Impact of Genomics on Chickpea Breeding

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Abstract

Chickpea is an economical source of vegetable protein for the poor living in the semi-arid regions globally. As a consequence of climate change and increasing climate variability, the incidences of drought and heat stresses and severity of some diseases, such as dry root rot and collar rot, have increased in chickpea crop, resulting in poor and unstable yields. By improoving the efficiency of crop breeding programs, climate resilient varieties with traits desired by the farmers, industries and consumers can be developed more rapidly. Excellent progress has been made in the development of genomic resources for chickpea in the recent past. Several national and international chickpea breeding programs have started utilizing these genomic resources and tools for genetic improvement of complex traits. One of such examples includes the introgression of "*QTL-hotspot*" containing quantitative trait loci (QTLs) for several drought tolerance-related traits, including root traits, through marker-assisted backcrossing (MABC) for enhancing drought tolerance in popular cultivars. Several drought-tolerant introgression lines with higher yield as compared to the popular cultivars have been identified. Multi-parent advanced generation intercross (MAGIC) populations developed from using 8 parents created large genetic diversity consequently several promising lines. Marker-assisted recurrent selection (MARS) has also been explored for yield improvement in chickpea. Development of diagnostic markers or the identification of candidate genes for several traits is essential for greater use of genomic resources in chickpea improvement.

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11.1 Introduction

Chickpea (*Cicer arietinum* L.) is a cool-season food legume grown mainly in arid and semi-arid regions of the world. Chickpea is cultivated in 13.9 m ha with a production of 13.6 m ton during 2014 (FAOSTAT 2016). Its cultivation and consumption are mainly concentrated in South Asia region, where India alone accounts for more than 70% of global chickpea area and consumption. Due to its cultivation under challenging soil and environmental conditions, the crop is exposed to several biotic and abiotic stresses. As a consequence of climate change, incidence of new races and also new diseases such as dry root rot and collar rot are posing serious threats to chickpea production. Besides classical breeding methods, genomic approaches are particularly useful in handling complex traits, which are usually controlled by several genes and highly influenced by environment. Genomic tools facilitate in the identification of genomic regions/QTLs and favorable alleles of small effects that generally remain unnoticed and are not included in the gene pool used for breeding (Morgante and Salamini 2003; Vaughan et al. 2007).

Most of the qualitative traits are characterized by high heritability and are easy to select for. However, favorable allelic combinations and genetic recombinations for complex traits are difficult to identify through conventional breeding strategies. Advances in genomic technologies enable to capture genome-wide diversity in natural and artificial populations. In recent years, large-scale genomic resources were developed in case of chickpea (Varshney et al. 2010). The draft genome sequence and resequence information of germplasm lines of chickpea (Varshney et al. 2013) including parental lines of several mapping populations (Thudi et al. 2016), varieties (Thudi et al. 2016) provided several thousands of simple sequence repeat (SSR) markers, millions of single nucleotide polymorphism (SNP) and indels for use in genomics-assisted breeding for chickpea improvement. The present chapter discusses the recent advances in the application and impact of the genomic tools in chickpea improvement.

11.2 Marker-Assisted Selection for Chickpea Improvement

In marker-assisted selection (MAS), the genotypes are selected based on the presence or absence of markers instead of the trait itself. The tight linkage between the markers and the major gene or QTL responsible for the trait is necessary for successful implementation of MAS in breeding programs. With the advances in new genomic tools and availability of a large amount of genomic resources, it is now possible to identify the strong associations between markers and traits.

Routine breeding programs involve the combining of two or more genes or QTLs controlling trait(s) of interest into a common genetic background. In this process, selection of plants having all favorable donor alleles based on phenotype for making backcrosses or generation advancement in each generation will be very difficult. In such circumstances, the application of MAS will be of a great help in the process of identifying plants carrying several targeted alleles whose effect on the phenotype is not recognizable. In chickpea, a large number of genomic resources were deployed for the identification of genes/QTLs controlling several qualitative and quantitative traits. Some of them are early-flowering-time genes (Gaur et al. 2016; Mallikarjuna et al. 2017), pod- and seed-related traits for enhancing heat tolerance (Pronob Paul, personal communication), vernalization response (Samineni et al. 2016), root-related traits for enhancing drought tolerance (Chandra et al. 2004; Varshney et al. 2014a), ascochyta blight resistance (Aryamanesh et al. 2010; Cho et al. 2004; Varshney et al. 2014b), fusarium wilt resistance (Sharma et al. 2004; Sharma et al. 2005; Tekeoglu et al. 2000), botrytis gray mold resistance (Anuradha et al. 2011), seed yield traits under salinity (Pushpavalli et al. 2015) and normal growing conditions (Gowda et al. 2011),

double podding (Rajesh et al. 2002; Cho et al. 2002; Ali et al. 2010), flower color, and several other traits. Among these traits, practical application of QTLs identified for improving drought tolerance, fusarium wilt, and ascochyta blight diseases has been successfully demonstrated using marker-assisted backcrossing (MABC).

Improvement of Drought Tolerance

In case of drought tolerance, multi-disciplinary activities were converged to improve the response of chickpea to drought stress conditions. The architecture and function of the root system are expected to directly relate to the transpiration efficiency (TE) which in turn is responsible for water balance in the plant during moisture stress conditions. The results indicated that increasing drought tolerance via deep roots along with higher TE was the key trait most likely to give higher grain yield under drought stress conditions (Soltani et al. 2000). Even though roots play a vital role in the extraction of water from the soil layers, very less information about the extent of variation and genetic behavior of these traits was revealed. The reason is obvious that phenotyping of these traits is highly labor-intensive and high influence of growing conditions on the results recorded.

Efforts from physiologists led to the identification of large variation for various root-related traits in the germplasm (Kashiwagi et al. 2005) and RILs (Serraj et al. 2004) that help reduce the negative effects of drought. In this direction, the root length density (RLD) in relatively shallow soil layers and the maximum root depth (RDp) were found to positively influence the seed yield under terminal drought environments (Gaur et al. 2008). One RIL population from Annigeri x ICC 4958 cross was developed and phenotyped for root traits (Serraj et al. 2004). Further, based on the results from screening of chickpea germplasm, two intraspecific mapping populations, namely ICC 4958 × ICC 1882 and ICC 283 × ICC 8261, were developed at ICRISAT (Gaur et al. 2008). These populations were evaluated at multi-locations over multi-seasons in India and genotyped with SSR markers. Results showed that a genomic region referred as "*QTL-hotspot*" showing 58.20% phenotypic variation for 12 drought tolerance-related traits including root traits was identified on CaLG04 (Varshney et al. 2014a). The "*QTL-hotspot*," validated in both RIL populations, increased the confidence of chickpea breeders to introgress this genomic region into popular chickpea cultivars for enhancing drought tolerance.

MABC aims to transfer one or more genes/QTLs of interest from one genetic background into popular or elite cultivar to improve the targeted trait. In this direction, chickpea varieties, JG 11, ICCV 10, and KAK 2 from India and Chefe from Ethiopia, were selected to introgress this genomic region from ICC 4958 genotype using MABC scheme. After making three backcrosses and selfing for 4 generations, more than 20 BC_3F_4 introgression lines were developed in each background of JG 11 and ICCV 10. A number of plants selected in each generation for making crosses and the markers used in the foreground and background selection for improving JG 11 were reported in Varshney et al. (2014a). These lines were evaluated at multi-locations for two years during 2011–2014 in India. Several lines giving at least 10% higher seed yield than recurrent parents (JG 11 and ICCV 10) were identified under both rainfed and irrigated conditions. Location-specific genotypes identified and very few genotypes found common in the top yielding lines due to high influence of environment. Interestingly, there was no relationship between yield under rainfed and irrigated conditions. Further, the seed size of most of the lines was increased which is similar to donor parent (ICC 4958). It indicates that the QTL-hotspot region was also influencing/close to genes controlling seed size in ICC 4958.

Heat Stress Tolerance

Increase in temperatures due to global warming reduces accumulation of assimilates, enhances

leaf senescence, disturbs fertilization activities, and thus drastically reduces seed yield of crops, especially in combination with drought stress. As a result, plants show shortened life cycles, less time for photosynthesis (Reynolds et al. 2010), a shorter reproductive phase, and lower yield potential (Ainsworth and Ort 2010).

Being adapted to cool-season environments, cultivation of chickpea under increased day and night temperatures is a big challenge ahead. Recent screening efforts identified several heat-tolerant genotypes in chickpea (Wang et al. 2006; Krishnamurthy et al. 2011; Upadhyaya et al. 2011; Devasirvatham et al. 2012; Gaur et al. 2015). The ability of heat tolerance varies with cultivars and could involve changes in both morphological and physiological traits (Karim et al. 2000; Kumar et al. 2012), and therefore, heat-tolerant genotypes could be of great promise toward achieving stable yields under increasing temperatures. In this direction, a recent study was conducted to identify genomic regions related to heat tolerance in $F_{8–9}$ recombinant inbred line (RIL) population of the cross ICC 4567 (heat sensitive) × ICC 15614 (heat tolerant). Phenotypic evaluation was done under field conditions with no stress and heat stress treatments. Genotyping-by-sequencing (GBS) approach based on 271 single nucleotide polymorphisms (SNPs) covering the whole genome of chickpea was used for genotyping. The QTL analysis revealed two consistent genomic regions harboring eight QTLs on CaLG05 and CaLG06. Four major QTLs for number of filled pods, number of seeds, grain yield, and % pod setting, located in the CaLG05 genomic region, were found to have cumulative phenotypic variation of above 50%. Moreover, QTL × environment interaction effects were non-significant except for harvest index and biomass (Pronob Paul, personal communication). Validation of these QTLs in other populations is in progress, and once these are validated, MAS can be effectively implemented in regular breeding programs for enhancing heat tolerance.

Enhancement of Genetic Diversity Through MAGIC (Multi-parent Advanced Generation Intercrossing) Lines

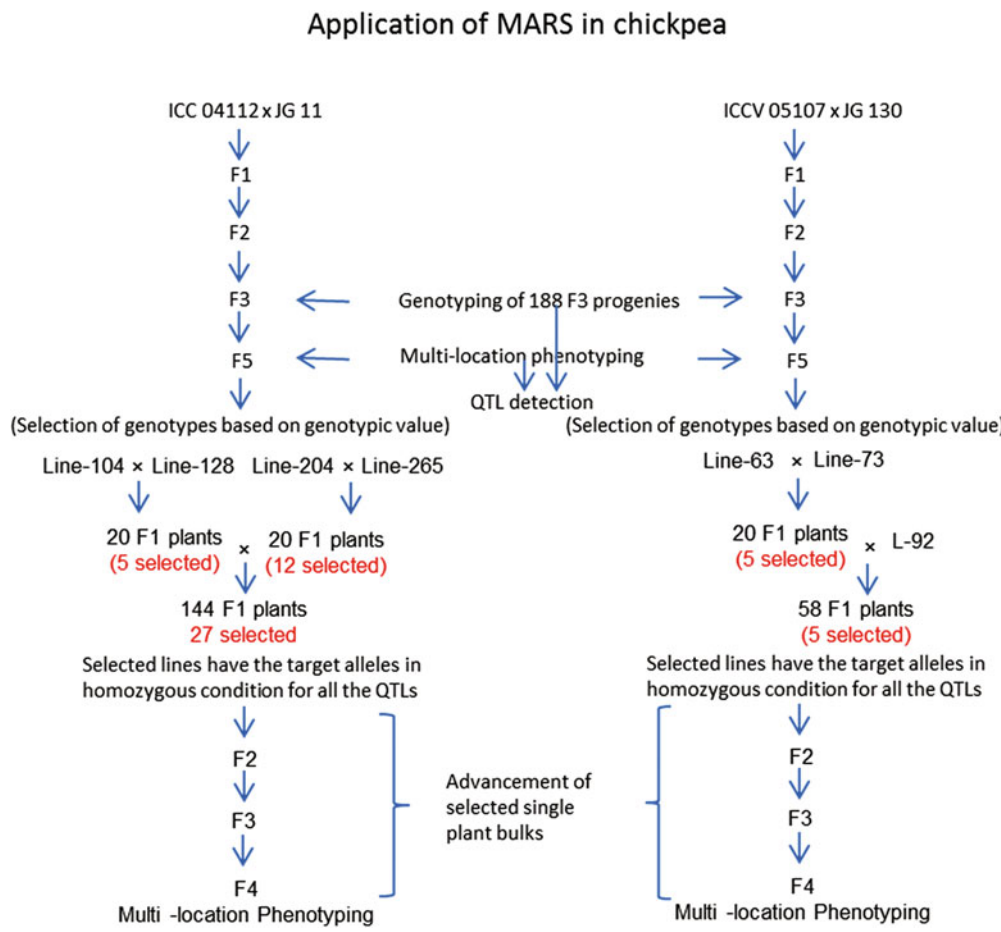
The existence of genetic diversity in the breeding populations is crucial to develop new varieties with resistance to various biotic and abiotic stresses. Using different hybridization techniques, plant breeders create variability for various traits of economic importance, which will expose the rare or important alleles in homozygous condition. In this direction, MAGIC lines were developed in chickpea using eight diverse genotypes selected from South Asia and sub-Saharan Africa. In this development scheme, more number of recombinations and greater genetic diversity in MAGIC lines greatly help in detection of QTLs with high precision. Further, these lines can be used directly in breeding programs for the development of cultivars suitable to diverse agro-ecologies in Asia and sub-Saharan Africa. The incorporation of multiple parents ensures the population segregates for multiple QTLs for multiple traits. Further, MAGIC lines can act as a base for gene discovery, characterization, and deployment of genes for understanding complex traits (Glaszman et al. 2010). The power of such populations has been demonstrated in maize to understand the genetic architecture of several traits (Buckler et al. 2009; Poland et al. 2011).

The parents (ICC 4958, ICCV 10, JAKI 9218, JG 11, JG 130, JG 16, ICCV 97105, and ICCV 00108) of the MAGIC lines from Ethiopia, Kenya, and India were crossed in direct fashion excluding reciprocals. Twenty-eight two-way, 14 four-way, and 7 eight-way crosses were made to develop a MAGIC population. Over 1200 F_2 plants from 7 eight-way crosses were advanced to F_8 using single seed descent (SSD) method and seed was harvested from 1136 $F_{7:8}$ progenies. These progenies were evaluated for two years (2013 and 2014) under field conditions with rainfed and irrigated treatments. Large

variability in phenology (days to flowering: 34–69 d) and yield-related traits (seed yield: 170–4554 kg/ha); 100 seed weight: 10–45 g) was observed under two treatments (Gaur et al. unpublished data). Several promising lines with significantly higher seed yield than the best parents were also identified. On the other hand, eight parents used in the development of MAGIC lines were genotyped using 70 SSR and 747 SNP markers. In addition, the parental lines were resequenced (with 5.79–16.08X coverage) and variable number of SNPs and indels were identified among the parental lines by aligning to CDC Frontier reference genome. The F_8 progenies were also genotyped for identification of diverse MAGIC lines based on haplotype distribution. MAGIC lines will be a valuable source for establishing marker-trait association using genome-wide association study (GWAS) for several complex traits in chickpea.

Marker-Assisted Recurrent Selection (MARS) for Yield Enhancement

Many complex traits are controlled by several minor QTLs. Gene pyramiding becomes very difficult as the number of QTLs increases, and in such cases, MABC has limited application. The more effective strategy would be to deploy MARS to increase the frequency of favorable alleles in the populations. This molecular breeding scheme differs from traditional QTL or MAS studies in that the new mapping study is conducted on each breeding population. This technology was developed first by major commercial maize breeding programs, and it has shown promising in increasing the rate of genetic gain. To evaluate the application of MARS scheme in self-pollinated crops such as chickpea, experiments were conducted with the support from Generation Challenge Program (GCP) during 2010–2014 at ICRISAT, Patancheru, India. Choice of populations was driven by yield performance of genotypes. Two crosses JG 11 × ICCV 04112 and JG 130 × ICCV 05107 were made to combine the favorable alleles of yield QTLs from the respective parents with an assumption that each population had a different set of QTLs involved. 188 F_3 plants each in two crosses were genotyped using SSR markers. Further, F_3-derived F_5 progenies were evaluated at multi-locations. QTL analysis of phenotyping and genotyping data resulted in identification of few major and several minor QTLs contributing to yield, and yield contributing traits (RK Varshney, personal communication). Based on the QTL(s) information for seed yield, harvest index, biomass, and seed size in different F_5 progenies, 4 lines were selected in JG 11 × ICCV 04112 and 3 lines in JG 130 × ICCV 05107 having different combinations of favorable alleles for recombination cycle. Multiple cycles of MARS increased the frequency of favorable marker alleles associated with agronomic traits. The selected lines were subjected to 1st and 2nd recombination cycles. F_1 plants (27 and 5) having all favorable alleles of QTLs from both parents for seed yield and other yield-related traits were identified in JG 11 × ICCV 04112 and JG 130 × ICCV 05107, respectively. Finally, F_1 plants with all favorable alleles in homozygous condition were grown. Each selected F_1 plant was advanced to F_4 generation separately for field evaluation. On the other hand, for comparing the advantage of MARS over the traditional method of recurrent selection, top 8 high-yielding F_5 progenies were also selected and intercrossing is being completed in each cross. Practical utility of this scheme in regular breeding programs will depend on the genetic gain achieved in terms of selection efficiency, selection accuracy, marker-trait associations, and distribution of favorable alleles between the selected parents used for crossing. Further, marker technology helps in the identification of individual plants having all favorable alleles among large populations when the number of *loci* of interest is higher, and in identifying whether the genotype combining favorable alleles is present in the population (Ishii and Yonezawa 2007). The utility of MARS decreases as the information of the number of small-effect QTLs associated with the trait decreases (Charcosset and Moreau 2004; Bernardo and Charcosset 2006). However, Bernardo and Charcosset (2006) reported that the higher genetic gain was feasible through MARS compared to MABC.



Introgression of Fusarium Wilt and Ascochyta Blight Resistance into Elite Cultivar

In chickpea, genes from different sources which confer resistance against fusarium wilt and ascochyta blight (*Ascochyta rabiei*) diseases have been successfully transferred and genotypes were developed with resistance to fusarium wilt and ascochyta blight diseases. Wilt is the most commonly occurring disease in warm and dry regions. Several stable sources of resistance were identified (Haware and Nene 1982; Nene et al. 1989; Pande et al. 2006) and successfully integrated into the backgrounds of high-yielding lines in the regular breeding programs for enhancing the wilt resistance. Further, the available field and laboratory screening technologies are cost-effective, yet reliable. However, availability of molecular markers associated with wilt resistance genes could accelerate the selection of resistant genotypes. Using the marker-assisted selection, markers tightly linked to wilt resistance genes can be used to screen a large number of genotypes for the presence of these genes. For example, SSR marker "TA59" has been used to tag genes for wilt resistance in the NIL development (Castro et al. 2010). Several studies suggest the existence of a genomic region harboring several resistance genes in linkage group 2 (LG2), including a cluster of six fusarium wilt resistance genes: foc-0, foc-1, foc-2, foc-3, foc-4, and foc-5 (Tekeoglu et al. 2000; Winter et al. 2000; Cobos et al. 2005; Milla´n et al. 2006; Sharma and Muehlbauer 2007; Halila et al. 2009). Identifying reliable race-specific

diagnostic markers will further enhance the application of molecular markers in regular breeding programs. These markers help in the identification of sources of resistance to different races simultaneously, which has been a difficult task under field screening.

Ascochyta blight (AB) is a major disease of chickpea, especially in areas where cool, and humid weather persists during the crop season. Several sources of resistance to AB were identified (Reddy and Singh 1984; Singh and Kapoor 1985; Singh and Reddy 1990). Breeding efforts at ICRISAT led to the development of varieties with moderate to good level of resistance to AB were released in the names of "Myles" and "Howzat" in USA and Australia, respectively. Genetic studies reported that AB resistance of chickpea is oligogenic in nature. Studies on RILs suggest that several genomic regions (QTLs) were involved in controlling resistance to AB dispersed on different linkage groups (LG2, LG3, LG4, LG6, and LG8) in the genome. LG4 has been reported by several researchers to contain QTLs for AB resistance (Santra et al. 2000; Tekeoglu et al. 2002; Cho et al. 2004; Stephens et al. 2014), while other reports highlight LG2 (Udupa and Baum 2003; Cho et al. 2004), LG3 (Flandez-Galvez et al. 2003b; Anbessa et al. 2009; Kanouni et al. 2009), and LG8 (Lichtenzveig et al. 2006). Markers closely linked to major QTLs have been reported. Two QTLs for pathotype II located on LG4, one is linked to markers CaETR or GAA47 and the other is linked to TA72/ScY17 (Udupa and Baum 2003; Cho et al. 2004). Furthermore, loci TS12b and STMS28 on LG1 and TS45 and TA3b on LG2 were found significantly associated with the disease reaction under controlled environments (Flandez et al. 2003a and b). Similarly, a codominant marker (CaETR) located in the QTLAR1 region of LG4 was also reported (Madrid et al. 2013). However, these markers linked to different AB QTLs need to be validated in diverse populations for their utility in regular breeding programs.

In this direction, an attempt was made to introgress the QTLs controlling FW and AB into a cultivar, C 214 (Varshney et al. 2014). In the foreground selection, six SSR markers (TR19, TA194, TAA60, GA16, TA110, and TS82) linked to foc-1 for FW, and eight markers (TA194, TR58, TS82, GA16, SCY17, TA130, TA2, and GAA47) linked to ABQTL-I and ABQTL-II for AB were used in MABC scheme. After three backcrosses, FW-resistant lines with more than 90% recovery and AB-resistant lines with more than 80% recovery of recurrent parent genome were selected. These lines need to be evaluated under field conditions for disease response and agronomic performance in multi-location trials for possible application of these markers.

11.3 Conclusion

New genomic advances, many of which are already being developed, will make it easier for breeders to obtain new cultivars with improved characteristics, either by facilitating selection or by improving the variation available by using precision breeding approaches. In particular, the present and new genomics tools add great value in the process of genetic dissection and breeding of complex traits. So far, the genomic tools played a key role in QTL identification, and their use in chickpea breeding programs is limited to improving drought tolerance. Identification of reliable diagnostic markers for several other important traits should be given more emphasis for rapid spreading of this technology in NARS breeding programs.

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