Genetics of Flowering Time in Chickpea and Its Bearing on Productivity in Semiarid Environments

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Chickpea (*Cicer arietinum* L.), a grain legume of Near-East origin has a unique natural history. The crop cycle in most of its traditional growing areas is completely different from the autumn germination, spring flowering, and summer maturation of its wild progenitor, *Cicer reticulatum* Ladiz., in eastern Turkey. Millennia of summer cropping in the Near-East and later dissemination into the lower latitude growing areas of eastern Africa and the Indian subcontinent, as a postrainy season crop, had profound effects on allelic variation in major adaptive loci of chickpea. In this chapter we discuss the consequences of the traditional cropping practices on the flowering time genes of chickpea. The recently identified genes for flowering

time are described with special reference to their effect on chickpea adaptation, seed weight, seed yield, and stability under semiarid Near-East and Indian subcontinental growing environments. It is suggested that the genetic research on flowering time of this species and its wild relatives needs much attention, as only two genes affecting this trait are identified so far. Genes allowing a reduced crop cycle will provide pathways for new cropping systems and increased population density. Reduced crop duration may also help chickpea escape damage by the major biotic and abiotic stresses that mostly affect the crop at flowering and podding stages. It is concluded that the relatively simple inheritance of flowering time opens up new possibilities for breeding high yielding and stable chickpea cultivars for the semiarid and arid regions globally

I. INTRODUCTION

Chickpea (*Cicer arietinum* L.), with total annual production of 9.1 million tons from an area of about 11.1 million ha, ranks third among the world's food legumes or pulse crops (FAO, 1999). The Indian subcontinent (India, Pakistan, Myanmar, Bangladesh, and Nepal) accounts for about 80% of the global production while the rest is produced in eastern Africa, Mediterranean and Near-East countries, Australia, southern Europe, and North and South America. Chickpea provides high-quality protein and starch to the predominantly vegetarian population in India and large population sectors in other South Asian and Near-East countries and is considered a health food in developed nations. Chickpea does not contain any specific major antinutritional factors such as ODAP in grasspea (*Lathyrus sativus* L.), vicin in faba bean (*Vicia faba*), and trypsin inhibitors in soybean (*Glycin max*), although it has oligosaccharides which cause flatulence (Williams and Singh, 1987).

At present the demand for this popular pulse in the developing countries is higher than their current production. The major reason for this trend is the expansion of cereal cropping, with progressively smaller and marginal areas being devoted to legume crops like chickpea and lentil. During the past 4 decades, the productivity of chickpea has not kept pace with the dramatic increases in the cereal production, thus it has lost and is still losing traditional areas to wheat, which produces higher and more stable yields under high input irrigated environments (Kelley and Parthasarthy, 1994). The relegation of chickpea to marginal lands, with lower productivity, further aggravates the situation, since low productivity is also accompanied by yield instability. Therefore, international trade is on the increase. For instance, a lucrative chickpea industry developed recently in Australia (FAO, 1999; Siddique and Sykes, 1997), mostly for export to India. Area under chickpea in Australia rose from practically nil to ca. 200,000 ha with total production of

nearly 180,000 tons in 1998 (FAO, 1999) We consider these figures as a trend unlikely to reverse in the foreseeable future and stress the urgency in achieving a major leap in chickpea production in the Indian subcontinent, eastern Africa and the Mediterranean region, where the bulk of the produce is consumed

The semiarid tropics include parts of 49 countries in South Asia, northern Australia, sub-Saharan Africa, parts of southern and eastern Africa and some countries of Latin America One-sixth of the world population, the poorest on Earth, inhabits these regions Half of them live on less than U S $1 per day and " work hard to sustain a living through daily and seasonal struggle to protect poorly endowed natural resources, conserve scarce water, improve soil fertility, and diversify crop choices" (Barghouti, 1999) Chickpea is one of the vital crops that can produce sustainable seed and stover yield in these harsh environments to provide quality-protein food to the inhabitants Chickpea is also important in the cropping systems outside the semiarid tropics, e g , in Asia, northern Africa, southern Europe, North and South America, and southern Australia Thus it contributes to sustainability of agriculture in all these regions

A major rationale for including chickpea in the cropping systems of the semiarid environments is its demonstrated potential to contribute to enhancement of the natural resource base used for the production of the other crops that are staple foods of the poor communities who rely on marginal rainfed lands The crop's natural drought resistance makes it eminently suitable for such lands Its benefits to traditional cropping systems in the Indian subcontinent are well documented (Ryan, 1997) Although chickpea can fix up to 140 kg N ha^{-1} in a growing season, reported values usually range from 20 to 60 kg N ha^{-1} Inclusion of more legumes like chickpea in cropping systems should enhance N fixation in the system and can reduce the need for fertilizer, saving inputs and preventing environmental degradation The additional benefits include disruption of disease cycles affecting nonlegumes and higher water use efficiency by disruption of cereal--cereal rotations

We believe that lack of genetic knowledge is responsible for the slow progress in chickpea breeding Even after a quarter-century of international effort the addition to the chickpea gene map is minimal Only a few linkages are worked out at the end of the century (Muehlbauer and Kumar, 1999) and its molecular map is still sketchy and based on an interspecific cross (Winter *et al*, 1999) In contrast the pea (*Pisum sativum* L) gene map, particularly with its flowering genes, is perhaps among the best genetically characterized systems (Marx, 1985, Weller *et al*, 1997) A comprehensive classic gene map of *Pisum* was developed in the late 1940s (see Marx, 1985) and detailed DNA marker maps are available (Ellis *et al*, 1992)

Flowering is a major adaptive trait material to survival and cultivation (Marx, 1985) Genetic analysis of flowering time and its bearing on agronomic performance is fundamental to crop improvement The need to manipulate flowering time stems from the fact that chickpea growing season is generally too long for

obtaining a meager mean seed yield of about 0.8 t ha^{-1} (Kumar *et al.*, 1996). This could be produced in a much shorter period. Therefore, it is dangerous to let such an attractive crop remain in the field for a longer period than is necessary. It is estimated that major biotic and abiotic stresses reduce at least 50% realizable potential yield of this crop in the major production regions of the world (Ryan, 1997). Much of these losses occur at flowering and podding time during February/March in the subtropical Indian subcontinent, where the bulk of the crop is grown. If chickpea can be harvested early, much of these losses could be avoided (Kumar *et al.*, 1996). In this chapter, we describe the natural history with special emphasis on its direct bearing on the phenology of the central chickpea stocks and the newly reported flowering genes. In addition, the potential role of these genes for future improvement of chickpea in the semiarid environments is discussed.

II. EVOLUTION OF THE CROP AND GENETIC VARIATION

A. The Origin of the Crop

Chickpea is a self-pollinating diploid species having basic chromosome number 8. The genus *Cicer* holds more than 40 species (van der Maesen, 1987), nine of which (including the cultigen) are annuals. Two among the eight wild annual *Cicer* species, native to eastern Turkey, are closely related to the cultigen. The first, *Cicer echinospermum* P. H. Davis (echinate seed coat), grows in steppe plant formations on soils of basaltic origin. The second closely related species is *Cicer reticulatum* Ladiz (reticulate seed coat), which is found in oak shrub formations on hilly limestone bedrock (Ladizinsky, 1975). Based on meiotic chromosomes pairing data, *C. reticulatum* was suggested as the immediate wild progenitor of domesticated chickpea (Ladizinsky and Adler, 1976a, 1976b). This early identification is also supported by seed storage protein profiles (Ladizinsky and Adler, 1975) and by more recent morphological comparisons (De Leonardis *et al.*, 1996) as well as by DNA marker analyses (Patil *et al.*, 1995).

C. reticulatum was first collected and described in 1974 (Ladizinsky, 1975). Ever since, only 10 populations have been located in southeast Turkey (Ladizinsky, 1995). However, the ICARDA catalog of wild annual *Cicer* species (Robertson *et al.*, 1995) lists 51 *C. reticulatum* accessions. Upon close examination of the catalog entries, one realizes that ICARDA currently maintains 10 original collections (Robertson *et al.*, 1995) while the remaining are selections from the original material. Unfortunately, the number of *C. reticulatum* accessions utilized in genetic analyses is also small; that is, not all the 10 accessions have been utilized (e.g., Gaur and Slinkard, 1990a, 1990b; Singh and Occampo, 1997). We believe that the meagre number of *C. reticulatum* accessions deposited in gene banks

reflects a low interest in this species at the time of its discovery, and in recent years is an unfortunate consequence of the uncertain political situation in Turkish Kurdistan

The earliest remains of chickpea seeds were unearthed from archaeological digs within or near the known distribution range of *C reticulatum* (Zohary and Hopf, 1993) The earliest excavated chickpea remains were dated to the Pre-Pottery Neolithic B period of a number of Near-East sites (Zohary and Hopf, 1993) Unlike cereals' archaeobotanic remains, in most cases it is impossible to distinguish between wild and cultivated pulses Due to the very limited distribution of the wild progenitor, the common view is that chickpea was domesticated somewhere in the west arch of the Fertile Crescent alongside the rest of the founder crops of the Near-East Neolithic agriculture (Zohary and Hopf, 1993, Lev-Yadun *et al* , 2000) It is interesting to note that the area delimited by the actual range of *C reticulatum* is the only region in the Fertile Crescent where all the wild progenitors of the founder crops of the Near-East Neolithic agriculture grow together This includes the wild species of diploid and tetraploid wheat, barley, lentil, pea, bitter vetch, and flax as well as wild rye (Lev-Yadun *et al* , 2000) The earliest occurrence of chickpea in India dates back to 2000 BC at Atranjikhera in Uttar Pradesh, although it may have been introduced independently to the southern parts of the country by sea (Chowdhury *et al* , 1971, van der Maesen, 1987)

A few morphological characters and geographic distribution are commonly used for classification of chickpea into two main cultivar groups The desi type, grown mainly in the Indian subcontinent and East Africa, is characterized by pink flowers and small (100- to 200-mg), usually angular, and yellow-brown-(or other) colored seeds The kabuli type, native to the Mediterranean and Near-East region, possess white flowers and large (200- to 680-mg) smooth or wrinkled light-colored seeds Vavilov (1950) suggested two primary centers of diversity, Southwest Asia and the Mediterranean center, and designated Ethiopia as a secondary center He observed that large-seeded varieties were cultivated in the Mediterranean basin and progressively small-seeded varieties abounded eastward It is believed that kabuli chickpea was introduced into India through Kabul, Afghanistan (therefore named kabuli) in the mid-to late 17th century The spread of chickpea to tropical Africa, North and South America, and Australia has occurred in more recent times

B. Natural History of the Crop under Domestication

Five major cool-season food legumes, garden pea, lentil, faba bean, grass pea, and chickpea, originated in a fairly well-defined area of the eastern Mediterranean basin They have developed two distinct patterns of distribution subsequent to their domestication (Smartt, 1990) The garden pea and faba bean show northward spread and can be cultivated throughout Europe Lentil, grass pea, and chickpea show limited adaptation to northern Europe This may be related to the duration of

growing season required Satisfactory maturation of their pods may not occur in cool, moist conditions with declining autumnal daylength They have spread east and west, covering the latitudes of the place of their origin, and moved southward, probably due primarily to their drought tolerance

1. The Mediterranean and the Near-East Gene Pool

The Greek botanist Theophrastus (1977, in translation) and the Roman historian Pliny (1971, in translation) have described chickpea as a summer crop (sown in March/April and harvested in June/July) Such a crop begins and completes its life cycle under increasing photoperiod and rising temperatures and depends mainly on stored soil moisture (Khanna-Chopra and Sinha, 1987; Kostrinski, 1974) It is unclear whether the chickpea crop cycle in the initial stages of domestication was similar In any case, the crop cycle described in the ancient reports is entirely different from that of the wild ancestor In the wild, *C reticulatum* germinates after the autumn rains and develops vegetatively during the rainy winter under shortening photoperiod and cool temperatures Flowering and reproduction occur in the late spring when mean temperatures are high and the days are long Spring-sown, wild *C reticulatum* plants in Rehovot, Israel, yield less than 1/5th of total biomass and seed produced by the winter sown crop (S Abbo, HUJ, Rehovot, Israel, unpublished observations) What could have been the reason for the readiness to compromise to such an extent on seed yield? The common view is that the incipient farmers were fully aware of the devastating effects of the blight disease caused by the fungus *Didymella rabiei* (Kovacevski) v Arx [anamorph *Ascochyta rabiei* (Pass) Labr] In the Near East, the climatic conditions favoring spread of the disease occur from early February until early April Since an autumn-sown crop would have a fully closed canopy by this time, an ascochyta epidemic is likely to destroy the crop completely Indeed, ascochyta blight is the major biotic constraint for chickpea production in the Mediterranean basin to this very day (Singh and Reddy, 1996, Vir *et al* , 1975) In other parts of the world where chickpea has been introduced, ascochyta blight epidemic can occur The disease destroyed much of the chickpea crop in Australia, during 1998 In South Australia, which also has a Mediterranean climate, the area planted to this crop in 1999 was reduced to 8,000 ha from over 80,000 in 1997 (Jan Bert-Brouwer, Victoria Dryland Agricultural Institute, Horsham, Australia, personal communication) Since the disease is not a serious problem in spring-sown chickpea, it is considered as the prime reason for the ancient practice of chickpea spring sowing

This change in the plant cycle following domestication is unique to chickpea (and to some extent to lentil) The founder crops of the Near-East agriculture, einkorn and emmer wheat, barley, pea, bitter vetch, and flax, all retained their original plant cycle (as winter crops) in the ancient and traditional Near-East farming (Zohary and Hopf, 1993, Elazari-Volcani, 1930) This is because both

chickpea and lentil are poor competitors with the aggressive winter weeds and, probably more importantly, both crops are susceptible to closely related species that cause ascochyta blight (Khare, 1981, Vir *et al*, 1975)

Whatever the primary reason was for the first attempts of spring sowing, and the adoption of this cropping system, we argue that its success was a major junction in the natural history of the crop This is because shifting from the natural wild plant cycle to spring sowing was accompanied with selection in the direction of increased daylength sensitivity Timing of flowering independent of the daylength usually means that the plant would enter reproduction upon accumulation of a certain biomass value (often expressed as number of internodes) typical to the genotype (Sachs, 1999) Indeed, Roberts *et al* (1985) have demonstrated this phenomenon in chickpea using daylength-sensitive types and a daylength-insensitive (ICC 5810) chickpea cultivar Interestingly, in Roberts *et al* 's (1985) experiment, in only two of the nine tested cultivars did flowering commence below the 15th internode It should be stressed that in the Middle East, spring-sown chickpea often completes its life cycle with about 15–19 internodes or less In our experience, winter- and spring-sown (in Rehovot, Israel) *C reticulatum* rarely flowers at the 15th internode and values of 19–22 are more common (S Abbo, HUJ, Rehovot, Israel, unpublished observations) Following spring sowing, a delay of flowering until a relatively large number of nodes have developed might imply that the plant would enter reproduction when soil moisture is nearly depleted and only a meager seed yield (if any) might be expected On the other hand, following spring sowing, increased daylength sensitivity might turn into a major adaptive advantage This is because it might allow the plant to enter reproduction early enough in the season regardless of its developmental stage (node number) In such a way, seed set and pod development will take place before the onset of the summer drought and the grain yield (although modest) will be secured

The long-term consequence of selection under millennia of spring sowing was a (nearly complete) fixation of the relatively high daylength sensitivity in the Mediterranean kabuli germplasm This is evident from data of cultivar screens (Roberts *et al*, 1985) and from the phenology of recently developed modern ascochyta tolerant germplasm (Singh and Reddy, 1996) In an effort to produce blight resistant cultivars for winter sowing in Mediterranean environments, an extensive crossing and selection scheme was developed in ICARDA (Singh and Reddy, 1996) In the selection procedure, the F_3 and the F_6/F_7 generations were grown in an off-season nursery in Terbol (Beka Valley, Lebanon) "under normal day-length conditions to eliminate the late maturing types" Looking at the products of this selection scheme, it appears that in most cases, following autumn sowing in Syria, mean number of days to 50% flowering never occurred before 130 days from germination (Singh and Reddy, 1996) Assuming germination on the 1st day of December this means that flowering of the ICARDA material starts from mid-April onward In another report from ICARDA (Singh *et al*, 1997), it is

mentioned that winter sowing took place between November 20th and December 5th and that the mean value of days to 50% flowering was 136 days (Singh *et al.,* 1997). Allowing 5 to 14 days for germination, this means that the crop commenced reproduction between late April and mid-May. Based on the above considerations, selection and/or seed increase in such off-season nurseries might imply that types of reduced daylength sensitivity would be relatively less productive if flowering is delayed until a critical number of nodes is accumulated. Consequently, such daylength-insensitive types might have been selected against as either less productive or relatively late to flower.

A relatively late start of the reproductive phase (April/May) in the Mediterranean might also impose selection in the direction of high temperature requirement of the reproductive process. This might have included high temperature requirement for proper pollen tube germination and growth, for the meiotic process, and for proper floral meristem development. Indeed, sensitivity of floral development to chilling was recently reported for modern Israeli material, bred and selected using relatively late sowing practice (Or *et al.,* 1999). Problems with proper pod set were also encountered in Australia, where chickpea is sown quite early in the cool season (Lawlor *et al.,* 1998). Accordingly, temperatures below 20°C were reported to have adverse effect on pollen germination and pollen tube growth (Savithri, 1980; Srinivasan *et al.,* 1999).

2. The Indian Subcontinent and the East African Gene Pool

Despite the Near-East origin of the crop, currently about 80% of its global production takes place on the Indian subcontinent. This remarkable adaptive success in an environment so very different from its native origin area must have depended upon the presence of allelic variation in major adaptation loci. As a rule, successful introduction of a new crop species into a new growing area (e.g., a Near-East species into India or Africa) is dependent on the presence of such allelic variation in the introduced plant material and adequate agrotechniques to ensure crop establishment and correct timing of flowering. In the absence of such allelic variation in the introduced plant material the newly introduced species will most likely fail to reproduce and consequently might be abandoned after a few cropping attempts.

In India, chickpea is mostly sown in October/November and in Ethiopia from August/September onward to January (van der Maesen, 1972) In both regions, the growing season is characterized with shortening photoperiod. Based on the Near-East origin of the first chickpea introductions to India and Ethiopia, one must assume that the first attempts of chickpea cropping encountered problems in terms of poor adaptation, namely incorrect timing of flowering. Furthermore, it is difficult to see how repeated sowing of nonadapted material took place until reduced daylength-insensitive types gradually occurred in the seed stocks. This is for two reasons: First, farmers are unlikely to spare seed for more than one sowing

season and, second, there is no incentive for repeated sowing of an ill-adapted crop.

We, therefore, suggest that the spread of chickpea into its Indian and East African growing areas and its most successful establishment as a staple protein crop therein must have required adequate allelic variation in flowering-time genes to be present in the founder seed stocks. The seasonal daylength variation in the low-latitude chickpea growing areas of India and Africa suggests that insensitive alleles at photoperiod response loci had a central role in the successful spread of chickpea into these regions. Such a variation might have included alleles at both major and minor photoperiod and perhaps temperature response loci as well. These off-types of reduced required daylength gave rise to the Indian and African chickpea gene pools. Recent screening results of a collection of Ethiopian land races and its performance compared to a set of Mediterranean chickpea stocks by Or *et al.* (1999) provide supportive evidence to the above considerations. Flowering time of the Ethiopian material in Rehovot (Israel, 32°N), ranged between 2 to 6 weeks earlier compared with local Mediterranean material (Or *et al.*, 1999). The inherent early flowering habit of the Ethiopian material as well as intravariation of its flowering time suggest the presence of either an allelic series at a major flowering locus and/or respective variation in minor (modifier) flowering time loci. Or *et al* (1999) attributed the inherent earliness of the Ethiopian material to the repeated selection under two contrasting seasonal daylength profiles following the sowing seasons in Ethiopia, one starting from August/September and the second (in the highlands) starting from April (van der Maesen, 1972).

III. THE FLOWERING GENES OF CHICKPEA

A. General

The literature covering the above topic in other crop plants is immense and we make no attempt to cover it in full, but rather use a number of selected references relevant to chickpea. The number of days taken from sowing to onset of flowering (flowering time) is a major component of crop adaptation, particularly in rain-fed environments (Subbarao *et al.*, 1995). The timing of flowering is dependent upon the genotype, the seasonal temperature profile, photoperiod, and vernalization responses of the plant. In indeterminate species, early flowering may enable the plants to prolong the reproductive phase, especially when the flowering duration is delimited by terminal drought that terminates seed set. Probably due to their central role in determining crop plant adaptation, the flowering genes of many crop plants and their role in environmental adaptation were studied thoroughly (e.g., reviews by Quinby, 1973; Worland, 1996). In most cases, major as well as minor gene effects involved in determining flowering time were reported. The involvement of

Table I

Ranges and Mean Number of Days to 50% Flowering for 25 Chickpea Genotypes at Three Contrasting Locations in India

Attribute	Hisar (29°N)	Gwalior (26°N)	Patancheru (18°N)
Range	80–102	71–78	40–61
Mean	95.6	75 5	51.3
SE±	6 4	3.9	1 3

several genetic systems responding to daylength and/or temperature, their possible interaction, and the genotype × environment interaction cause in many hybrid progeny analyses a typical continuous frequency distribution of flowering time. Therefore, the isolation of any major flowering gene effect is best done using defined genetic stocks (e.g., Weller *et al*. 1997), which is not always possible in conventional breeding material.

In chickpea, however, information on the genetic control of flowering time is only beginning to accumulate. This is despite the fact that early flowering mediated by photoperiod insensitivity was suggested as a means to increase chickpea adaptability nearly 3 decades ago (Sandhu and Hodges, 1971). Regrettably, no genetic studies followed until recent years (Kumar and van Rheenen, 2000; Or *et al.*, 1999).

The flowering time of chickpea genotypes varies with latitude and temperature variations ICRISAT conducted trials of breeding lines at three locations: Patancheru (18°N), Gwalior (26°N), and Hisar (29°N). The ranges for 25 genotypes tested in these locations did not overlap (Table I). The mean number of days to 50% flowering were 51, 76, and 96 for the three locations, respectively. Thus the genes controlling flowering time are sensitive to temperature and day length.

The existence of wide genetic variation for flowering time was documented by Pundir *et al* (1988), who evaluated the world chickpea germplasm maintained at ICRISAT and listed 43 accessions that flowered in less than 39 days at Patancheru (18°N). Most of these lines originated in tropical India (Maharashtra and Karnataka), a few in Ethiopia, and 2 in Mexico and 5 have their origin in Iran (>30°N). This might indicate that mutations for early flowering genes also survived in subtropical environments. They probably out-yielded the traditional long-duration varieties under severe drought conditions. Lack of knowledge on the genetic control of flowering time did not prevent Kumar *et al.* (1985) from developing extra-early chickpea ICCV 2 as a transgressive segregant from a cross of five chickpea lines. However, further manipulation of these genes is difficult without understanding individual effects of other genes governing this trait, interaction among them, and their responses to variations in temperature and daylength.

B. Genetic Control of Flowering Time

A major recessive gene "*efl-1*," for "early flowering," was identified in a cross between the extra-early variety ICCV 2 and the medium-duration variety JG 62 (Kumar and van Rheenen, 2000) This gene is responsible for about 3 weeks' difference in flowering time between the two parents at ICRISAT, Patancheru A super early chickpea segregant, ICCV 96029, was selected from the F_6 generation from a cross of two extra-early varieties, ICCV 2 and ICCV 93929. ICCV 96029 flowers about a week earlier than either of the parents (Kumar and Rao, 1996) The allele *efl-1* is common between the two parents. Thus other complementary genes with smaller effects exist between these two extra-early parents. Complementary gene action for flowering time was also evident in crosses between chickpea genotypes ICC 4958 (India) and Guamuchil (Mexico), two of the five parents of cv ICCV 2 (Kumar *et al.*, 1985). Thus at least two different loci control flowering time in ICCV 2. This observation was further corroborated by a diallel analysis among three extra-early lines, ICCV 2. ICCV 93929, and Harigantars (ICC 5810), that produced three different types of F_1s, indicating that more than two complementing genes operate flowering time in chickpea (Jagdish Kumar, ICRISAT, Patancheru, India, unpublished results). In these studies one of the three F_1s (ICCV 2 × ICCV 93929) flowered earlier than the mid-parent, the second at the same time as the mid-parent, and the third flowered later than the mid-parent.

The super-early genotype ICCV 96029 and control Pant G 114 were evaluated for their flowering time at Patancheru and at Hisar. The number of days taken to first flowering by ICCV 96029 were 24 and 43 at Patancheru and Hisar (Table II).

Table II

Performance of Superearly Chickpea ICCV 96029 and Long-Duration Controls at ICRISAT, Patancheru and CCS Haryana Agricultural University, Hisar, 1997/1998 and 1998/1999

	Patancheru(18°N) (two environments, mean)			Hisar (29°N) (three environments, mean)	
Character	ICCV 96029	C 235	Pant G 114 (projected)	ICCV 96029	Pant G 114
Days to first flower	24	61	58	43	83
Days to first pod	29	69	65	75	107
Plant height (cm)	40	46	46	54	45
Days to maturity	79	109	119	128	155
Seed yield plant-1 (g)	14	21	—	17	16
Biomass plant-1 (g)	—[a]	—	—	43	48

[a]Data not recorded

Source Kumar *et al* (2001a)

This difference for the long-duration control Pant G 114 was 25 days at the two locations (Kumar *et al.*, 2001a). First podding for ICCV 96029 was at 75 days after sowing and for Pant G 114 it was at 107 days at Hisar. The two produced similar seed yield under experimental conditions.

It was observed that the extra-early-duration cultivar ICCV 2 grew at a rapid pace and produced the first flower at 16th node at Patancheru (K. Anupama and Jagdish Kumar, ICRISAT, Patancheru, India, unpublished data). The slow-growing medium-duration cultivar JG 62 produced its first flower at the 23rd node. Under good management JG 62 out-yields ICCV 2. However, under severe drought conditions the latter out-yields the former. As moisture is often a major limiting factor in farmers' fields, early maturity is desirable.

Or *et al.*
early line ICC 5810 and a late-flowering Israeli cultivar (Hadas) at Rehovot (32°N), Israel. The flowering gap between these two genotypes was subject to considerable year-to-year variation. Similarly, the flowering range displayed by the progeny from the segregating generations changed across seasons (Or *et al.*, 1999). The above cross was designed to analyze the flowering syndrome of the Mediterranean chickpea stocks, hence the choice of the modern relatively late-flowering cv. Hadas. The early parent ICC 5810 (originated in Maharashtra, India) was chosen based on the screening of Roberts *et al.* (1985), who characterized it as a nearly day-neutral type. The 3:1 segregation of late:early individuals among the F_2 progeny was interpreted as an evidence to a major gene action affecting flowering time through determination of photoperiod response (*PPD*). In this cross, the late condition (photoperiod responsive allele) was dominant. Plants carrying the recessive allele were more prone to environmental effects (mainly temperature), while the flowering time values of individuals with the late allele were more stable (this may be the result of favorable temperatures during the later part of crop growth).

At present, it is unclear whether the *efl-1* gene described by Kumar and van Rheenen (2000) and the *PPD* gene reported by Or *et al.*
other. However, there are indications that the major recessive allele for earliness in ICC 5810 is located at the same locus as the *efl-1* gene in ICCV 2 (Jagdish Kumar, ICRISAT, Patancheru, India, unpublished data). Several major gene loci were reported to affect flowering time in sorghum and differences within the well-defined maturity groups were attributed to specific gene combinations rather than to allelic series operating in the *Ma* loci of sorghum (Quinby, 1973). In contrast, both in pea and *Arabidopsis,* allelic series were reported for some of the flowering loci (Weller *et al.*, 1997; Koornneef *et al.*, 1998). Test crosses are required to assess the situation in chickpea. While it is clear that at least three loci affect flowering time, at present there is no evidence for the existence of allelic series for these. Furthermore, in the absence of DNA markers linked to the chickpea flowering genes we are also unable to relate either gene to its homologous counterparts among the well-defined pea flowering genes (Weller *et al*, 1997). Despite clear evidence to

a certain degree of linkage group similarity between pea and chickpea (Kazan *et al*, 1993), the chickpea basic chromosome number of 8 [different from the basic number (7) of pea] makes such comparisons quite difficult without cloned-gene sequences from both species Major as well as minor gene actions affecting flowering time were recently reported in lentil (Sarker *et al*, 1999) These authors have suggested that the lentil gene is equivalent to the *SN* gene of pea (therein), but provided no experimental evidence or theoretical consideration to favor this suggestion over the alternative options that the identified gene was, perhaps, an equivalent of the pea *PPD* or the *DNE* loci

The flowering genes influence maturity type and crop yield through their effects on the onset of reproduction, duration of reproductive phase, number of branches, and number of flowers per node (Murfet and Reid, 1985) In pea it is known that photoperiod-sensitive types have a marked tendency to produce basal branches Thus knowledge of gene action and epistatic effects and genotype × environment (g × e) interaction enable selection of genotypes suited to particular regions In pea it is known that photoperiod-sensitive types have a marked tendency to produce basal branches

C. Association of Flowering Genes with Agronomic Traits

Abbo and co-workers have used the cross Hadas × ICC 5810 (and the reciprocal) to detect possible associations between the major flowering gene *PPD* and a number of agronomic traits The two parents involved in the crosses differ in many traits, with cv Hadas presenting partial resistance to ascochyta blight and large grain weight (450 mg) and ICC 5810 extremely susceptible to ascochyta and having a small grain size (150 mg) Both parents also differ in their developmental response to temperature in terms of internode length, branching and growth habit, and floral development (Or *et al*, 1999, S Abbo, HUJ, Rehovot, Israel, unpublished data) As a result, in comparisons conducted under Israeli environments, ICC 5810 exhibits its early flowering habit in an ill-adapted agronomic background

The phenotypic correlation estimate between flowering time and mean grain weight calculated from the F_2 data of the Hadas × ICC 5810 was 0 29 ($P<0$ 0001) Based on the data from the reciprocal population the respective r value was lower and not significantly different from zero Phenotypic correlation estimates from the F_3 progeny were 0 26 and 0 23 for the Hadas × ICC 5810 and the ICC 5810 × Hadas, respectively The differences between the reciprocal populations and the year-to-year variation were attributed to g × e interaction affecting the time to flowering trait (Or *et al*, 1999) Genotypic correlations between time to flowering and mean grain weight based on the variances and covariances between

and within F_3 families were 0 64 and 0 51 for the Hadas × ICC 5810 and the reciprocal cross, respectively (both with $P<0$ 0001) These data imply that flowering time loci as well as grain weight loci are scattered throughout the chickpea genome, and in some cases these loci are linked, as expressed by the r values calculated between the two traits (Hovav, 1999)

The large kabuli-seed phenotype also occurs in an extra-early flowering background, e g , ICC 7344 and ICCV 92311 (Pundir *et al* , 1988, J Kumar, ICRISAT, Patancheru, India, unpublished data) This fact is in accord with the assumption that the *PPD* locus is linked to grain weight gene(s) rather than affects the grain weight trait directly (pleiotropy) Under such a situation the daylength response locus as well as the grain weight loci may harbor either allelic variant at any of the loci affecting each trait, thereby allowing desired combinations to suit grower as well as consumer preferences

The days to first flower and data obtained from the F_3 families of the Hadas × ICC 5810 (and reciprocal cross) were correlated with the response to the pathogen of ascochyta blight (*Didymella rabiei*) in an infested field nursery of F_3's single-seed descendants (F_4 generation of the above crosses) The genetic correlation between resistance to *D rabiei* and days to first flower was significantly negative [$r > -0$ 4, $P(F)< 0$ 05] In the studied cross combinations, the tolerant parent was the late-flowering one The negative correlation means that some of the flowering loci are linked to quantitative loci governing resistance to ascochyta blight

Or *et al* (1999) suggested that in a Mediterranean environment, early flowering might allow a longer reproductive period expressed as a relatively large number of pods along the main branches of the plant Due to its indeterminate growth habit, such a trait might be an important yield component for chickpea Their comparisons showed that in certain genetic backgrounds early flowering types do set more pods along their main branches compared to late-flowering ones When measured under field conditions among the progeny of the Hadas × ICC 5810 crosses this trait was subject to large environmental influence The strong environmental effect on this trait was expressed in the absence of any correlation between time to flowering and number of pods along the main branches (Hovav, 1999)

Although flowering is a prerequisite for pod set, the latter phenotype is also dependent on the sensitivity of the reproductive process to temperatures (Savithri *et al* , 1980) and on the pod-set rate during the season The pod set feature might be related to the seed weight, with relatively large seed dictating a slower pod set compared with types possessing small seed This is because large seeds might pose a heavier sink load compared with smaller seeds Such a relationship was reported for lentil and served to suggest smaller seeded microsperma types as better adapted to drought-prone environments (Erskine, 1996) Our observations with late flowering kabuli types support such a relationship, e g , despite being later to flower, cv Bulgarit consistently produces more pods along its main branches compared with cv Hadas (Or *et al* , 1999, S Abbo, HUJ, Rehovot, Israel, unpublished data)

Possible effects on field productivity of the *PPD* allele were tested using bulks of F_4 seed material from the Hadas × ICC 5810 (and reciprocal) (Shai, 2000). The flowering, grain weight and color, and ascochyta response data of the field-tested F_3 families produced three comparisons between relatively early and relatively late F_3 families from the above crosses. The first comparison included large-seeded lines (ca. 250 mg and above) (late vs early to flower), regardless of seed color or ascochyta blight response. The second comparison included only beige-seeded lines (late vs early to flower) regardless of other traits, and the third comparison was made in a relatively ascochyta blight-resistanct background (late vs early to flower) regardless of seed size or color. Total biomass production and grain yields were compared following autumn sowing under current agronomic practice in Israel. In this way, a comparison of the possible *PPD* effect was held under three independent genetic backgrounds. In all three tested backgrounds, both the grain yields and total biomass production of the relatively late-flowering bulks were superior compared with those obtained from the early-flowering bulks. The superiority of the agronomic alleles donated by the late-flowering modern cultivar Hadas over those of the early-flowering parent in the tested environment is evident from their own performance (S. Abbo, HUJ, Rehovot, Israel, unpublished). The results of the above comparisons are nonetheless important. First, such *PPD* chickpea material was never tested in agronomic stand under Mediterranean conditions. Second, the field results support the genetic analyses performed on individual plant basis. Third, despite the clear evidence for the *PPD* gene action, flowering time is heavily affected by polygenes, similar to grain yield. Under such circumstances, it becomes clear that numerous combinations between promoting and demoting alleles at any linked flowering and yield loci (major and/or minor) may exist. Therefore, bearing in mind the poor adaptation of the ICC 5810 parent to the Israeli conditions such results of bulk comparisons are not surprising. The presumed loose associations between the flowering loci (*PPD* included) and agronomic performance affecting loci suggest that selection to produce desired combinations in any direction should be possible. These conclusions support the hypothesis proposed by Wallace and Yan (1998) that the majority of the genes of the plant control the flowering time.

D. Photothermal Modeling of Flowering Time

Ever since the early 1980s (Roberts *et al.*, 1980, 1985) attempts have been made to characterize chickpea varietal responses to environmental factors as expressed in the time to first flower or as the developmental rate to flowering. This approach resulted in the conclusion that in chickpea daylength and temperature have an additive effect on the time to first flower, assuming no interaction between these two environmental factors (Ellis *et al.*, 1994). Although the above model is well

supported by experimental evidence for a number of crop species, an alternative model was proposed, in which the photoperiod × temperature interaction is an integral part of the model (Yan and Wallace, 1996).

Such experimental approaches are most useful to predict the flowering time of the tested genotypes in a range of environments and to classify them according to the relative importance of the factors affecting their flowering time, i.e., temperature, photoperiod, or both. However, these models fail to fully describe the underlying genetic mechanisms governing the action of the loci responding to the environmental cues. Ideally, such experimental approaches should be applied to segregating progeny of the kind analyzed by Kumar and van Rheenen (2000) or Or *et al.* (1999). Indeed, Alcalde *et al.* (1999) have recently quantified the effects of the *Lf, Sn, E,* and *Hr* genes on time to flowering in pea. This was done using a set of standard pea lines homozygous for different allelic situations in the respective flowering genes. In a similar manner, comparisons of late vs early flowering progeny from the crosses studied by Kumar and van Rheenen (2000) and Or *et al.* (1999) could assess the effect of the *efl-1* and the *PPD* genes of chickpea. Such an analysis might assist in determining the relative importance of the temperature response in the different genetic backgrounds and help to allocate genes for earliness *per se* operating in either daylength-sensitive or daylength-neutral backgrounds of chickpea. We anticipate that such a combined approach may result in better understanding of major adaptive loci later to contribute to improved chickpea crop productivity.

E. Earliness-Mediated Drought-Escape as a Means to Increased Productivity

Drought is the major constraint to increased productivity, as nearly 90% of the world's chickpea is grown rainfed (Kumar *et al.,* 1996). It is estimated that if moisture stress is alleviated, up to a 50% increase in chickpea production could be achieved, with a present value of ca. U.S.$ 900 million (Ryan, 1997). One way to escape end-of-season drought is to develop varieties with early growth vigor, early flowering, and early maturity (Calcagno and Gallo, 1993; Johansen *et al.,* 1997).

In drought-prone environments such as those in the tropics normally a strong positive association exists between water transpired by the crop and biomass formation (Sinclair *et al.,* 1984). Therefore, rapid early growth of the crop is desirable. This will also ensure early attainment of full crop canopy and prevent soil-surface evaporation. Johansen *et al.* (1997) measured the relationship between early growth vigor and shoot mass and seed yield at harvest in 123 chickpea genotypes grown on a vertisol at ICRISAT, Patancheru (Fig. 1). There was a linear positive relationship between early crop growth and seed yield. They suggested that the most feasible way to increase productivity is to shorten the crop duration.

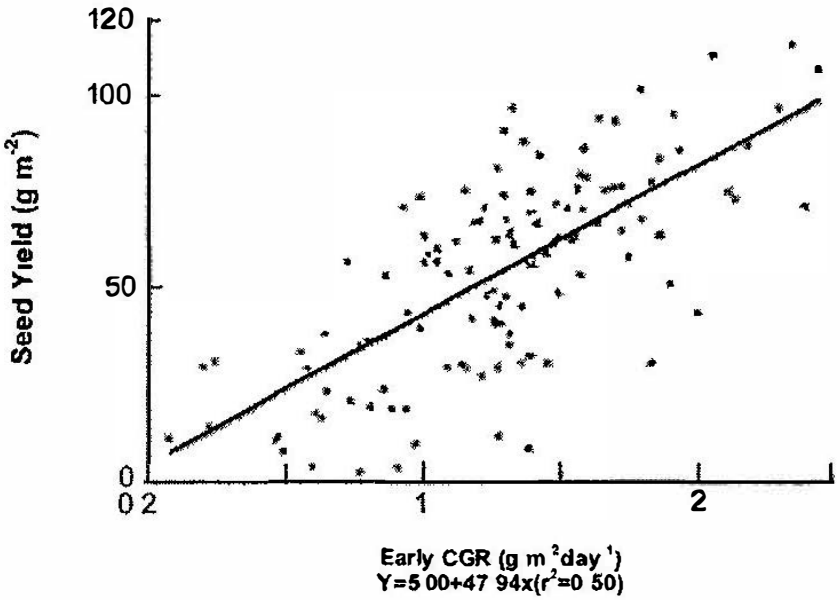

Figure 1 Relationship between early crop growth rate (CGR) and seed yield at harvest in 123 chickpea genotypes grown on a vertisol ICRISAT Center postrainy season 1988–1989 (from Johansen *et al* 1997)

Often end-of-season drought is associated with increasing temperature (Calcagno and Gallo, 1993, Singh, 1997) Sedgley *et al* (1990) suggested that early pod set should be a prime strategy for avoiding drought stress in environments prone to end-of-season moisture stress Thus development of early maturing varieties may help drought-escape and result in increased productivity and extending this crop to even more drought-prone areas (Kumar *et al*, 1996)

Earliness is considered important in cowpea, pea, and other grain legume crops (Hall and Patel, 1985, Sharma and Khan, 1997) Genes allowing a reduced crop cycle will provide pathways for new cropping systems (Ortiz *et al*, 1999) Early maturing varieties will also allow increased population per unit area and consequently help maximize yield in drought-prone environments

Penalties associated with earliness include short time available to accumulate biomass and development of a shallower root system The first can limit the grain yield potential and the latter will render plants vulnerable to adverse effects of intermittent drought (Johansen *et al*, 1997) However, relatively higher temperatures faced by the late maturing crop will also reduce seed yield Summerfield *et al* (1981) observed that the reproductive growth of chickpea suffered considerably in hot environments (35/18°C, day/night) This was reflected in yield reduction of almost 33% when compared with that in a milder controlled environment (30/10°C, day/night) Thus in farmers' situations a compromise is necessary between the reduced yield potential of short-duration cultivars and the losses caused by end-of-season drought

In order to test the above rationale, a series of experiments with standard late-flowering Israeli cultivars (cvs Hadas and Bulgarit), early-flowering material

(Ethiopian land races and ICC 11299), and very early flowering materials from ICRISAT (ICC 7344 and ICCV 95333) were conducted between 1995 and 1999 in several Israeli sites (Bonfil *et al*, in preparation) As expected, in a semiarid site, the early-flowering types produced ca 1 3 t ha^{-1} less biomass yield compared with the late-flowering high-yielding Israeli cultivars However, the grain yields of the early-flowering types (e g , ICC 8625) were equivalent to those of the modern Israeli varieties (3 3 t ha^{-1}) In other words, the early-flowering types were more efficient in terms of their harvest indices In the same site, in two successive seasons, the yields of the very early line ICC 7344 were inferior in biomass production and in its grain yields In a dry site (with average precipitation of 240 mm), yields in the range of 1 4 to 1 9 t h^{-1} were achieved with ICC 7344, ICC 11299, and ICCV 95333, with the Israeli cultivar Bulgarit yielding 0 7 t ha^{-1} These results demonstrate clearly the potential of restricting vegetative growth, and early flowering in semiarid environments, and the potential of very early onset of podding under extreme water shortage of less than 250 mm (Bonfil *et al*, in preparation)

Early flowering and podding restrict vegetative growth in indeterminate plants like chickpea (Saxena *et al*, 1997) In subtropical environments winter rains may induce excessive vegetative growth leading to dense canopy and high humidity Such conditions are conducive for the development of foliar diseases Thus restricted vegetative growth can help avoid seed yield losses in these environments Therefore development of early flowering and podding cultivars should be a major objective for chickpea improvement In our view this could be a major step toward stabilizing and increasing mean seed yields in subtropic environments (see Section III,B)

IV. CONSTRAINTS ON PRODUCTIVITY IN SEMIARID ENVIRONMENTS

Chickpea is predominantly grown under rainfed conditions in a postrainy season, on marginal lands, often without monetary inputs The crop is, therefore, vulnerable to various abiotic and biotic constraints occurring under these situations Drought at various stages of the crop cycle is a major yield reducer Plant stands may be spaise because of poor emergence (Saxena *et al*, 1997) Although the chickpea plant can produce extra vegetative growth (in a favorable moisture regime) to cover available space, poor plant stands and stunted growth are often a major cause of low seed yields in semiarid environments Adverse soil conditions such as salinity and toxicity may also cause poor plant stands and stunted growth The crop-growing season is often restricted by receding soil moisture Winter rains in the Indian subcontinent may help alleviate drought stress and increase productivity However, occasionally excess moisture is conducive to the spread of foliar diseases leading to seed yield losses in the subtropics Fusarium wilt, ascochyta blight, root

rots, botrytis gray mold, chickpea stunt, helicoverpa pod borer, and leaf miner are important diseases and pests that limit the crop productivity

All these constraints may not occur together in a particular region or year Drought, suboptimal plant stands, stunted growth, and root diseases are relatively more important in short-season tropical environments In subtropical environments early drought often may affects plant stands and late drought may affect seed filling Alternatively, excess winter rains can encourage overgrowth and foliar diseases In the following sections we analyze constraints to productivity in the major chickpea production systems

A. Traditional Systems

1. The Mediterranean Basin

In the traditional cropping systems of the Mediterranean basm chickpea is a summer crop sown in March/April and harvested by pulling in June (Elazari-Volcani, 1930) The crop is sown as soon as the temperatures are favorable for emergence The growing season is short, often 80–90 days, limited by increasing temperatures and drought Ground cover is never complete and leaf area index is low The erratic nature of the winter precipitation in the Middle East and the frequent hot spells typical of the Mediterranean spring usually result in relatively low and unstable yields ranging between 100 and 600 kg ha^{-1} (Elazari-Volcani, 1930, Kostrinski, 1974) Potential seed yield does not exceed 1 5 t ha^{-1} Besides limited water, low nutrients, salinity, high temperatures, root diseases, chickpea stunt, leaf miner, and weeds may cause seed yield losses

In past years, spring cropping was the only effective means to avoid ascochyta blight epidemics The spring crop is also nearly weed free, since presowing cultivation destroys most of the winter weeds The extremely short season (at best, late March to June) allowed a relatively short period of vegetative and reproductive growth, which in turn, relies completely on residual soil moisture Under such practice, flowering and podding occurs pretty close to the ground thereby preventing mechanical harvesting

2. The Indian Subcontinent and the East African Region

Chickpea is grown on conserved soil moisture as a sole or a mixed crop following rainy season fallow or after a short rainy-season crop Thus it often is subject to end-of-season drought which coincides with flowering and podding The effects of such drought are progressively enhanced by increasing temperatures, particularly in lower latitudes (<25°N) (Johansen *et al*, 1997) Although there may be overlaps, for discussion we broadly classify chickpea-growing environments on the Indian subcontinent into two categories as follows

In the subtropical Indian subcontinent, which used to be the principal chickpea-producing region, the crop is sown from October to November and can produce high seed yield in a growing season of 160 to 170 days (Smithson *et al.,* 1985). Where chickpea follows a rainy-season crop, its planting is determined by the harvest of the preceding crop and the turnaround period. Sorghum and maize or short-season legumes may mature in time to allow early planting of chickpea (Rahman *et al.,* 1995). However, crops like rice take a much longer time to mature, rendering large tracts of land to remain fallow in the postrainy season. Chickpea planting is often delayed in this situation. As the soil-moisture profile may not be full such planting results in poor emergence. Late planting also reduces the length of the growing season as rising temperatures enhance maturity. Farmers may intercrop chickpea with other postrainy-season crops such as wheat, barley, mustard, linseed, or even sugarcane. Diseases such as ascochyta blight, botrytis gray mold, chickpea stunt, and fusarium wilt and the pod borer are important biotic constraints. Drought and freezing temperatures can also limit seed yields substantially (Kumar *et al.,* 1996).

On the tropical Indian subcontinent the growing season is limited to between less than 90 days and 130 days by increasing temperatures and reduced soil moisture (Saxena *et al.,* 1993). Potential seed yield may range from about 1.5 to 2.0 t ha^{-1}(Saxena *et al.,* 1997). In these situations early planting when the soil moisture profile is fully charged is advantageous. However, the prevailing high temperatures early in the season could adversely affect the final seed yield. As chickpea tolerates partial shading, intercropping may be the best solution to guard against drought effects and take advantage of winter rains. Major constraints are drought, salinity and poor nutrition, fusarium wilt and root rots, chickpea stunt, and helicoverpa pod borer. Early maturity may help alleviate the major constraints to productivity.

In eastern Africa, chickpea is cultivated in Ethiopia, Tanzania, Malawi, Zambia, Uganda, and Kenya. It is grown between 1400 and 2300 m in the northern and central highlands of Ethiopia, but southward was introduced only recently (Smithson *et al.,* 1985). Sowing may be undertaken at the end of the rainy season, from August to September in Ethiopia and southward from February to April. In bimodal rainfall areas (e.g., Kenya) chickpea is cultivated at the ends of both rainy seasons Potential seed yields of 1 to 2 t ha^{-1} are possible. Major constraints include drought, pod borer, fusarium wilt, viruses, and poor management. Thus constraints to chickpea productivity on the tropical Indian subcontinent and the low-altitude East African region are generally similar.

B. Modern Systems

1. The Mediterranean Basin

Chickpea may be grown under nearly nonlimiting conditions of moisture supply and soil fertility through the application of inputs or natural endowment of

environment (Saxena *et al*, 1997) This can be achieved by advancing the sowing date from spring to winter, thereby providing a favorable moisture regime through the growing season In these environments the growing season can be as long as 6 months and the seed yields may range between 3 and 5 t ha^{-1} as a result of high biomass production of up to 10 t ha^{-1} The crop season can also be extended through irrigation to the spring-planted crop The seed yields can be increased by 25 to 30% of the traditional spring-season crop Nutrient supply and crop protection measures are undertaken to prevent yield losses The winter-sown crop is vulnerable to damage by ascochyta blight, high weed and orobanche parasite growth, and leaf miner and sometimes by freezing temperatures Other biotic constraints may not be of major concern Therefore, resistance to ascochyta blight and cold is necessary to achieve stable crop production (van Rheenen, 1991)

The first successful experiments with winter sowing of chickpea were conducted in Israel in 1959 when yields of about 3 t ha^{-1} were obtained with cv Bulgarit, a cultivar with high field resistance to ascochyta blight (Kostrinski, 1974) These experiments were initiated following repeated observations that chickpea volunteer plants (from a previous crop) develop well following the autumn showers, survive the chilling temperatures of the Israeli winter, commence flowering in late March or early April, and mature in June Kostrinski (1974) assumed that autumn (or winter) sowing would allow a higher plant stand in the field, more efficient utilization of the winter rains, higher biomass production per area unit, and consequently support higher seed yield Indeed, this was the case (Kostrinski, 1974) The adoption of Kostrinski's (1974) and Hawtin's (1975) ideas and the large-scale experimentation with winter sowing of chickpea across ICARDA's mandate area have promoted winter sowing of chickpea in many Mediterranean countries (Singh *et al*, 1997) An immediate consequence was the development of large-scale research programs in the two international centers ICRISAT and ICARDA, focusing on ascochyta blight epidemiology, chemical control, and breeding for resistance (Saxena and Singh, 1984, Singh and Reddy, 1996)

Eshel (1967) and Keatinge and Cooper (1983) were the first to provide a detailed crop development analysis of winter-sown chickpea Keatinge and Cooper (1983) have demonstrated that winter-sown chickpea (in northern Syria) develops higher green area indices and consequently build-up higher biomass yield per area unit compared with spring-sown crop This is mainly due to reduced evaporation from the bare soil before full canopy closure occurs and the better water extraction capacity of the root system of the winter sown chickpea The increased productivity of the winter crop is also evident in impressive seed yield figures from a range of semiarid environments in Australia (Loss *et al*, 1998)

Despite yield increases following winter sowing, reported from many Mediterranean countries, a number of workers have noticed that still higher yields could be expected should the reproductive phase of the crop be extended Eshel (1967) has demonstrated a strong positive correlation between the duration of the growth period and chickpea seed yield Looking at Eshel's (1967) flowering data

it appears that higher yields were indeed obtained when flowering duration was longer A yield increase of about 56% was obtained with supplementary irrigation, which extended the reproductive phase by nearly 10 days (Saxena *et al*, 1990) Bonfil and Pinthus (1995) have conducted a detailed crop growth comparison of chickpea and wheat under a typical semiarid Mediterranean environment In their experiments, both crops were sown so that flowering would start at the same time Comparing canopy development, dry-matter accumulation of both crops, prior and after the initiation of flowering, and seed yields the authors showed that the inherent need to support both reproductive and vegetative growth in chickpea is a major constraint on seed yield build-up (Bonfil and Pinthus, 1995) Or in other words, due to the indeterminate growth habit of chickpea, the duration of the reproductive phase is a major yield determinant

In most Mediterianean chickpea-growing areas, the duration of the reproductive phase of the crop is delimited between the initiation of flowering and the summer drought that terminates seed set Therefore, the prospects for extending the reproductive period into the summer season are quite limited and depend mainly on water availability for supplementary irrigation to allow further growth (Auld *et al*, 1988, Saxena *et al*, 1990) Mild seasonal tempeiature profile is also required to allow proper seed set and further pod development Since the end of the growing season is almost fixed under dryland conditions in the Mediterranean environments, an alternative option for extending the reproductive phase of chickpea could be through early flowering (Or *et al*, 1999)

2. The Indian Subcontinent and the East African Region

a The Indian Subcontinent

The world chickpea outlook is greatly influenced by that of the Indian subcontinent Among legumes the potential chickpea seed yields are large More than 5 t ha^{-1} seed yields have been harvested from large plots in the subtropical and up to 3 t ha^{-1} in irrigated plots in tropical regions (Smithson *et al*, 1985) Howevei, the mean seed yields of around 0 8 t ha^{-1} show that most farmers do not obtain such high productivity because of the constraints mentioned earlier (see Section IV,A,2) The cereals' "green revolution" relegated chickpea to less endowed lands (Kelley and Parthasarthy, 1994) As the increase in the genetic potential and stability of productivity has not kept pace with the major competing crops (wheat, mustard, and sunflowei), farmers do not prefei to grow chickpea in their more productive lands Chickpea has lost more than 1 million ha in the high input subtropical environments Indian subcontinent's share of 87% of the world's production (1971–1973) is fast declining (78% in 1989–1991) This downward trend is likely to continue unless a major breakthrough in its mean productivity is achieved to enhance its competitiveness through yield and price increases (Kelley and Parthasarthy, 1994) Such stability can be possible for a determinate crop with

resistances to major stresses Early maturity can help escape major end-of-season constraints

Chickpea, being an indeterminate crop, puts up excessive vegetative growth under high input conditions in the subtropics Such a canopy is prone to damage by foliar diseases, pod borer, lodging, and even rotting Usually overgrown crop does not produce stable high seed yields Therefore, farmers are reluctant to commit their best land and resources to an unstable crop They are, however, willing to cultivate chickpea with assured 2 t ha^{-1} seed yield, the value of which at the current prices is equivalent to about 5 t wheat Attaining this seed yield is possible with the available cultivars What is lacking is the stability of production

Ryan (1997) analyzed estimated damages caused by major constiaints to chickpea productivity and observed that the cumulative losses attributed to these may actually be more than the current production Kumar *et al* (1996) further analyzed the timing of occurrence of these stresses and observed that much of the adverse effects of these constraints were limited to the flowering and podding stages of the crop In subtropical environments this coincides with rising temperatures They concluded that if the crop duration is genetically reduced by about a month, the mean seed yield in these environments could be doubled using an escape mechanism

It is necessary to restrict chickpea vegetative growth at a reasonable canopy level and induce fruiting A determinate chickpea plant is still elusive (van Rheenen *et al*, 1994) The currently grown cultivars in the subtiopical areas continue to develop vegetatively during the cool winter months and pod only when the temperatures start rising The earliness gene *efl-1* becomes ineffective in freezing temperatures Although chickpea flowers in cool temperatures, it does not pod at <8°C Srinivasan *et al* (1998) observed in controlled environments that pod set in chickpea could occur at night temperatures of 0° to +5°C as long as the day temperatures were above 20°C Such genotypes may produce sufficient pods during the cool months and thus grow less prolifically under good growing conditions Early growth vigor, early flowering, and podding through cool temperatures may help the crop mature before severe onset of drought, foliar diseases, and pod borer attacks (van Rheenen *et al*, 1997) A few such genotypes have already been developed, and these could avoid damage by most of the abiotic and biotic stresses, as they mature in relatively cooler temperatures (Kumai *et al*, 1996) A newly developed genotype ICCV 96029 combines *efl-1* and other genes for earliness, early growth vigor, and chilling tolerance In experiments conducted at Hisar (29°N) over 2 yeais this genotype matured about 4 weeks earlier than the local control Pant G 114 (Kumar *et al*, 2001a) (Table II) It produced similar seed yield as the longer duration control Pant G 114 Its agronomic potential is being evaluated further in a few locations

In recent years in this subcontinent chickpea cultivation has moved toward the tropics Its area increased by nearly 750,000 ha in the tropical region (Kelley and Parthasarthy, 1994) This has partly offset the area loss in the subtropical region mentioned above Development of short and extra short duration chickpea

varieties combined with fusarium wilt resistance has dramatically increased their competitiveness (Kumar, 1997). Traditional chickpea varieties took 90–130 days to mature in the tropics and succumbed to fusarium wilt. Hall and Patel (1985) also found that short-duration varieties produced high seed yield in cowpea. ICRISAT in collaboration with the Indian National Agricultural Research System (NARS) released ICCV 2 and ICCC 37 in the state of Andhra Pradesh in 1989 and ICCV 10 in Central Zone in 1992. ICCV 2 was released in Maharashtra in 1992. Chickpea production in Andhra Pradesh registered a sevenfold increase in the past 10 years (Kumar, 1997). The productivity of the <90-day crop increased from less than 0.3 t ha^{-1} to nearly 0.8 t ha^{-1}. This is now equivalent to the Indian national mean, which is based mostly on a 130- to 170-day crop. Chickpea seed yield in Maharashtra also showed significant increases. However, Karnataka, where the new variety adoption is low, has not shown much improvement, as the improved-variety seed has not been multiplied on a large scale (J. Kumar, ICRISAT, Patancheru, India, unpublished data).

One way to increase chickpea competitiveness is to ensure high returns to the farmers. Kabuli chickpea, which covers 10 to 15% of the total chickpea area in the world, commands up to three times the price paid for the more common desi types (Kumar, 2000). The bulk of the international trade involves mainly kabuli types, with the exception of the Australian desi export. The available kabuli cultivars are long duration and require the cooler environments of the subtropics for their cultivation. Development of the extra short duration, fusarium wilt-resistant cultivar ICCV 2 has extended kabuli cultivation to tropical regions (Kumar *et al.*, 2001b). ICCV 2 has been named as a national kabuli check cultivar by the Indian NARS. Based on the present requirement of breeder seed it is the most popular kabuli cultivar in India (Fig. 2). The variety has now been released in Myanmar and Sudan. It has also shown promise in Ethiopia, Tanzania, and Egypt (Kumar *et al.*, 2001b). Its sister line, ICCV 3 has been released in Myanmar and is under consideration for release in Brazil.

A major prospect for chickpea area expansion is under fallow replacement in rice-based cropping systems (Kumar *et al.*, 1994). Of the estimated 20 m ha rice fallows, 4 m ha is suitable for chickpea cultivation in the Indian subcontinent. Farmers have little choice of crops capable of producing enough seed yield under receding moisture in the difficult-to-manage paddy soils. The present relatively longer duration varieties do not fit in the available window as rice may be harvested too late, leaving little available moisture in the top layers. However, recent successes in the Barind region in northwestern Bangladesh indicate that rice farmers are willing to compromise on rice yield to accommodate chickpea in their cropping systems (Rahman *et al.*, 1995; Musa *et al.*, 1999). If chickpea seed can be planted soon after the harvest of rice when the topsoil still has sufficient moisture, it can emerge and produce reasonable seed yields of probably higher value than the main season rice crop (Mazid *et al.*, 1998). Here again, short-duration varieties

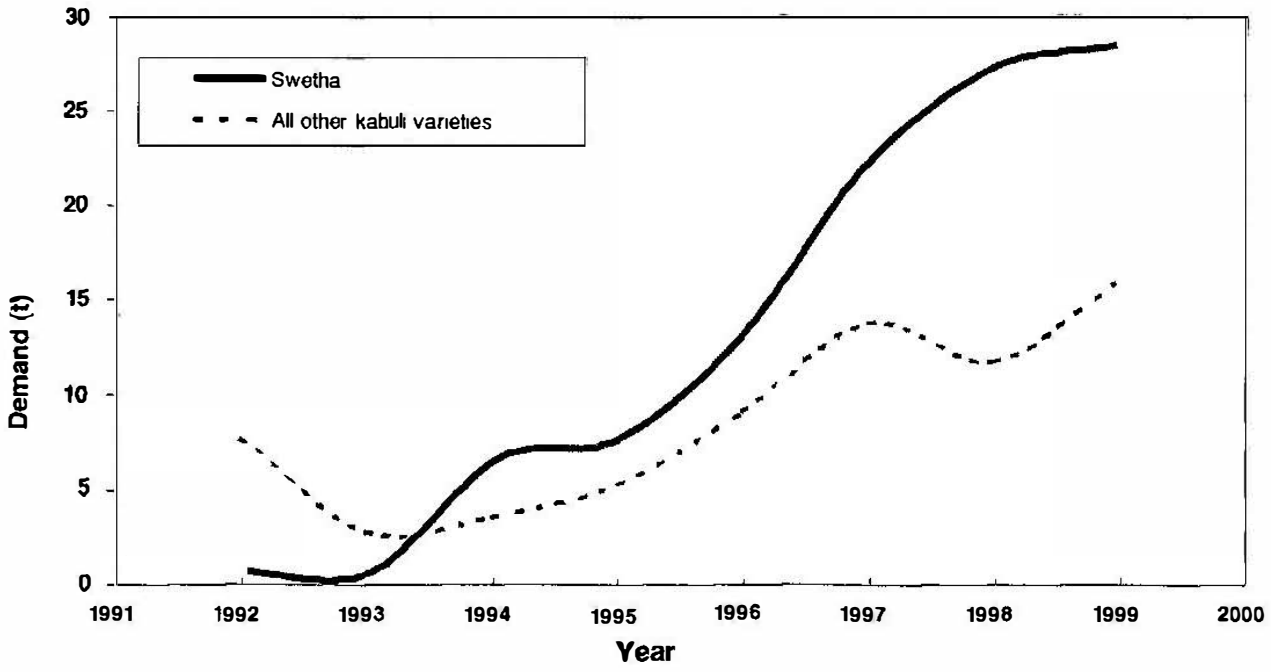

Figure 2 Breeder seed demand for all of India for kabuli variety Swetha (ICCV 2) and that for all other kabuli varieties of chickpea Source Chickpea breeder seed requirements, Indian Institute of Pulses Research, Kanpur, 1998 and 1999 (limited circulation).

of both chickpea and of rice can play a pivotal role in the fallow replacement and in sustaining and increasing the productivity of one of the most fragile agricultural ecosystems of the world (Rahman *et al.*, 1995). Scientists are now breeding shorter duration cultivars of rice.

b. The East African Region

One way of increasing yield in East African highlands is to advance the sowing date so that the crop will have much better moisture regime for early growth and produce larger biomass. Seed yields of around 3 t ha^{-1} are possible in the cooler highlands. Short-duration cultivars can help extend fruiting period and increase productivity. However, chickpea is susceptible to foliar diseases, especially when rains create high humidity and wash off the plant-acid exudates. It appears that fast-growing shorter duration cultivars with resistances to fusarium wilt, root rots, and pod borer will enhance stability and productivity of chickpea in this region. Super early chickpea ICCV 96029 appears to produce relatively high seed yield under experimental conditions in Kenya (R. Jones, ICRISAT-Nairobi, Kenya, personal communication) This also indicates drought as a major constraint in that region. The super early lines may extend chickpea cultivation to even drier regions.

Extension of chickpea cultivation to wheat-based farming systems of Southern Africa may be possible, as the two crops have a similar range of adaptation. Such a development will help diversify crop choices and may thus enhance sustainability of agriculture in the region. We believe short-duration cultivars will have greater

scope for success However, experimental data on chickpea genotypes are required to understand the system

V. CONCLUSIONS AND FUTURE OUTLOOK

Understanding flowering behavior is fundamental to crop adaptation There is a large gap in our knowledge of flowering genes of chickpea Only two genes controlling flowering time have been identified so far (Kumar and van Rheenen, 2000, Or *et al*, 1999) Much genetic information is available on this aspect for the closely related genus *Pisum* (Weller *et al*, 1997) More research should be undertaken to identify new loci controlling flowering behavior in chickpea so that a wider array of adapted cultivars could be developed

Chickpea breeders, geneticists, pathologists, and physiologists are open to criticism They have tended to follow models on wheat and rice where the crop environments were modified to complement genetic improvement of these crops to achieve stable and high productivity Such favorable environments, when provided to chickpea in the subtropics, often induce excessive vegetative growth and result in decreased seed yield Therefore, the chickpea crop ideotypes need to be modified (Singh, 1997, Saxena *et al*, 1997) There is an urgent need to develop near-determinate ideotypes with early flowering and podding through the cooler season for these environments These ideotypes might produce restricted vegetative growth and mature early Such cultivars may respond to high-input conditions without producing excessive canopy Early maturity should help avoid the losses caused by late-season biotic and abiotic constraints that are often faced by this crop Thus development could help produce much higher seed yields than are presently realized and ensure that chickpea becomes competitive among predominant cropping systems of the subtropics

There is also an urgency to collect more accessions of wild *C. reticulatum* to better define its ecogeographic range and obtain greater insight into the biology and genetics of this important species This development will be essential for widening the genetic base of the cultivated chickpea

The genetics of chickpea are not well investigated Knowledge of other traits is also scanty (Kumar, 1997) Established rules for chickpea genetic studies, following the pea model (Marx, 1985, Muehlbauer and Kumar, 1999), would be very useful Chickpea breeders/geneticists will need to establish some selected standard genotypes to relate newly characterized genetic differences These genetically defined "Type lines" should form a basis for identification and naming new genes This information is essential to develop integrated genome maps

The fast-developing fields of recombinant DNA technology and bioinformatics have given a huge boost to genome research These techniques have the potential to increase the span of coverage, speed, efficiency, and precision of genetics and

breeding research to a great extent. Although the present level of genetic understanding of chickpea lags behind most economically important cereals and legumes, molecular markers can narrow these differences in a matter of years. Winter *et al.* (2000) published a most advanced 303-marker map for *Cicer* that covers a distance of 2080 cM. The synteny chickpea shares with field pea and lentil should be useful in developing the chickpea genome map more quickly (Kazan *et al.*, 1993; Simon and Muehlbauer, 1997).

Chickpea with only a few known linkages is being investigated as never before. Recently, several workers have demonstrated the power of DNA marker techniques to complement breeding efforts in chickpea. Patil *et al* (1995), Ahmad (1999), and Udupa *et al.* (1999) have studied genetic relationships in and among annual *Cicer* species. Sant *et al.* (1999) showed the potential of simple sequence repeat markers to predict heterotic performance in Indian chickpea germplasm. Staginnus *et al.* (1999) studied the molecular structure and chromosomal location of major repetitive chickpea DNA elements. Molecular markers linked to resistance genes and QTL to ascochyta blight were reported by Santra *et al.* (2000). DNA markers linked to fusarium wilt resistance genes were reported by Mayer *et al.* (1997), Tullu *et al.* (1998), and Ratnaparkhe *et al.* (1998a, 1998b). A successful attempt to develop marker tags to a flowering locus was recently made in an ICCV 2 × JG 62 RIL population (Cho *et al.*, 2001). In contrast to earlier reports on restricted resolution power of the AFLP system in chickpea, 9 polymorphic primer combinations of a total of 64 were found between the Israeli cultivar Hadas and the Indian accession ICC 5810 (I. P. Singh and K. Upadhyaya, Jawaharlal Nehru University, New Delhi, India, in preparation). Such efforts are likely to result in a better genomic understanding in terms of coding and noncoding sequences, a high-resolution genetic map, and, most important, in tags for agronomic traits.

It is necessary to reverse the trend of humans' overdependence on a narrowing range of crop species. This negative aspect of the green revolution that has relegated most of the high-protein crops like chickpea to marginal lands should be corrected. The potential seed yield of the chickpea crop is not really in question, but its mean productivity is far behind competing cereals and well-researched legumes such as pea and soybean. Therefore, it is necessary to substantially increase and stabilize its mean seed yield to ensure that it becomes a competitive crop in high-input environments. The earliness genes can play a major role in increasing and stabilizing chickpea seed yield.

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