However, because of the low heritability estimates, selections must be evaluated in progeny tests.

Cross combinations; Giza9 x FLIP84 - 1 L, Family 370 x Pant.L,406 and Precoz x ILL121 may be recommended for improving seed protein. These crosses had the highest protein content level (Table 41) and also had the highest SCA effects (Table 60).

It should be emphasized that those crosses which had the highest protein content produced the lowest seed yield per plant, as shown in Table 33. This may be due to a negative, or lack of, correlation between seed yield and seed protein content. Therefore, these crosses could be used where a high level of seed protein is the main objective, or they may be used, in later generations, as a source of high protein in hybridization programs.

However, when two characters are negatively correlated, the breeder should use special breeding programs to break linkage. One such approach is to intercross segregating populations; another may be the use of mutagenesis.

Table 60 Estimates of specific combining ability (SCA) effects for seed protein per cent in the F_1 and the F_2 generations from an 8-parent diallel cross in lentil*

Parents	Fam. 370	78S26004	Precoz	Pant L406	FLIP 84,1-L	ILL 274	ILL 121
Giza 9	0.14	0.05	0.05	0.97	-0.13	-0.78	-0.45
	0.33	0.50	-1.12	0.45	1.61	-0.52	-0.98
Fam. 370		0.31	0.49	0.47	-0.64	-0.45	-0.25
		0.51	-0.11	1.67	-1.37	-0.71	0.09
78S26004			-1.11	0.26	0.66	-0.89	-0.41
			-0.54	0.18	-0.91	-0.09	-0.30
Precoz				1.61	-0.06	0.94	0.67
				-0.59	0.02	0.04	0.93
Pant L406					-1.29	0.07	-0.90
					0.00	-0.24	-1.84
FLIP 84,1-L						-0.49	0.34
						-0.53	0.37
ILL 274							0.25
							0.28

* F_1 and F_2 data are in the first and the second row, respectively.
S.E. of the difference between effects of two crosses having one parent line in common is 0.71 for F_1's and 0.64 for F_2's.
S.E. of the difference between effects of two crosses having no parent line in common is 0.67 for F_1's and 0.61 for F_2's.

CHAPTER IV

GENERAL DISCUSSION

Since quantitative characters are controlled by both genetic and environmental effects, a progeny variance estimated from a single selection in one year contains interaction variance in addition to the true genetic variance, inflating the estimation of genetic variance (Allard, 1960; Johnson et al. 1955). In this study, the experiments were conducted across very diverse conditions at five environments in two years. Thus, the components of variance due to genotype-environment, genotype-year and genotype-environment-year interactions were estimated and removed from the estimate of the genetic variance component. Therefore, the data provided improved estimates of genetic variance.

The results showed that number of pods per plant had a high genotypic variance and potential genetic advance, and in addition had strong positive phenotypic and genotypic correlations with seed yield. Variation in number of pods was thus largely responsible for the considerable variation in seed yield. Consequently this character may be useful for indirect selection for seed yield/plant.

The absence of strong negative phenotypic and genotypic correlations between seed yield and seed protein content indicated the possibility of selecting for high yield and protein simultaneously amongst these genotypes. The close relationship between seed size and cooking time eliminates the need for screening early generation lentil genotypes for cooking time, since for all practical purposes the cooking time was predictable on the basis of seed size. Selection of the early generation genotypes for quality then becomes simply a matter of determination of seed size and protein content, which were found to be highly heritable characters in this study.

There was a strong positive correlation between seed size and dehulling percent. However, the results showed a wide range of

dehulling percent within each of the macrosperma and microsperma genotypes. The low heritability and genetic advance of this trait in addition to its high genotype-environment and genotype-year interaction variances increase the difficulty for its use in selection.

Much work is needed to investigate the relationships between the dehulling ability and tannin and lignin contents in lentil seeds and also to study the inheritance of these characters. Also, there is a need to study the relationships between the variation of dehulling and seed characters (such as seed shape, seed coat patterns and colour) which may help the lentil breeder in screening for high dehulling genotypes.

The main objective of lentil breeding programs is to increase seed yield. A neglected aspect of the crop's improvement is its straw yield. The straw is very important to farmers in the Middle East as a livestock feed, and sometimes the sale price of lentil straw is as large as that of the seed (Nordblom and Halimeh, 1982).

In this study thephenotypicand genotypic correlations between both seed and straw yields were positive (r_{ph} = 0.25, r_g = 0.23). These relationships indicate the possibility of selecting for a high performance of both characters. The indeterminate growth habit of the lentil allows the number of reproductive nodes to be proportional to the size of the vegetative frame and, hence, straw yield (Erskine, 1983). Therefore, selection for seed yield will not reduce straw yield, but may increase it.

As Allard (1960) mentioned 'If the breeder wishes to exercise control over some particular components of environments, he can design experiments to identify and measure such specific components of environment and their interactions with genotype.'

In this study environments differing widely in water supply (irrigation and rainfall) were employed, in order to identify their effect on lentil characters. Since lentils are grown under irrigation (as in Egypt, Sudan and elsewhere) an understanding of the genotype-irrigation interaction is of particular value in enabling an efficient breeding strategy to be formulated.

The predominance of environments as a source of variance for seed yield and most other characters in these experiments may be due to the breadth of environments sampled, representing differences mainly in water supply levels and partially in temperature and soil types, employed in this study. The magnitude of environmental variance, however, also suggests the possibility of raising yield levels through improved management practices, especially irrigation. The average seed yield with two irrigations (total of 446 mm water) was higher by 19% than the yield with no irrigation (346 mm), and was more than three times as great as that with 248 mm water.

Genotypic effects were highly significant and high. The genotypes used in this study showed wide genetic diversity, allowing selection for higher-yielding genotypes under irrigation. As there are more than 5,000 accessions of lentil in ICARDA germplasm collections, there is considerable scope for selection. Such germplasm evaluation must be made under irrigated conditions.

Genotype-environment interaction is another important source of variation for seed yield. Hill (1975) reported that the presence of genotype-environment interactions automatically implies that the behaviour of the genotype in the trial depends upon the particular environment in which they are grown. Thus the performance of any one of the genotypes relative to the remaining genotypes grown in the same environment will be unique.

The results revealed differences between the highland and lowland environments which showed that altitude (i.e. temperature) was more important than rainfall in adaptation (at Terbol). In order to select for wide adaptation, it will thus be important to test in both highland and lowland environments, rather than confining selection to either.

The linear regression technique was used to describe the behaviour of genotypes over a range of environments. The regression analyses of genotype-irrigation and genotype-environment interactions showed that a large portion of variation in seed yield per plant was due to linear regression on environmental means. Four genotypes exhibited response

to irrigation, these being; 74TA264, 74TA276, FLIP84-27L and ILL 241. These genotypes could be recommended as promising genotypes under irrigated conditions. Consequently, these entries will probably be used in lentil breeding programs in Egypt and Sudan as introductions and parents in the crossing block.

Also, a considerable range of variation in stability was noted amongst genotypes under different environments. The results showed that several genotypes were stable and had high seed yield/plant. However, FLIP 84-67L had the highest seed yield among those entries and therefore it can be recommended as a most stable genotype under rainfed conditions.

All genotypes which showed response to irrigation were medium-large seeded types, whereas the genotypes which exhibted adaptability to dry conditions were very small seeded. Also, the former genotypes showed high yield and possessed favourable rooting characteristics. These results, in addition to the positive correlation between seed size and seed yield, are an interesting discovery for countries such as Egypt and Sudan, where only small seeded genotypes are grown. Also, in lentil breeding programmes in these countries selection is practised for small seeded and very early types, discarding large seeded lines, so that much potentially valuable material may have been lost in this way.

Two reasons are given for growing solely small seeded lentil in these countries; firstly because temperatures rise quickly during March (the period of reproduction growth) early maturing genotypes are preferred, and secondly, the people are used to consuming small-seeded lentils.

The results in this study indicated that genotypes adapted to irrigation were not late maturing types, but matured only 8 days later than the very early genotypes. The second reason for preferring small seeds is also invalid, since large seeded lentil is now imported into Egypt and is available in the market.

Consequently, the evaluation of new medium-large seed size and early maturing introductions under irrigation in both Egypt and Sudan will be a very desirable objective.

The morphological and anatomical adaptation to irrigation in roots observed in this study might be used as a preliminary seedling selection criterion in screening for response to irrigation in lentil breeding programmes. Further screening of additional irrigation responsive lines and irrigation ill-adapted lines is required to test the method. Irrigation-responsive genotypes are particularly valuable when irrigated lentils are grown in a heavy clay soil with a high watertable as in Egypt. Under this environment the use of lentil genotypes, which can adapt their root structures and systems, is very important for yield improvement.

The technique used for the morphological and anatomical screening in this study is simple, easy, inexpensive and effective for screening large numbers of accessions in a short period. There are also some other techniques which can be used to induce anearobic conditions (oxygen deficiency), such as growth of plants in nutrient solution, either aerated or nitrogen-flushed, (Wiedenroth and Erdmann, 1985 and Erdmann et al., 1986) or growth of plants in sand media flooded with water or nutrient solution (Erdmann et al., 1986). Other techniques for studying roots subjected to oxygen stress have been described by Drew et al. (1980).

Further investigations are needed to identify the most effective combination of physiological mechanisms that may suit a particular irrigation environment. Also more work is needed to improve resistance to diseases under irrigation, especially root-rot which is common under irrigation in hot countries. In addition, genetic studies are needed to investigate the inheritance of root system characters under irrigation (root length, branching, shoot/root ratio).

The study of heterosis indicates the percentage increases of the F_1 over mid-parent or the better parent and thus helps in selecting out the best crosses. Rejection of crosses showing no heterosis would enable the breeder to concentrate on fewer more productive crosses, which would be helpful in building useful breeding materials especially if resources are limited.

The degree of heterosis in this study varied from character to character, the highest value being 40.3% (over mid-parent) in number of

pods per plant. The results indicated that number of pods per plant influenced hybrid vigour in seed yield.

Despite the presence of heterosis in lentil, it cannot be exploited commercially because artificial hybridization is technically difficult. Assuming a male sterility mechanism will be discovered in lentil and the technical problems of cross pollination solved, hybrid lentil could be produced from inbred lines derived from parents such as those showing high SCA effects in this study. Alternatively, hybrids could be developed using recurrent selection (Hull, 1945) to make efficient use of inbred lines showing high SCA effects.

Despite the importance of heterosis, it fails to identify the possible causes for the superiority of hybrids. Studies on combining ability, on the other hand, provide information on the overall gene action controlling quantitative characters and helping the breeder in the choice of appropriate parents.

This fact leads to the importance of using diallel analysis techniques. As outlined by Jinks (1954) and Hayman (1954 a,b) the diallel analysis attempts to partition phenotypic variation into genotypic and environmental components and to further subdivide genotypic variation into its additive and dominance components. These values can be used to draw inferences about the genetic system. In addition, the diallel is a systematic method for identifying those parents and hybrids that have superior combinations of the characters of interest. This information is required because the breeding methods employed for maximum genetic improvement of qualititive traits are dependent upon the types and relative amounts of genetic variability for those traits in the population of interest.

The use of three diallel analysis techniques in the present study allowed comparison of results obtained from each method and increased confidence in the results. Since the parents and F_1 and F_2 crosses in this experiment were grown under irrigation, the results provided information on the genetic system in these lentil populations in response to irrigation. Because one of the main objectives in this study was to identify lines with potential as parents, method 2 for combining ability analysis was used.

The present study showed that the diallel cross analysis provided an overall genetic and performance evaluation. It has also provided useful information about the relative importance of general and specific combining ability. In addition it provided information on the genetic identity of the characters under investigation, on dominance-recessive relationships and on genetic interaction.

The results showed insignificant correlation between parental means and general combining ability values for seed yield per plant. This indicated that the performance of the parents per se is not necessarily a good indicator of their combining ability in later generations for this trait. However, the genotypes 78S26004, ILL274 and ILL121 may be recommended as parents for the improvement of seed yield. On the other hand, the results indicated that both Egyptian genotypes; Giza 9 and Family 370, are not good combiners for seed yield per plant.

The additive variance, which is the variance of breeding values, is the most important component since it is the chief cause of resemblance between relatives and therefore the chief determinant of the observable genetic properties of the population and of the response of the population to selection (Falconer, 1981). Consequently a knowledge of the additive variance is important because it assists in defining appropriate breeding methods.

As the results showed, 100 seed weight, number of seeds per pod, time to flowering and time to maturity character had a large additive component. Therefore, all methods of breeding and selection are appropriate and should be effective to the improvement of these traits. For seed yield per plant and the remaining characters in this study, the non-additive component was more important.

Variation due to non-additive gene action in seed yield could be exploited in hybridization programmes. Consequently, the five F_2 crosses which showed superiority in seed yield and SCA effects should be carried forward. These being Giza 9 x ILL121, 74TA26004 x Precoz, 74TA26004 x Pant.L,406, ILL274 x ILL121 and Pant.L,406 x ILL274.

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Appendices

Appendix Table 1. Array covariance (W_r), variance (V_r) and their differences for 100-seed weight in the F_1 and F_2 generations from an 8-parent diallel cross in lentil

Parents	F_1			F_2		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Giza 9	0.1414	0.0245	0.1169	0.1543	0.1243	0.0300
2. Family 370	0.1557	0.0786	0.0771	0.3729	0.1700	0.2029
3. 78S26004	0.3829	0.240	0.1429	0.5414	0.4014	0.1400
4. Precoz	0.6457	0.4429	0.2029	0.6623	0.5829	0.0814
5. Pant.L, 406	0.4986	0.2286	0.2700	0.1286	0.1243	0.0043
6. FLIP 84,1-L	1.0100	0.8086	0.2014	1.13	0.9486	0.1814
7. ILL 274	0.5871	0.3000	0.2871	0.4229	0.260	0.1629
8. ILL 121	0.4529	0.2371	0.2517	0.3071	0.1586	0.1486
Intercept	0.155			0.089		
	b = 1.116 ± 0.11			b = 1.086 ± 0.095		

Appendix Table 2 Array covariance (W_r), variance (V_r) and their differences for no. of seeds per pod in the F_1 and F_2 generations from an 8-parent diallel cross in lentil

Parent	F_1			F_2		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Giza 9	0.0043	0.0029	0.00143	0.0271	0.0229	0.0042
2. Family 370	0.0114	0.0086	0.00286	0.0143	0.0171	-0.0028
3. 78S26004	0.0300	0.0529	-0.0229	0.0357	0.0386	-0.0029
4. Precoz	0.0371	0.0386	-0.0014	0.0343	0.0257	0.0086
5. Pant.L,406	0.0414	0.0443	-0.00286	0.0243	0.0243	0.00
6. FLIP 84,1-L	0.0371	0.0300	0.00714	0.0243	0.0243	0.00
7. ILL 274	0.0342	0.0357	-0.00142	0.0057	0.0114	-0.0057
8. ILL 121	0.0314	0.0343	-0.00286	0.0286	0.0214	0.0072
Intercept	0.0078			-0.0015		
	$b = 0.668 \pm 0.16$			$b = 1.11 \pm 0.26$		

Appendix Table 3 Array covariance (W_r), variance (V_r) and their differences for time to flowering in the F_1 generation from an 8-parent diallel cross in lentil

Parents	All parents included			Parent 4 eliminated		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Giza 9	32.57	25.94	6.67	32.56	28.88	3.68
2. Family 370	4.66	1.85	2.81	5.69	2.16	3.53
3. 78S26004	24.33	17.55	6.78	29.48	20.43	9.05
4. Precoz	6.92	23.71	-16.79	-	-	-
5. Pant.L406	6.59	23.70	-17.11	14.52	25.48	-10.96
6. FLIP 84,1-L	50.74	32.25	18.50	42.88	25.24	17.64
7. ILL 274	68.70	63.12	5.58	54.81	43.76	11.05
8. ILL 121	67.45	63.41	4.04	70.85	71.12	- 0.27
Intercept	-2.278			6.116		
	b = 1.11 ± 0.23			b = 0.96 ± 0.19		

Appendix Table 4 Array covariance (W_r), variance (V_r) and their differences for time to flowering in the F_2 generation from an 8-parent diallel cross in lentil

Parents	All parents included			Parent 4 eliminated		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Giza 9	40.76	23.21	17.55	40.09	24.49	15.60
2. Family 370	22.58	15.21	7.37	20.91	16.37	4.54
3. 78S26004	30.54	21.64	8.90	27.02	21.81	5.21
4. Precoz	4.40	3.50	0.90	-	-	-
5. Pant.L406	58.57	22.29	16.28	32.35	18.56	13.79
6. FLIP 84,1-L	52.48	35.91	16.57	44.79	29.22	15.57
7. ILL 274	57.01	40.28	16.73	44.88	25.24	19.64
8. ILL 121	66.07	62.36	3.71	49.26	36.74	12.52
Intercept	33.09			4.038		
	$b = 0.213 \pm 0.45$			$b = 1.34 \pm 0.33$		

Appendix Table 5 Array covariance (W_r), variance (V_r) and their differences for time to maturity in the F_1 and F_2 generations from an 8-parent diallel cross in lentil

Parents	F_1			F_2		
	W_r	V_r	W_r-V_r	W_r	V_r	W_r-V_r
1. Giza 9	7.23	8.91	-1.68	26.04	14.03	12.01
2. Family 370	15.15	5.44	9.71	12.29	3.93	8.36
3. 78S26004	15.44	9.41	6.03	4.99	3.11	1.88
4. Precoz	47.27	46.34	0.93	45.15	41.39	3.76
5. Pant.L406	15.20	16.98	-1.78	24.06	22.28	1.78
6. FLIP 84,1-L	9.71	5.46	4.25	11.29	8.07	3.22
7. ILL 274	6.96	6.32	0.64	11.78	7.25	4.53
8. ILL 121	8.02	7.48	0.54	10.07	11.00	-0.93
Intercept		3.407			4.687	
$b = 0.919 \pm 0.11$				$b = 0.974 \pm 0.13$		

Appendix Table 6 Chemicals and supplier Companies

Chemical	Company
Ammonium persulphate	BDH Chemical Ltd., Poole,
Acetic acid	Dorset, U.K.
Methanol	"
N, N, N, methylene-bis-acrylamide (BIS)	"
N, N, N', N', tetramethyl ethylene-diamine (TEMED)	"
Sodium dodecyl sulphate (SDS)	"
Acrylamide	Sigma Chemical Company,
Coomassie brilliant blue R 25°	Poole, Dorset, U.K.
Glycerine	"
Trizma base [tris (hydroxy methyl) amino methane]	"
L-leucyl-ß-naphthylamide HCl, puriss, CHR, A.R.	Koch-Light Laboratories Ltd. Colnbrook.