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Allelic relationships of flowering time genes in chickpea

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Abstract Flowering time and crop duration are the most important traits for adaptation of chickpea (*Cicer arietinum* L.) to different agro-climatic conditions. Early flowering and early maturity enhance adaptation of chickpea to short season environments. This study was conducted to establish allelic relationships of the early flowering genes of ICC 16641, ICC 16644 and ICCV 96029 with three known early flowering genes, *efl-1* (ICCV 2), *ppd* or *efl-2* (ICC 5810), and *efl-3* (BGD 132). In all cases, late flowering was dominant to early-flowering. The results indicated that the *efl-1* gene identified from ICCV 2 was also present in ICCV 96029, which has ICCV 2 as one of the parents in its pedigree. ICC 16641 and ICC 16644 had a common early flowering gene which was not allelic to other reported early flowering genes. The new early flowering gene was designated *efl-4*. In most of the crosses, days to flowering was positively correlated with days to maturity, number of pods per plant, number of seeds per plant and seed yield per plant and negatively correlated or had no correlation with 100-seed weight. The double-pod trait improved grain yield per plant in the crosses where it delayed maturity. The information on allelic relationships of early flowering genes and their effects on yield and yield components will be useful in chickpea breeding for desired phenology.

Keywords Allelic relationship · Chickpea · Early flowering · Early maturity · Inheritance

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Introduction

Globally chickpea (*Cicer arietinum* L.) is the second most important food legume after dry beans. During 2013, it was grown on about 13.5 million ha and 89.2 % of the area was in Asia, 4.2 % in Oceania, 3.6 % in Africa, 2.4 % in Americas and 0.5 % in Europe (FAOSTAT 2014). Though chickpea is grown in over 50 countries, the major chickpea producing, countries contributing to about 95 % of the global production during 2013, include India (67.4 %), Australia (6.2 %), Pakistan (5.7 %), Turkey (3.9 %), Myanmar (3.7 %), Iran (2.3 %), Ethiopia (1.9 %), Canada (1.3 %), and USA (1.2 %).

Phenology (time to flowering, podding and maturity) plays critical role in adaptation of chickpea cultivars to different environments (Berger et al. 2004, 2006; Gaur et al. 2008a, 2008b). Early phenology is a key trait for adaptation of chickpea to short-season environments as it helps the crop escape terminal (end-of-season) stresses (drought, high/low temperature).

Terminal drought (the soil moisture stress that occurs at the pod filling and seed development stage of the crop with increasing severity at the end of season) is a major constraint to chickpea production in over 80 % of the global area. This is because the crop is largely grown under rainfed conditions in the post-rainy season (Gaur et al. 2008a, 2008b). Early maturity is also important in temperate environments for escaping end-of-season frost. For example, the chickpea growing season is short (110–120 days) in Canada and late maturing cultivars suffer severe losses in grain yield and quality due to frost (Warkentin et al. 2003).

Development of short-duration cultivars is an important breeding objective at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). The main chickpea breeding program of ICRISAT is located at its headquarters in Patancheru (near Hyderabad) in Telangana state of India. As Patancheru is located at 17°53′ N latitude, 78°27′ E longitude and 545 m altitude, the winter season (in which chickpea is grown) is short and temperatures are mild. The chickpea crop experiences increasingly higher temperature at the post flowering stage. Genotypic discriminations in terms of flowering and maturity are more apparent in such warmer short-season environments than in cooler long-duration environments (Saxena 1984). Thus, Patancheru is an ideal location for studying variability for phenology in chickpea.

Several early flowering accessions of desi and kabuli types have been identified from germplasm collections and most of these originated from India, Ethiopia, Mexico, Iran and Pakistan (Pundir et al. 1988; Upadhyaya et al. 2007). In addition, ICRISAT has developed two super-early lines ICCV 96029 and ICCV 96030 which flower in less than 30 days and mature in less than 85 days (Kumar and Rao 1996). These are good sources for earliness in developing short-duration cultivars that can escape terminal drought and high/low temperature stresses.

Flowering time (or days to flowering), which refers to number of days from sowing to the appearance of the first fully opened flower (Reid 1979), gives a good indication of a genotype's crop duration and can be recorded with greater precision than days to maturity. This is particularly useful when observations are to be recorded on individual plants in segregating generations. Studies conducted on genetics of flowering time in chickpea indicate that this trait is controlled by one major gene (Gumber and Sarvjeet 1996; Or et al. 1999; Kumar and van Rheenen 2000; Anbessa et al. 2006; Hegde 2010). The major gene for flowering time initially identified from the desi chickpea landrace ICC 5810 was designated as *ppd* (Or et al. 1999), while that identified from kabuli chickpea cultivar ICCV 2 was designated as *efl-1* (Kumar and van Rheenen 2000). Kumar and Abbo (2001) speculated that that the recessive early flowering gene *ppd* of ICC 5810 and *efl-1* of ICCV 2 could be alleles of the same locus. However, later Hegde (2010) showed that *ppd* (designated *efl-2* by Hegde) and *efl-1* are non-allelic and identified a new flowering gene (we designate this as *efl-3*) from BGD 132. Thus, three early flowering genes, *efl-1* (ICCV 2), *efl-2* or *ppd* (ICC 5810) and *efl-3* (BGD 132), are known in chickpea.

This study was conducted to establish the allelic relationships of the three earlier reported early flowering genes (*efl-1, efl-2* and *efl-3*) with the early flowering genes present in ICC 16641, ICC 16644 and ICCV 96029. In addition, the relationships of early phenology with grain yield and its components were also evaluated.

Materials and methods

Six early flowering genotypes, which included three landraces (ICC 5810, ICC 16641, ICC 16644), two breeding lines (ICCV 96029 and BGD 132), and one released cultivar (ICCV 2), were used as parents for the 19 crosses used in this study. Two of these genotypes were desi types (ICC 5810, ICCV 96029) and the remaining genotypes were kabuli. The origin, pedigree and key traits of these genotypes are given in Table 1.

Initially, five parental lines (ICC 5810, ICCV 2, ICCV 96029, ICC 16641 and ICC 16644) were used in this study. Crosses in all possible combinations including reciprocals (full diallel) were made between four parental lines (ICC 5810, ICCV 96029, ICC 16641 and ICC 16644). Crosses of ICCV 2 with other parental lines were made only in one direction. Segregation for flowering time was studied in the F_2. F_2 populations along with parental lines and F_1s were grown during the post-rainy season in 2007/08 (Oct to Feb) in the field at ICRISAT-Patancheru, India.

A row to row spacing of 60 cm and plant to plant spacing of 10 cm was maintained. The crop was

Table 1 Origin, pedigree and key traits of the parental genotypes used in this study

Genotype	Origin/pedigree/alternative name(s)	Key traits
ICC 5810	A landrace from Maharashtra Province of India. Also known as '*Harigantras*'	Desi type, pink flower, semi-spreading growth habit, black seed, and small seed size. Roberts et al. (1985) described it as the earliest flowering and the least photoperiod sensitive genotype
ICCV 2	A breeding line developed at ICRISAT in India from a multiple cross [F_3 (K 850 × GW 5/7) × P 458] × F_3 (L 550 × Guamuchil)-2 that included three desi (K 850, GW 5/7, P458) and two kabuli parents (L 550, Guamuchil). Released as *'Swetha'* in India, *'Wad Hamid'* in Sudan, *'Yezin 3'* in Myanmar	Kabuli type, white flower, semi-spreading growth habit, extra-early maturity white seed, and medium seed size
ICCV 96029	A breeding line developed at ICRISAT, India from a cross between two extra-early lines ICCV 2 (kabuli) and ICCV 93929 (desi)	Desi type, pink flower, double-podded, semi-erect growth habit, and brown seed. It flowered about a week earlier than both extra-early parents and thus called 'super-early' (Kumar and Rao, 1996). It was reported to be the world's earliest flowering chickpea germplasm (Kumar et al. 2001)
ICC 16641	A landrace from Punjab province of Pakistan	Kabuli type, white flower, semi-spreading growth habit, super-early, white seed, and medium seed size
ICC 16644	A landrace from Punjab province of Pakistan	Kabuli type, white flower, semi-spreading growth habit, super-early, white seed, and medium seed size
BGD 132	A breeding line developed by Indian Agricultural Research Institute (IARI), at Dharwad center (IARI 2006; Hegde 2010)	Kabuli type, white flower, semi-spreading growth habit extra-early, white seed, and medium seed size

grown on residual soil moisture without any supplementary irrigation. The crop received a total rainfall of 16 mm during the entire crop season. The minimum and maximum temperatures ranged between 8.2–19.9 and 24.9–33.4 °C, respectively. Recommended agronomic practices (Gaur et al. 2010) were followed for raising a healthy crop. No incidence of pest or disease was observed during the experiment.

Observations were recorded on individual plants. There were 10–20 plants in the parents, 5–10 plants in F_1s and 149–267 plants in F_2 populations. F_3 progenies were evaluated during the post-rainy season in 2008/09. Observations were recorded on flowering time or days to flower (DF), days to maturity (DM), number of pods per plant, number of seeds per plant, grain yield per plant and 100-seed weight on each plant. In addition, single-flower and double-flower plants were identified in the crosses where ICCV 96029 was one of the parents.

Flowering time was recorded when the first fully opened flower was observed on a plant. As no significant differences were observed for mean values of days to flowering between direct and reciprocal crosses, data from these crosses were pooled for statistical analysis and representing distribution of flowering time on graphs. Standard statistical procedures like student *t* test, Chi square and simple correlations were used to analyze the data using GENSTAT (version. 15.0).

In 2010, Hegde (2010) reported early flowering gene *efl*-3 from BGD 132. Thus, BGD 132 was included in this study later. It was crossed with three genotypes (ICCV2, ICC 5810 and ICC 16344) having different early genes to confirm the allelic relationship of *efl-3*.The F_2 populations from these crosses were grown during the 2013–2014 crop season.

Results and discussion

Allelic relationships of flowering time genes

The days to flowering of parental lines varied from 27–35 days (Table 2). As late flowering is known to be dominant over early flowering in chickpea (Gumber and Sarvjeet 1996; Or et al. 1999; Kumar and van Rheenen 2000; Anbessa et al. 2006; Hegde 2010), each of these lines is expected to have at least one

Table 2 Days to flowering and maturity of the parents, F_1 and F_2 populations of different crosses

S no	Parents	Days to flower		Days to maturity		N*
		Mean ± SE	Range	Mean ± SE	Range	
1	ICCV 96029	28.8 ± 0.28	27–30	81.6 ± 0.78	78–85	10
2	ICC 16644	27.9 ± 0.20	27–30	80.3 ± 0.53	76–83	15
3	ICC 16641	28.2 ± 0.20	27–30	84.0 ± 0.68	79–87	20
4	ICC 5810	30.1 ± 0.43	27–34	85.9 ± 1.12	80–90	17
5	ICCV 2	33.2 ± 0.45	30–35	87.0 ± 0.45	82–89	15
6	BGD 132	27.4 ± 0.53	25–30	89.3 ± 0.75	85–92	13

	Cross	F_1				N	F_2				N
		Days to flower		Days to maturity			Days to flower		Days to maturity		
		Mean ± SE	Range	Mean ± SE	Range		Mean ± SE	Range	Mean ± SE	Range	
1	ICCV 96029 × ICC 16644	52.3 ± 1.01	51–55	111.4 ± 0.57	110–114	7	50.7 ± 1.28	20–83	99.7 ± 1.42	60–130	184
2	ICC 16644 × ICCV 96029	52.6 ± 0.90	47–55	109.3 ± 1.10	105–114	8	46.9 ± 1.00	18–78	95.8 ± 1.30	52.129	169
3	ICCV 96029 × ICC 16641	56.7 ± 0.99	55–60	111.1 ± 0.40	110–112	8	49.9 ± 1.28	20–83	100.1 ± 1.45	65–127	183
4	ICC 16641 × ICCV 96029	55.8 ± 0.73	53–58	107.2 ± 2.18	97–114	10	46.8 ± 1.35	18–90	96.9 ± 1.81	50–132	149
5	ICCV 96029 × ICC 5810	47.8 ± 0.81	45–52	96.7 ± 1.29	93–103	9	40.8 ± 0.56	23–63	89.2 ± 0.65	75–110	234
6	ICC 5810 × ICCV 96029	46.8 ± 0.63	45–49	93.7 ± 1.44	91–97	8	39.9 ± 0.60	20–65	91.9 ± 0.70	56–129	231
7	ICC 16644 × ICC 16641	28.1 ± 0.46	27–31	76.5 ± 1.34	70–80	10	27.9 ± 0.27	20–41	80.2 ± 0.32	50–90	244
8	ICC 16641 × ICC 16644	29.4 ± 0.97	27–32	80.3 ± 1.10	75–86	9	28.2 ± 0.23	23–39	72.1 ± 0.82	50–102	185
9	ICC 16644 × ICC 5810	47.1 ± 0.33	46–49	100.0 ± 0.67	97–103	10	44.0 ± 0.89	23–78	94.7 ± 1.09	62–127	220
10	ICC 5810 × ICC 16644	51.2 ± 0.72	49–55	109.0 ± 1.10	102–112	10	47.4 ± 0.90	23–82	99.6 ± 0.90	66–128	217
11	ICC 16641 × ICC 5810	52.4 ± 1.92	48–63	105.6 ± 3.54	96–110	9	43.9 ± 0.80	22–76	95.4 ± 1.02	55–125	235
12	ICC 5810 × ICC 16641	55.8 ± 0.75	52–59	109.3 ± 1.10	105–114	10	43.8 ± 0.90	21–73	100.0 ± 1.1	70–130	201
13	ICCV 2 × ICCV 96029	32.9 ± 0.93	29–35	84.2 ± 1.30	78–90	9	36.5 ± 0.40	23–49	86.0 ± 0.60	70–110	149
14	ICCV 2 × ICC 16644	58.7 ± 1.91	55–62	113.7 ± 0.87	112–115	5	50.8 ± 1.39	21–89	101.9 ± 1.28	70–129	165
15	ICCV 2 × ICC 16641	53.5 ± 0.87	52–59	110.6 ± 1.51	102–114	8	48.9 ± 1.00	24–90	100.7 ± 0.10	70–130	267
16	ICCV 2 × ICC 5810	43.3 ± 0.86	40–47	95.6 ± 1.09	92–103	9	41.9 ± 0.54	26–76	91.8 ± 0.91	72–129	196
17	BGD 132 × ICCV 96029	43.5 ± 0.84	42–45	102.1 ± 1.41	100–104	5	40.9 ± 1.04	20–68	97.1 ± 0.89	60–120	152
18	BGD 132 × ICC 5810	46.2 ± 1.02	45–47	106.6 ± 1.35	102–108	4	37.9 ± 1.06	18–66	97.5 ± 0.60	68–112	150
19	BGD 132 × ICC 16641	48.3 ± 0.71	47–50	115.7 ± 1.66	113–117	5	38.4 ± 0.91	20–66	117.4 ± 0.20	110–127	172

* *N* number of plants

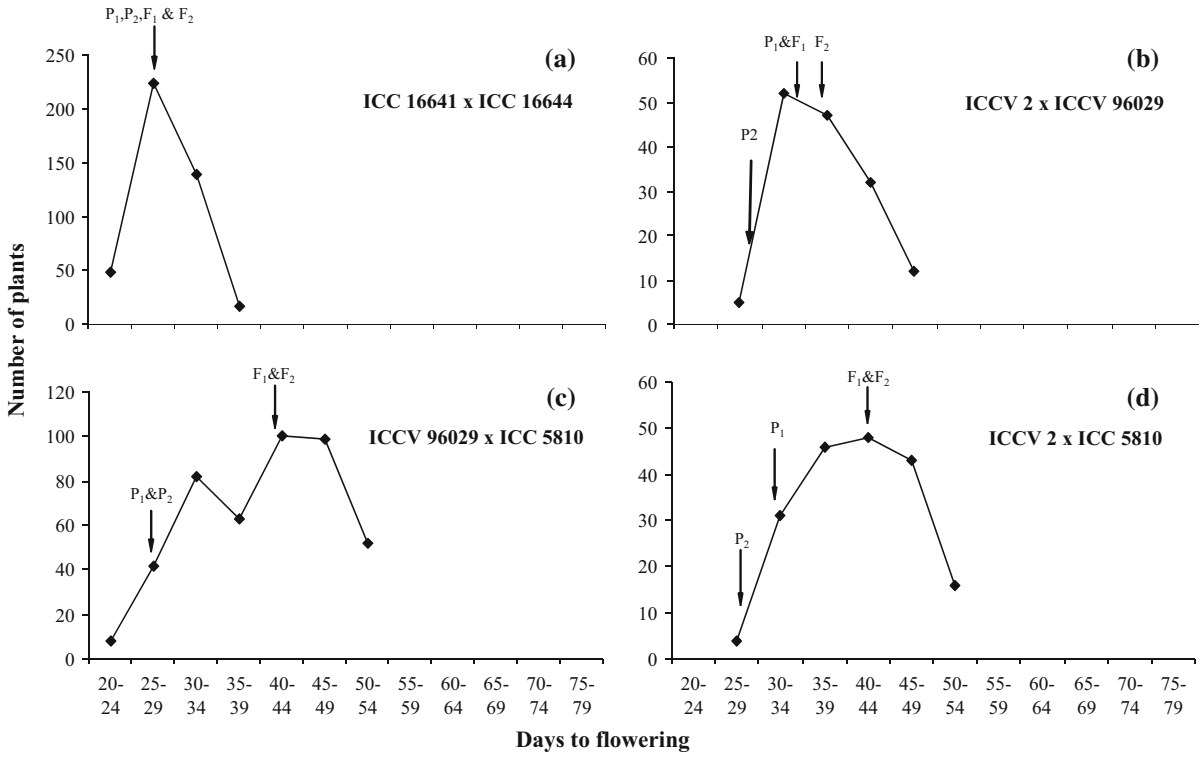

Fig. 1 Distribution of flowering time in F_2 populations of the crosses **a** ICC 16641 × ICC 16644, **b** ICCV 2 × ICCV 96029, **c** ICCV 96029 × ICC 5810 and **d** ICCV 2 × ICC 5810. The mean values of flowering time of F_1 and F_2 are close to the parents (P_1 and P_2) in the *top two crosses* **a** & **b** indicating that the major early flowering genes contributed by the parents are the same (allelic) in these crosses, and far from parents in the *bottom two crosses* **b** & **c** indicating that the major early flowering genes contributed by the parents are different (non-allelic) in these crosses

flowering time gene in the homozygous recessive condition. The hybrids between ICC 16641 and ICC 16644 (Table 2, Cross # 7 and 8; Fig. 1a) and also between ICCV 2 and ICCV 96029 (Table 2, Cross # 13; Fig. 1b) were found to be as early as their parents while the F_2 populations showed a narrow range for flowering time indicating no segregation for major flowering time genes. The average flowering time of parents, F_{1s} and F_{2s} coincided in these crosses (Table 2; Fig. 1). The F_1 and F_2 of the crosses between two early flowering lines will be similar to parents in earliness only when both the parents contribute the same recessive allele for flowering time at least at one flowering locus. Thus, these results suggested that ICCV 16641 and ICCV 16644 shared the same gene for earliness. Similarly, the major gene for earliness between ICCV 2 and ICCV 96029 was the same. The latter case was expected since ICCV 2 was used as one of the parents in the development of ICCV 96029 (Kumar et al. 2001). Kumar and van Rheenen (2000) identified a major recessive gene *efl-1* for flowering time from ICCV 2, so we suggest that ICCV 2 and ICCV 96029 both have the major recessive gene *efl-1*in homozygous condition.

ICCV 96029 flowered 4–5 days earlier than ICCV 2 indicating presence of other minor gene(s) affecting flowering. The F_2 population from their crosses had a wider range of variability for DF and DM in F_2 compared to the parents (Table 2; Fig. 1), which suggested segregation of minor gene(s). Even in the crosses between ICC 16641 and ICC 16644, which had the same major gene for flowering time, segregation of minor genes was apparent as the F_2 had a wider range than that which existed in the parents. The F_2 population of ICCV 2 × ICCV 96029 cross showed comparatively greater variability than the F_2 population of the crosses between ICC 16641 and ICC 16644 (Table 2; Fig. 1). These results suggest that the minor gene(s) differing between ICCV 2 and ICCV

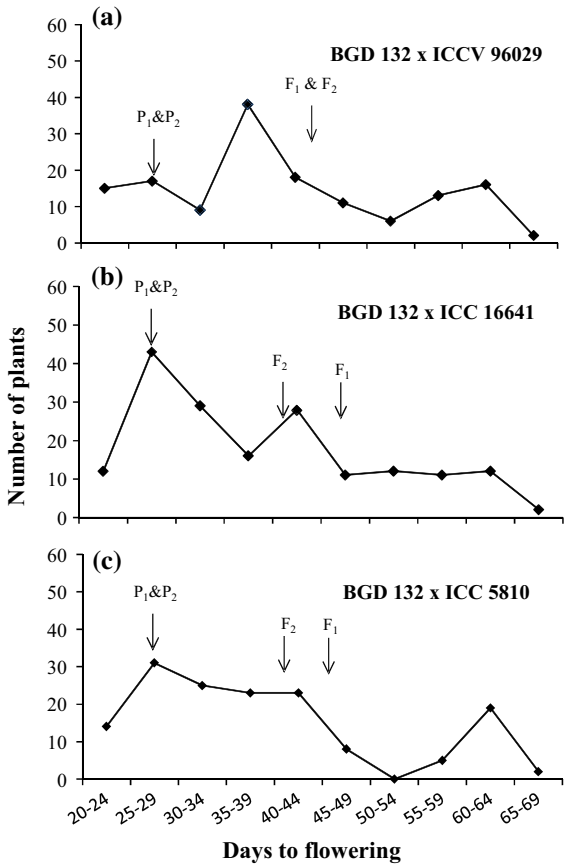

Fig. 2 Distribution of flowering time in F_2 populations of the crosses of BGD 132 with **a** ICCV 96029, **b** ICC 16641 and **c** ICC 5810. The *mean values* of flowering time of F_1 and F_2 are far from parents in all the *crosses* indicating that the early flowering gene of BGD 132 was not allelic to the early flowering genes of other parents

96029 had larger effects on phenology than the minor gene(s) differing between ICC 16641 and ICC 16644.

The hybrids obtained from crosses between ICCV 96029 and ICC 5810 and also between ICCV 2 and ICC 5810 (Table 2, Cross # 5 and 6) were 18 days late to flower (DF 45–52 days) compared to their parents (DF 27–34) (Table 2). The F_2 populations from these crosses showed a wide range in DF (23 to 63 in crosses of ICCV 96029 with ICC 5810 and 26–76 in crosses of ICCV 2 with ICC 5810) (Table 2; Fig. 1c,d). Hybrids between the two early flowering lines flower late when the parents contribute different (non-allelic) recessive alleles for flowering time. For example, one parent has the genotype *efl-1 efl-1 Efl-2 Efl-2* and contributes gametes with alleles *efl-1 Efl-2,* while the other parent has the genotype *Efl-1 Efl-1 efl-2 efl-2* and contributes gametes with alleles *Efl-1 efl-2*. The hybrid will have the genotype *Efl-1 efl-1 Efl-2 efl-2* and flower late because none of the flowering loci has flowering time gene in homozygous recessive condition. The F_2 segregates at two flowering loci and showed a wide range in flowering time. Thus, late average flowering of F_1s and F_2s compared to parents and wide variation in flowering time of F_2 in crosses of ICC 5810 with ICCV 2 and ICCV 96029 suggested that the major early flowering gene (*efl-1*) present in ICCV 2 and ICCV 96029 was not allelic to the early flowering gene of ICC 5810. Or et al. (1999) reported that early flowering in ICC 5810 was due to a recessive gene *ppd* that determines photoperiod response. Later, Hegde (2010) studied allelic relationships between early flowering genes of ICCV 2 (*efl-1*) and ICC 5810 (*ppd*) and found that these genes were non-allelic. He renamed the *ppd* gene of ICC 5810 as *efl-2*. Results of this study further support the findings of Hegde (2010) that early flowering genes of ICCV 2 and ICC 5810 are different (non-allelic).

A new early flowering gene *efl-3* was reported by Hegde (2010) from the early flowering line BGD 132 by studying its allelic relationships with early flowering genes of ICCV 2 (*efl-1*) and ICC 5810 (*efl-2*). The crosses of BGD 132 with ICCV 96029 and ICC 5810 were evaluated in this study. The hybrids from these crosses were 13–15 days late in flowering (DF 43–46) as compared to the parents (DF 28–31) and the F_2 populations showed a wide range of variation for DF from 18 to 66 (Table 2, Cross # 17 and 18; Fig. 2a,c). These results confirm the findings of Hegde (2010) that the early flowering gene of BGD 132 is non-allelic to the early flowering gene of ICCV 2 (*efl-1*) and ICC 5810 (*efl-2*).

The allelic relationships of the early flowering gene of ICC 16641/ICC 16644 with the early flowering genes of ICCV 96029/ICCV 2 (*efl-1*), ICC 5810 (*efl-2*) and BGD 132 (*efl-3)* were examined in this study. Hybrids from all these crosses were late flowering (DF 48–57 days) and the F_2 populations showed wide variation for days to flowering (18–90 days) (Table 2; Figs. 2, 3). An example of the lateness of hybrids between two early lines is given in Fig. 4. These results suggested that the major early flowering gene of ICC 16641/ICC 16644 was not allelic to any of the early flowering genes identified earlier. This new early

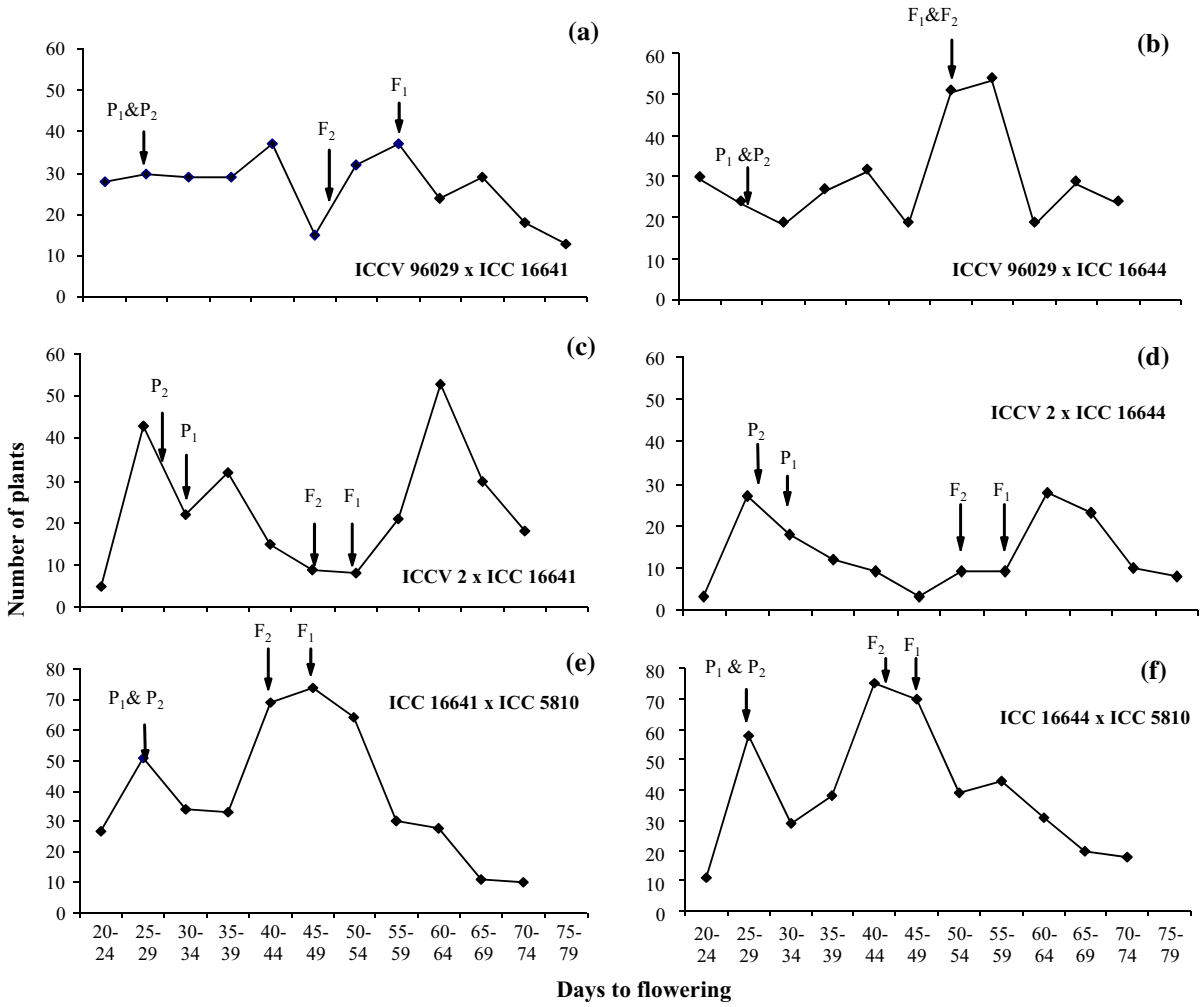

Fig. 3 Distribution of flowering time in F_2 populations of the crosses of ICC 16641/ICC 16644 with ICCV 96029, ICCV 2 and ICC 5810. The *mean values* of flowering time of F_1 and F_2 are far from parents in all the *crosses* indicating that the early flowering gene of ICC 16641/ICC 16644 was not allelic to the early flowering genes of other parents

flowering gene identified in this study is designated *Efl-4*.

Thus, so far four major genes for flowering time, *efl-1* (ICCV 96029, ICCV 2), *efl-2* (ICC 5810), *efl-3* (BGD 132) and *efl-4* (ICC 16641, ICC 16644), have been identified in chickpea (Kumar and van Rheenen 2000; Kumar and Abbo 2001; Hegde 2010 and this study). A cross between any two of these genotypes that differ in flowering time genes would show segregation for two major genes in the F_2. The F_2 gives a wide variation in flowering time and the segregation pattern may vary from cross to cross depending on the effects of individual major genes and segregation of additional minor gene(s) influencing flowering time. As late flowering is dominant over early flowering, the number of plants with late flowering is much higher than the plants with early flowering (Tables 2, 3; Figs. 1, 3). For example, the F_2 from a cross between ICCV 96029 and ICC 16644 (both flower in about 30 days) showed a range in DF from 18 to 83, and out of 376 F_2 plants, 216 plants flowered late (Tables 2, 3). Like this F_2 population, all F_2 populations segregating for two flowering time genes had some transgressive segregants which flowered 8–10 days earlier than the parents (Tables 2, 3; Figs. 1, 3). These plants are expected to be double recessive homozygotes (e.g. *efl-1 efl-1 efl-4 efl-4* in a cross between ICCV 96029 and ICC 16644) and can

Fig. 4 A hybrid (*middle*) with late maturity from a cross between two early *lines*, ICCV 96029 (*left*) and ICC 16641 (*right*), indicating that the genes for earliness in the two parents are different (non-allelic)

be valuable sources of developing super-early lines. F_2 plants that flowered much earlier than the parents were selected in all the crosses and grown as F_3 progenies. The F_3 progenies were as early as the mother F_2 plants and did not show segregation for flowering time (data not shown). These results further support that the super-early F_2 plants obtained were double recessive homozygotes. It may be possible to further reduce flowering time by developing triple or quadruple recessive homozygotes for flowering time genes.

Di-genic mode of inheritance for flowering time genes in chickpea has been reported earlier (Anbessa et al. 2006; Hegde 2010). The F_2 plants gave a good fit to a 9:7 (Anbessa et al. 2006) or 9:6:1 (Hegde 2010) ratio depending on how the plants were classified in different classes. A 9:7 ratio is possible when the F_2 plants are classified only in two classes—late and early (includes extra-early), and a 9:6:1 ratio is obtained when the F_2 plants are classified into three classes—late, early and extra-early. For simplicity, we classified F_2 plants in two classes, late and early (early + extra early) and found good fit to a 9:7 ratio in all crosses (Table 3). Classification of F_2 segregants into early and late flowering classes varied among the crosses, because of variable effects of major and minor genes.

The number of flowering time genes identified in other legumes varies considerably. For example, six major genes have been identified in pea (Murfet 1985), eight in soybean (Bernard 1971; Buzzell 1971; Buzzell and Voldeng 1980; McBlain and Bernard 1987; Cober and Voldeng 2001; Bonato and Vello 1999; Ray et al. 1995), two in pigeonpea (Koebner et al. 1991; Craufurd et al. 2001), one in lentil (Sarker et al. 1999) and one in common bean (Coyne and Mattson 1964). In all cases lateness was dominant to earliness, except for pigeonpea (Saxena and Sharma 1990) and common bean (Coyne and Mattson 1964) where early flowering was found to be dominant to late flowering.

Relationships of flowering time with maturity and other traits

The data collected on individual F_2 plants were used to estimate correlation coefficients between flowering time and other phenological, morphological and yield traits (Table 4). Days to flowering showed significant positive correlations with days to pod initiation in all the crosses, suggesting that early flowering leads to early podding. Days to flowering and days to maturity were positively correlated in all the crosses, except two crosses (ICCV 2 × ICC 16644, BGD 132 × ICC 5810) where values of correlation coefficients were not significant. These results suggest that, in general, the early flowering lines also mature early. The observations on days to flowering can be recorded

Table 3 Goodness-of-fit $\chi 2$ test for a 9:7 ratio for late and early flowering plants observed in F_2 of different crosses involving both early flowering parents

S no	Cross	F_2 observed phenotype		$\chi 2$
		Early flowering	Late flowering	
1	ICCV 96029 × ICC 16644	160	216	0.22 ns
2	ICCV 96029 × ICC 16641	163	205	0.04 ns
3	ICCV 96029 × IICC 5810	198	270	0.39 ns
4	ICC 16644 × IICC 5810	172	270	3.22 ns
5	ICC 16641 × IICC 5810	181	251	0.35 ns
6	ICCV 2 × IICC 16644	67	97	0.56 ns
7	ICCV 2 × IICC 16641	115	151	0.03 ns
8	ICCV 2 × IICC 5810	101	153	1.57 ns
9	BGD 132 × IICCV 96029	61	91	0.81 ns
10	BGD 132 × IICC 5810	70	87	0.05 ns
11	BGD 132 × IICC 16641	83	100	0.19 ns

$\chi 2$ significance was calculated at 5 % LOS)

ns non-significant

with more precision than on days to maturity, particularly in long growing season environments, thus days to flowering can be used to select for early maturity. However, the efficiency of selection will depend on genetic background. In ICCV 2 × ICC 16644 and BGD 132 × ICC 5810 crosses, where the correlation coefficients between days to flowering and days to maturity are not significant, it is possible to select plants with early flowering and late maturity (longer reproductive period). Subbarao et al. (1995) suggested that early flowering in chickpea may extend the duration of the reproductive period because of the indeterminate growth habit of the crop. However, in this study, the early flowering did not result in extending the duration of the reproductive period which may be because the crop was grown on residual soil moisture without any supplementary irrigation.

In most of the crosses, flowering time showed positive and significant correlation with plant height, plant width, number of pods per plant, number of seeds per plant and grain yield per plant (Table 4). These results indicate that extra-early and early plants of these F_2 populations matured very early and could not accumulate enough biomass (had less plant height and plant width), had fewer pods and seeds per plant and thus gave lower yields than the late maturing plants. Singh et al. (1990) reported that days to flowering and days to maturity contribute to seed yield in chickpea mainly via biological yield and harvest index. Thus, reducing growth period after a threshold level may have a penalty on grain yield.

Flowering time showed either significant negative correlation or no correlation with 100-seed weight. Hovav et al. (2003) also observed no correlation between days to first flower and mean seed weight in early-flowering segregants in the crosses where desi genotype ICC 5810 (*efl-2*) was one of the parents. Thus, there are no constraints in combining large seed size with earliness in chickpea. This is also supported from the fact that there are many large-seeded kabuli varieties with early maturity (Gaur et al. 2007).

Relationships of double flowering trait with maturity and other traits

Most chickpea cultivars produce a single flower at each flowering node. A few cultivars with two flowers per node (twin-flower or double-flower) resulting into two pods per node (double-pod) are also found. The double-pod trait was found to reduce days to maturity in tropical environments of western Canada (Anbessa et al. 2007).

ICCV 96029 was the only double-flower line among the parents used in this study. Three F_2 populations from the crosses where one of the parents was ICCV 96029 (ICCV 96029 × ICC 16644, ICCV 96029 × ICC 16641 and ICCV 96029 × ICC 5810) were used to compare single-flower and double-flower plants for various traits (Table 5). In two crosses, ICCV 96029 × ICC 16644 and ICCV 96029 × ICC 16641, significant differences were observed between single-flower and double-flower plants for all the traits studied. As compared to the single-flower plants, the double-flower plants were later in pod initiation and

Table 4 Correlation coefficients between days to flower and other studied traits (correlations were calculated on total number of plants in both direct reciprocal crosses)

S no.	Cross	Days to pod initiation	Days to maturity	Plant height	Plant width	Pods per plant	Seeds per plant	Yield per plant	100 seed weight
1	ICCV 96029 × ICC 16644	0.994*	0.901*	0.786*	0.738*	0.241*	0.201*	0.176*	−0.239*
2	ICCV 96029 × ICC 16641	0.996*	0.893*	0.732*	0.728*	0.295*	0.245*	0.219*	−0.263*
3	ICCV 96029 × ICC 5810	0.942*	0.585*	0.385*	0.395*	0.227*	0.180*	0.160*	−0.099 ns
4	ICC 16644 × ICC 5810	0.986*	0.827*	0.58*	0.646*	0.243*	0.194*	0.209*	−0.053 ns
5	ICC 16641 × ICC 5810	0.985*	0.794*	0.582*	0.621*	0.280*	0.236*	0.219*	−0.171 ns
6	ICCV 2 × ICC 16644	0.990*	0.079 ns	0.616*	0.608*	0.172*	0.111 ns	0.067 ns	−0.122 ns
7	ICCV 2 × ICC 16641	0.983*	0.852*	0.695*	0.705*	0.221*	0.189*	0.128*	−0.202*
8	ICCV 2 × ICC 5810	0.947*	0.123*	0.263*	0.371*	0.157*	0.105 ns	0.113 ns	0.095 ns
9	BGD 132 × ICCV 96029	**	0.355*	**	**	0.312*	0.339*	0.265*	0.061 ns
10	BGD 132 × ICC 5810	**	0.081 ns	**	**	0.433*	0.440*	0.430*	0.010 ns
11	BGD 132 × ICC 16641	**	0.148*	**	**	0.318*	0.305*	0.284*	−0.198*

* 5 % level of significance; *ns* non-significant

** Data not recorded

maturity; taller and had more plant width; produced more pods per plant, number of seeds per plant, and grain yield per plant; and had smaller seed. Though the double-flower trait did not hasten maturity, it increased the grain yield per plant by increasing number of pods (and then number of seeds) per plant. The only drawback is that the double-flower plants had comparatively smaller seeds. Kumar et al. (2000) also found similar results regarding reduced seed size in double-flower segregants compared to single-flower. However, some studies have reported no significant difference between single and double-pod segregants for seed size (Rubio et al. 2004; Anbessa et al. 2007).

In the F_2 population of the cross ICCV 96029 × ICC 5810, the double-flower and single-flower plants differed significantly only for number of pods per plant, number of seeds per plant and 100 seed weight. These results indicate that crop growing environment and the genetic background would significantly influence the advantages of the double-flowering trait. In an earlier study, Sheldrake et al. (1978) obtained 6–11 % higher yield in double podded plants compared to single-podded plants under rainfed conditions.

Prospects of using different flowering time genes in chickpea breeding

Information on allelic relationships of flowering time genes would be useful in developing effective breeding strategies for improving earliness in chickpea. It provides options for choosing a specific early flowering gene or a combination of such genes based on the desired background (e.g. kabuli or desi) and linkage relationships of the flowering time genes with other traits. For example, there are reports that suggest that ascochyta blight resistance was negatively correlated with days to flowering (Aryamanesh et al. 2010). In

Table 5 Comparison of single-flower (SF) and double-flower (DF) F_2 segregants for phenology and agronomic traits in different crosses

		Days to flower	Days to pod initiation	Days to maturity	Plant height	Plant width	Pods per plant	Seeds per plant	Yield per plant	100 seed weight
ICCV 96029 × ICC 16644										
DF	Mean	57.7 ± 2.04	65.2 ± 2.11	108.0 ± 2.23	40.7 ± 1.41	54.3 ± 2.4	85.8 ± 7.24	107.4 ± 9.77	15.2 ± 1.4	14.3 ± 0.44
	Range	36–83	41–90	80–128	20–60	31–84	13–236	18–349	1.9–31.3	7.1–21.3
SF	Mean	48.4 ± 1.5	55.4 ± 1.51	96.6 ± 1.64	34.0 ± 0.98	41.4 ± 1.74	61.3 ± 3.92	76.7 ± 5.02	11.8 ± 0.76	15.6 ± 0.28
	Range	20–82	27–92	60–130	8–63	3–83	3–240	3–360	0.3–50.7	7.3–24.1
	t-prob	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.004*	0.006*	0.04*	0.01*
ICCV 96029 × ICC 16641										
DF	Mean	59.2 ± 2.22	66.7 ± 2.16	110.9 ± 2.19	41.8 ± 1.51	51.5 ± 2.19	102.5 ± 7.52	122.5 ± 9.8	17.8 ± 1.5	14.6 ± 0.4
	Range	35–83	61–90	85–126	22–62	18–75	17–205	17–298	3.3–50	10–20.5
SF	Mean	47.1 ± 1.41	53.4 ± 1.43	96.6 ± 1.63	32.3 ± 0.86	36.7 ± 1.46	68.5 ± 4.16	84.9 ± 5	13.3 ± 0.76	16.3 ± 0.26
	Range	20–92	28–96	66–127	10–60	7–75	6–225	6–252	0.9–44	8.3–24.8
	t-prob	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	0.001*	0.001*
ICCV 96029 × ICC 5810										
DF	Mean	39.8 ± 1.26	46.3 ± 1.31	88.1 ± 1.19	32.9 ± 0.81	37.0 ± 1.73	122.0 ± 5.54	146.9 ± 10.09	17.6 ± 1.2	12.1 ± 0.17
	Range	23–54	29–62	75–110	20–50	17–73	26–324	36–360	1.2–43.2	8.8–14.5
SF	Mean	41.1 ± 0.62	47.6 ± 0.67	89.4 ± 0.62	33.8 ± 0.47	37.0 ± 0.89	101.3 ± 3.97	124.4 ± 5	15.9 ± 0.63	12.9 ± 0.13
	Range	25–63	31–73	75–110	17–54	7–68	5–265	7–356	0.7–45.6	5.8–22.5
	t-prob	0.24 ns	0.36 ns	0.34 ns	0.32 ns	0.97 ns	0.03*	0.04*	0.21 ns	0.003*

such a case, another flowering time gene, not linked to the locus for ascochyta resistance, can be used for earliness.

There have been rapid advancements in development of genomic resources in chickpea in the recent years (Varshney et al. 2013a; Gaur et al. 2014b). The draft genome sequence of chickpea has also been published (Varshney et al. 2013b). Molecular markers have been identified for genes/quantitative trait loci (QTLs) controlling several agronomic traits, including flowering time. The major flowering time gene from ICCV 2 (*efl*-1) was mapped on linkage group (LG) 4 (Chao et al. 2002; Jamalabadi et al. 2013). There are other reports on mapping of flowering time QTLs on LG 3 (Cobos et al. 2009; Aryamanesh et al. 2010; Hossain et al. 2010; Rehman et al. 2011), but in these cases the sources of earliness were different. The major flowering time gene from ICC 5810 (*efl-2* or *ppd*) was mapped on LG 4 (Cobos et al. 2007). The flowering time genes *efl-3* and *efl-4* are yet to be mapped. QTLs for flowering time have also been mapped on LG 1 (Lichtenzveig et al. 2006; Rehman et al. 2011), LG 2 (Lichtenzveig et al. 2006), LG 4 (Cobos et al. 2007 Rehman et al. 2011) and LG 8 (Lichtenzveig et al. 2006; Rehman et al. 2011). Some of these mapped QTLs have minor effects.

The chickpea genotypes carrying the flowering time genes of known allelic relationships, i.e. ICCV 2/ICCV 96029 (*efl-1*), ICC 5810 (*efl-2*), BGD 132 (*efl-3*), and ICC 16641/ICC16644 (*efl-4*) would be useful genetic stocks for establishing allelic relationships with other flowering time genes. There is a need for mapping *efl-3* and *efl-4* genes and developing near isogenic lines (NILs) for all four flowering time genes to study effects of individual genes.

Early maturity is an important trait in chickpea for its adaptation in short growing season environments. As chickpea has indeterminate growth habit and is both thermo- and photo-sensitive, days to maturity for a variety may vary considerably across locations. For example, a variety that matures in 90–95 days in southern India, may take 110–120 days in central India and 130–150 days in northern India. Berger et al. (2011) also observed such differences in genotypic responses at different chickpea growing locations globally. Thus, classification of varieties based on maturity will vary from one location to another. At ICRISAT (located in southern India), we classify a variety early if it matures in 90–99 days, extra-early if it matures in 85–89 days and super-early if it matures in less than 85 days.

One extra early (ICCV 2) and several early (e.g. JG 11, JG 14, KAK 2, JAKI 9218, Yezin 4) chickpea cultivars have been developed through collaborative research efforts of ICRISAT and National Agricultural Research System (NARS) institutes in Asia and Africa and have shown high impacts on area and productivity of chickpea in short growing season environments. For example, the extra-early cultivar ICCV 2 (Yezin 3) occupied 55 % of the chickpea area and the early variety ICCV 88202 (Yezin 4) occupied 22 % of the chickpea area during 2004/05 in Myanmar. As a result, the chickpea area increased by 23.5 % (from 166,000 to 205,000 ha), production increased by 2.6 times (from 92,000 to 239,000 t) and yields almost doubled (from 588 to 1,171 kg ha^{-1}) during a period of 10 years from 1995/96 to 2004/05 (Than et al. 2007). Similarly in Andhra Pradesh state of Southern India, the early maturing chickpea cultivar JG 11 covered 70 % of the chickpea area during 2008/09, where the chickpea production increased 9.3 fold (95,000 to 884,000 t) during a period of 10 years from 1999/00 to 2008/09 because of a 3.8-fold increase in area (102,000 to 602,000 ha) and 2.4 fold increase in yield levels (583 to 1,407 kg ha^{-1}) (Gaur et al. 2012).

Several super early chickpea breeding lines are available (Kumar and Rao 1996). These super early lines are generally lower yielding than the extra-early and early cultivars. However, these can be used in special niches, such as a short duration catch crop between two major crops (Gaur et al. 2008b) or for harvesting plants for immature green grains to be used as vegetable (Sandhu et al. 2007).

Conclusions

Early maturity will continue to remain an important trait for chickpea because of a large shift (about 4 million ha, which is about 30 % of total chickpea area) in its area from cooler long season environments to warmer short season environments and increasing incidence of reproductive stage heat stress (Gaur et al. 2014a). The information on allelic relationships of flowering time genes provided here would be useful in chickpea breeding programs aimed at improving earliness in chickpea.

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