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A LINKAGE MAP OF CHICKPEA (*Cicer arietinum* L.) BASED ON POPULATION FROM ILC3279×ILC588 CROSSES: LOCATION OF GENES FOR TIME TO FLOWERING, SEED SIZE AND PLANT HEIGHT

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Quantitative traits of seed size, plant height and days to flowering were studied in a chickpea intraspecific $F_{3:4}$ lines population derived from a ILC3279×ILC588 cross. The lines were genotyped with random amplified polymorphic DNA (RAPD), universal rice primer (URP) and sequence tagged microsatellite site (STMS) markers, and a genetic map composed of 7 linkage groups (LGs) covering 285.3 cM was constructed. Quantitative trait loci (QTLs) for the three characters were detected in LG2, LG3 and LG4. Two QTLs for days to flowering were detected on LG2 and LG3. These two QTLs accounted for 58% of the total phenotypic variation for days to flowering. A QTL for plant height was located in LG3 explaining around 42% of the variation. This trait was shown to be under a major gene control. For 100-seed weight, a QTL located in LG4 explained around 37% of the phenotypic variations. This information can be used to formulate the an efficient breeding strategy for improvement of time to flowering in short-season temperate environments, plant height with more reproductive biomass and improved yield with bigger seed size in chickpea.

Key words: Chickpea, Mapping, QTLs, Yield related traits.

INTRODUCTION

Chickpea (*Cicer arietinum* L.) is a self-fertilizing diploid ($2n = 2x = 16$) grain legume, grown in more than 30 countries of Central and South Asia, southern Europe, northern and eastern Africa, Australia, South America and North America. It is the second most important

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pulse crop worldwide in terms of area under cultivation (11.2 Mha) after dry beans, but ranks third in production (9.1 Mt) following dry beans and peas (FAOSTAT Database http://www.faostat. fao.org/, 2006). The cultivated chickpea, *Cicer arietinum* L., is often divided into two types: Desi and Kabuli. Kabuli chickpea (white flower, large, cream-coloured seeds) have traditionally been grown around the Mediterranean basin and central Asia, whereas Desi chickpea (purple flower, small, dark, angular seeds) are mainly produced on the Indian subcontinent, in east Africa, central Asia and to a limited extent the Mediterranean Basin. Yield is a complex trait, resulting from complete development of the plant. Therefore, yield usually shows low heritability. In chickpea, correlations have been reported between seed yield and its components (seeds per pod, pods per plant, seeds per plant, yield per plant, seed size, etc.) (MUEHLBAUER and SINGH, 1987; MAYNEZ *et al*., 1993; KARAMI, 2011; TALEBI *et al*., 2011; TALEBI and KARAMI, 2011). However, results obtained do not tend to corroborate each other possibly because of the differences in the material used (collections or segregate populations) or environments (different locations or years). Number of days to flowering is an important trait for crop adaptation and productivity, especially under dryland farming systems that experience terminal drought conditions. Therefore, the ability to manipulate flowering time is an essential component of chickpea improvement (KUMAR and ABBO, 2001). The low yield of chickpea is mostly due to its susceptibility to various biotic and abiotic stresses. Molecular marker based linkage maps have been useful in identifying and localizing important genes controlling both qualitatively and quantitatively inherited traits in a wide range of species (TANKSLEY *et al*., 1989). Marker assisted selection (MAS) of agronomical desirable traits such as yield, quality, biotic and abiotic stress resistance, etc. requires an intra-specific linkage map saturated with co-dominant and single-locus PCR based markers like SSRs. SSRs also enable transfer of linkage information among maps developed from different populations and can be used as anchors to combine the maps to develop a highly saturated consensus map. A highly significant QTL for seed size has been located in LG4 using both intra-specific (CHO *et al*., 2002) and inter-specific populations (ABBO *et al*., 2005). In addition, COBOS *et al*. (2007) found two QTLs that were located in LG4 and LG8. There are limited reports on quantitative trait locus (QTL) mapping of days to flowering and other yield related traits in chickpea. In relation to days to flowering, OR *et al*. (1999) found a single gene (*Ppd/ppd*) controlling photoperiodic response in chickpea and that insensitivity was recessive. In addition, KUMAR and VAN RHEENEN (2000) also identified a gene called *elf-1* from an intra-specific recombinant inbred line (RIL) population. These genes have not yet been located on the chickpea map. Identification of QTLs located on different LGs shows that there may be several genes for flowering time in chickpea. Seed size measures like 100-seed weight is an important yield component easy to manage in breeding programmes. Other traits such as plant height could be positively related with higher biomass. Therefore, the purpose of this study was to analyze quantitative agronomic traits by combining classic quantitative genetics and molecular marker analysis to identify QTL(s) that control seed weight, days to flowering, and plant height using an $F_{2:3}$ populations derived from ILC3279×ILC588 cross.

MATERIALS AND METHODS

Plant materials and phenotyping assessment

Studies were made on 111 $F_{2:3}$ plants of chickpea, *Cicer arietinum* L., one from each F_2 individual, from the cross 'ILC3279/ILC588'. Seeds of the parental lines were obtained from

ICARDA. ILC3279 is known for its high yield potential, long day to flowering and high plant height. ILC588 reported the presence of a major gene for early flowering (KUMAR and ABBO, 2001). Seed size in ILC588 significantly is smaller than ILC3279. $F_{3:4}$ Lines of the population, together with the parents, were evaluated for three morphological traits (days to flowering, plant height (cm) and 100-seed weight (g)) in field experiments at the Department of Agriculture, Islamic Azad University, Sanandaj Branch, during two years (2009 and 2010). Ten seeds from each $F_{3:4}$ lines were sown following a randomized complete block design with three replications. Each replication consisted of two rows (2m/row) planted with 20 seeds/row and 30 cm row spacing.

Genomic DNA extraction and marker analysis

Healthy leaves harvested from the parents and 111 $F_{2:3}$ plants were used for DNA extraction. Healthy young leaves from the spring crop of 2009–10 were immediately frozen in liquid nitrogen and stored at –80ºC. Isolation of DNA was carried out using the CTAB method (SAGHAI-MAROOF *et al*., 1984) with minor modification. DNA quantity and quality were assessed with a UV-Photometer. The primers used in the present study included 10 RAPD, 48 STMS markers (WINTER *et al*., 1999), 6 URP markers (KANG *et al*., 2002) and 50 chickpea STMS markers. Optimal PCR conditions were established for each primer type and all the marker loci were scored at least twice to minimize interpretation errors. The RAPD (Operon Technologies Inc., Alameda, California) and URP primers (KANG *et al*., 2002) were analyzed as described by WINTER *et al*. (2000) and KANG *et al*.(2002), respectively. The amplification products were electrophoretically separated on 1.5% agarose gels and the banding patterns were visualized on a UV-transilluminator after staining the gels with ethidium bromide. Only clear and reproducible polymorphic bands were scored as loci. The genotype profiles produced by STMS markers were as A, B and H for each allele presented in ILC3279, ILC588 and heterozygote lines, respectively. The STMS analysis included 50 primers reported by WINTER *et al*. (1999). PCR amplifications were performed in 25µl reaction volumes as described by WINTER *et al*. (1999) with minor modifications. The amplification products were separated on 3% MetaPhor agarose gels followed by staining with ethidium bromide.

Construction of linkage map and QTL analysis

Linkage analysis was conducted with JOINMAP 3.0 (STAM and VAN OOIJEN, 1995). Recombination fractions were converted into map distances by the Kosambi function (KOSAMBI, 1944). The output from JOINMAP was converted to a graphical format using the program WinQTL 2.5 (WANG *et al*., 2010) and the QTL analysis was performed using the genotypic and phenotypic data from the 111 $F_{2:3}$ lines obtained from cross between ILC3279 and ILC588. Composite interval mapping (CIM) was performed to account for the masking effects of other QTLs on detected QTLs, using a stepwise regression analysis enabling additive genetic models and the selection of markers as cofactors to declare the presence of a putative QTL in a given genomic region. Finally, the location of a QTL was defined as a position where the LOD score value exceeded 2.5 based on permutation test.

RESULTS

Morphological traits analysis

The two parents (ILC3279 and ILC588) of the cross used to develop $F_{2:3}$ population were distinctly different for scored agronomic traits (Table 1). The 111 F_3 lines were evaluated for three morphological traits including days to flowering, 100-seeds weight and plant height (growth habit). As expected, two of the traits (100-Seed weight and plant height) appeared to be controlled by single major gene and clearly fit a 1:1 segregation ratio ($p>0.05$) (Table 1). Frequency distributions of F_3 lines for each quantitative trait evaluated were plotted and are shown in figure 1. For all three morphological traits in the field, F_3 lines showed transgressive segregation towards higher and lower value (Figure 1a, 1b, 1c). There was a negative significant correlation between plant height with 100-seed weight ($r=-0.77$, $p<0.01$, $n=111$) and days to flowering ($r=-0.52$, $p<0.01$, $n=111$) in ILC3279, while it was positive in ICCV2. In the case of days to flowering, the data could be classified into one of the two parental types even though the F_3 lines had wide variation typical of a quantitatively inherited trait (Figure 1b). Days to flowering segregated into a 1:2:1 among F_3 lines and appeared to be controlled by at least two genes.

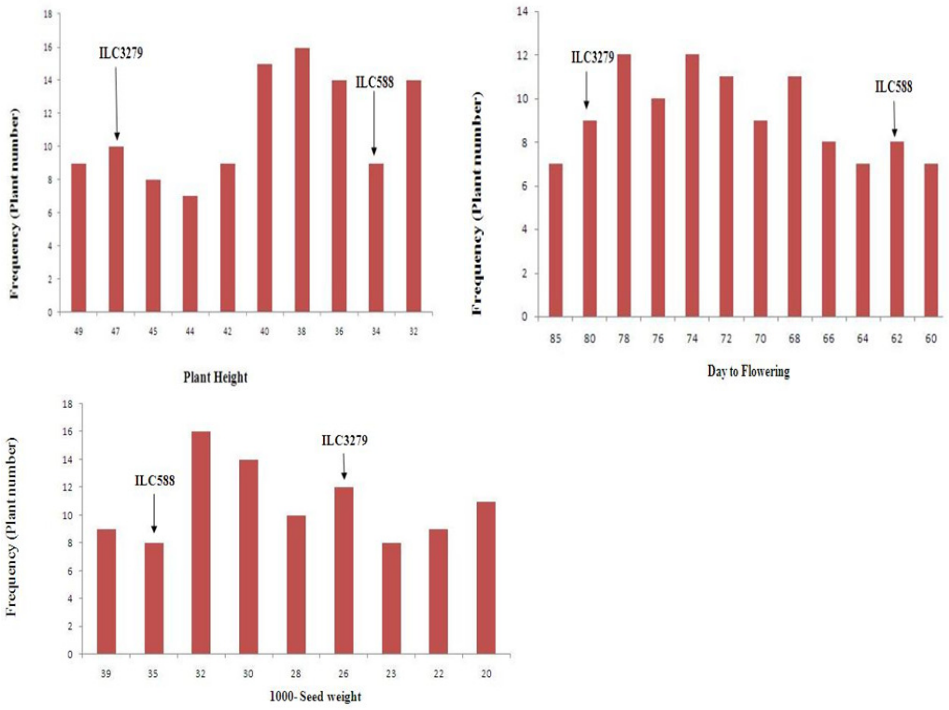

Figure 1. Frequency distribution of $F_{3:4}$ lines for three quantitative traits in chickpea (a=Plant Height; b=Days to Flowering; c=100-seed weight)

Table 1. Parental and $F_{3:4}$ population characterizations obtained from ILC3279×ILC588 cross evaluated under field condition in 2009-2010

Variable	Parents		F_3 segregation				
	ILC3279	ILC588	Maximum	Minimum	Mean ±SE	Expected ratio	$P(\chi^2)$
Days to Flowering	81	63	86	60	75±4	1:2:1	0.3142
Plant Height	47	34	49	32	41.25±3.18	1:1	0.1154
100-seed weight	26	36	39	20	28.1±3.11	1:1	0.1241

Linkage map and marker analysis

Polymorphic bands between the two parental lines were found for 37 STMS, 25 RAPD, and 13 URP markers. Therefore, three morphological and 75 molecular markers were available for linkage analysis and mapping. Sixty five of 75 markers fit the expected 1: 1 segregation ratio ($p > 0.05$). Thirty three (15 STMS, 8 URP, 10 RAPD, and 3 morphological markers) of the 75 markers were mapped to 7 linkage groups (Figure 2) covering 285.3 cM with an average distance of 8.6 cM between markers. Naming of LG was in accordance with presence of the anchor markers from the most extensive chickpea genome map of WINTER *et al*. (2000). The present map revealed relatively similar marker distribution among LGs with other published chickpea genetic maps reported by WINTER *et al*. (2000), TARAN *et al*. (2007) and ARYAMANESH *et al*. (2010).

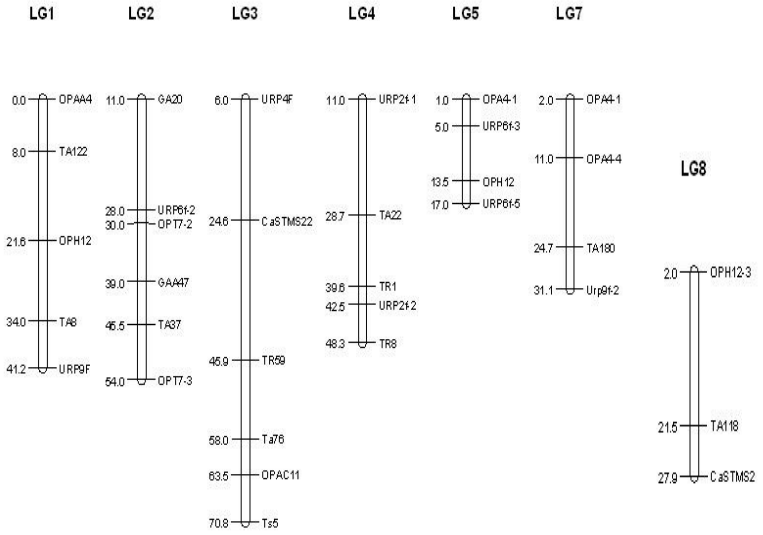

Figure 2. Linkage map of chickpea based on the intra-specific $F_{2:3}$ population derived from a cross between ILC3279 and ILC588.

QTL analysis

The non-parametric Kruskal Wallis test detected highly significant association between some markers on LG2, LG3 and LG4 and the traits studied ($p<0.001$) (days to flowering, plant height and 100-seed weight). The analysis of three morphological traits related to seed yield revealed four potential QTLs with an LOD ≥ 3 (Table 2). In the case of day to flowering, two QTLs were mapped on LG2 and LG3 ($P<0.001$) with unequal variances. The QTLs on LG2 and LG3 explained 23% and 35% of the phenotypic variation flanked by markers GGA47 (1 cM) and Ta37 (3.1 cM) in interval 4 and markers CaSTMS 25 (13 cM) and TR59 (6.8 cM) in interval 2, respectively (Figure 3). For plant height, QTL were mapped on LG3 with an LOD≥2.94 explaining 42% of the phenotypic variation flanked by markers CaSTMS22 and TR59 (3.6 cM) (Figure 4). A QTL peak with a maximum LOD score of 3.04 in LG4 was identified for 100-seed weight. This QTL was located between STMS markers TR1 and URP marker URP2f-2 with two intervals. The marker TR1 was the most closely linked explaining 37% of the total phenotypic variation (Figure 5).

Table 2. Summary of QTL analysis for morphological traits of the ILC3279×ILC588 $F_{3:4}$ population. QTL analysis were carried out by composite interval mapping (CIM)

Trait	Locus name	Linkage group	Source	LOD	VE
Days to Flowering	DTF	2	ILC588	3.11	23%
	DTF	3	ILC588	3.49	35%
Plant Height	PH	3	ILC3279	2.94	42%
100-seed weight	100-SW	4	ILC588	3.04	37%

VE= percentage of explained phenotypic variance; LOD= logarithm of odds

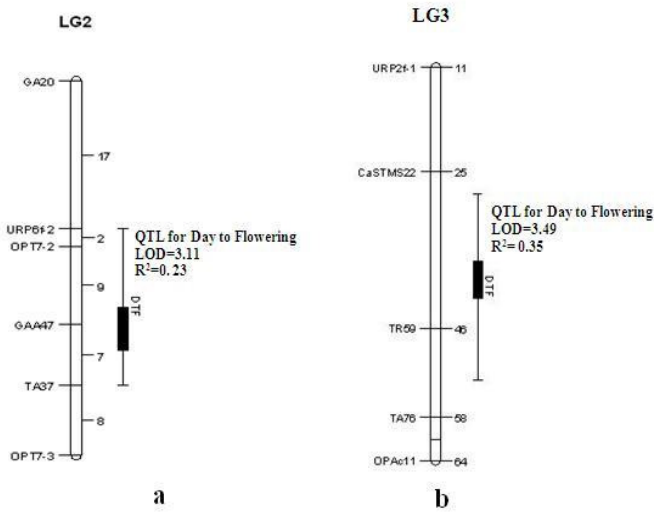

Figure 3. Localization of quantitative trait loci (QTLs) for days to flowering on LG2 (a) and LG3 (b) in the $F_{2:3}$ intra-specific populations derived from a cross between ILC3279 and ILC588.

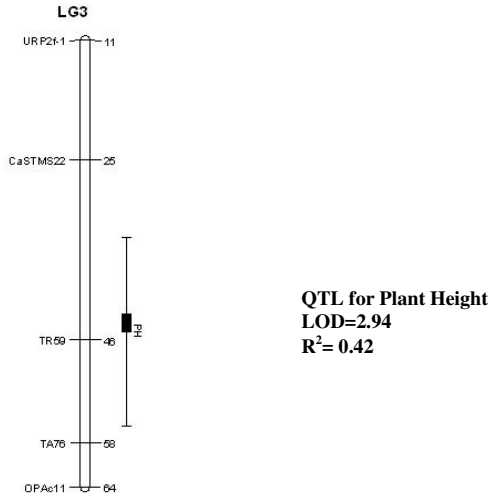

Figure 4. Localization of quantitative trait locus (QTL) for plant height on LG3 in the $F_{2:3}$ intra-specific population derived from a cross between ILC3279 and ILC588.

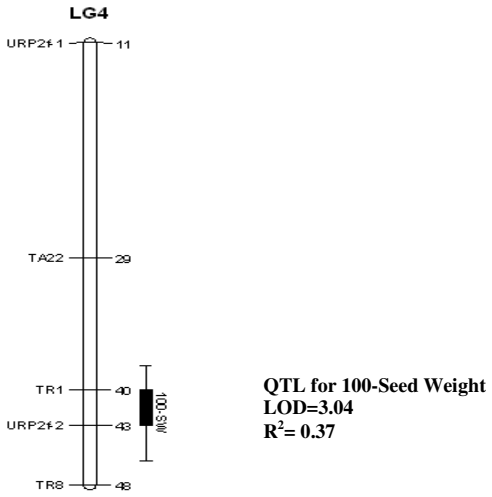

Figure 5. Localization of quantitative trait locus (QTL) for 100-seed weight on LG4 in the $F_{2:3}$ intra-specific population derived from a cross between ILC3279 and ILC588.

DISCUSSION

Seven of the eight LGs obtained from the ILC3279 × ILC588 were previously characterized STMS loci, so that these could be readily related to those constructed from other chickpea mapping populations. Seed yield is a complex character controlled by several genetic and environmental factors and also dependent on interaction of many other characters. In this study we mapped a major gene for some yield related traits such as days to flowering, 100-seed weight and plant height. Days to flowering is considered to be an important adaptive trait because crops have to grow in different thermal and photoperiod regimes (KHANNA-CHOPRA and SINHA, 1987). Mediterranean chickpea seem to have evolved towards high day-length sensitivity, while on the Indian subcontinent and in East Africa, they have evolved towards short photoperiods (ROBERTS *et al*., 1985; KUMAR and ABBO, 2001). In this study, we mapped two QTLs for days to flowering on LG2 and LG3. The inheritance of days to flowering in chickpea was controlled by two QTLs with epistatic interaction (HEGDE, 2010). Oligogenic inheritance of flowering time has been reported by GUMBERM and SARVJEET (1996) and ANBESSA *et al*., (2006) who suggested that two genes controlled time to flowering. KUMAR and VAN RHEENEN (2000) suggested the presence of a major gene (Efl-1/efl-1) and minor polygenes for this trait. However, OR *et al*. (1999) reported a single recessive major gene for time to flowering. The differences among these reports are probably due to differences in the parents used and environmental influences such as day length and temperature. Although our QTLs were found on LG2 andLG3, their locations on the linkage groups were different from CHO *et al*. (2002), COBOS *et al*. (2009), and ARYAMANESH *et al*. (2010); suggesting the presence of different genes for the control of flowering time or may it reflected to different population, markers and linkage map analysis. A QTL for plant height was mapped on LG3. To our knowledge, this is the first mapping analysis for plant height in chickpea, which we found to be under major gene control. ILC3279 is a vigour erect plant so in this case high plant can be much related with erect habit which it has been also mapped in LG3 in previous study (ARYAMANESH *et al*., 2010). QTL for 100 seed weight was found on linkage group 4. Our QTL might be the same QTL for seed size reported by CHO *et al*. (2002), ABBO *et al*. (2005) and COBOS *et al*. (2007) in LG4. ABBO *et al*. (2005) and COBOS *et al*. (2007) located their QTL flanked by markers GA02, STMS11 and TA130, respectively. These markers were not polymorphic in our map where TR1 was the closest to our QTL. UPADHYAYA *et al*. (2006) reported that seed weight was controlled by at least two major genes, but only one significant QTL identified in the present study might correspond to one of these genes. On chickpea maps published before now, this genomic region was poorly saturated, so to obtain more robust markers in this interesting region, STMS markers will be more informative and effective. Comparison of the present intra-specific map of chickpea with the inter-specific map developed by WINTER *et al*. (2000) revealed high linkage conservation in all linkage groups. However, the map distances and marker orders of the common SSR markers differed, possibly due to the intra-specific nature of our mapping populations. In conclusion, markers linked to days to flowering, plant height and 100-seed weight would enable simultaneous selection to be performed for all three traits at an early stage. The present intra-specific map will be helpful for mapping and tagging of the genes or QTLs governing traits such as biotic and abiotic stress resistance, other yield related agronomic characters and quality in chickpea breeding programs.

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MAPA UKOPČANOSTI GENA KOD LEBLEBIJE (*Cicer arietinum* L.) ZASNOVANA NA POPULACIJI DOBIJENOJ UKRŠTANJEM ILC3279×ILC588: LOKACIJA GENA KOJI KONTROLIŠU VREME CVETANJA, VELIČINU SEMENA, VELIČINU I VISINU BILJKE

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Izvod

Vršena su ispitivanja kvantativnih osobina: veličina semena, visine biljaka i trajanja perioda do cetanja u intraspecijskmh $F_{3:4}$ linijama unutar populacije dobijene ukrštanjem genotipova ILC3279×ILC588. Karakterizacija linija je vršena metodama RAPD, korišćenjem univerzalnog prajmera pirinča (URP) i STMS markera. Genetička mapa je konstruisana od 7 grupa ukopčanih genas (LGs) koje pokrivaju 285.3 cM. QTLs za tri osobine su detektovani u LG2,LG3 i LG4 Dva od QTLs za broj dana do cvetana su detektovana u LG2 i LG3T. Ova dva lokusa kontrolišu 58% ukupnog fenotipskog variranja broja dana do cvetanja. QTL za visinu biljaka lociran u LG3 i objašnjava oko 42% variranja. Pokazano je da se ova osobina nalazi pod kontrolom major gena. QTL za težinu 100 zrna, lociran u LG$ objašnjava oko 37 % fenotipskih varijacija. Ove informacije mogu da se koriste za formulisanje efikasne strategije oplemenjivanje leblebija na poboljšanje vremena cvetanja u uslovima kratkog dana, visine biljaka sa više reproduktivne biomase i povećanje prinosa sa povećanjem veličine zrna.

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