9 Requirement of Whole-Genome Sequencing and Background History of the National and International Genome Initiatives

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Abstract

Chickpea is the second most important grain legume for food and nutritional security in the arid and semi-arid regions of the world. The genome sequence provides the basis for a wide range of studies, from the important goal of accelerated breeding to identifying the molecular basis of key agronomic traits, in addition to understanding the basic legume biology. The discussions during 5th International Conference on Legume Genetics and Genomics, held during July 8–10, 2010 in Asilomar, USA, provided the platform for the genesis of International Chickpea Genome Sequencing Consortium (ICGSC http://ceg.icrisat.org/gt-bt/ICGGC/ICGSC.htm), and as result of global research partnership co-led by ICRISAT, UC-Davis, and BGI-Shenzhen, involving 49 scientists from 23 organizations in 10 countries the draft genome of kabuli genotype CDC Frontier was published. On the other hand, the Next Generation Challenge Programme on Chickpea Genomics (NGCPCG) initiative unraveled the genome sequence of desi genotype ICC 4958. This chapter summarizes the background history of two independent efforts to generate draft genome sequence of kabuli and desi chickpea genomes. In addition, the chapter also highlights key developments of application of genome sequence for crop improvement.

9.1 Introduction

The genus *Cicer* is a member of the monogeneric tribe *Cicereae* Alef; subfamily *Papilionaceae*, family *Leguminosae,* which includes 9 annual and 34 perennial species (van der Maesen 1987). Chickpea (*C. arietinum* L.) is the only *Cicer* species cultivated on a large scale, self-pollinated diploid ($2n = 2x = 16$) with a genome size

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of ~740 Mbp (Arumuganathan and Earle 1991). It is the second most important pulse crop in the world covering an area of 13.9 mha (FAO 2016). Two distinct chickpea types, different in their morphology and used in different ways of processing have been described: desi and kabuli. Desi-type chickpeas have purple flower and small, dark, and angular seeds; it is largely consumed in India and Pakistan. Kabuli chickpeas have white flower and large, cream-colored seeds; it is preferred in the Mediterranean Basin and Central Asia, mainly consumed as whole seed. The kabuli type constitutes only ~15% of global chickpea production, but good quality large-seeded kabuli chickpea are very much appreciated in the market and fetches three times higher price than desi cultivars. Although India is the largest producer, it imports chickpea from Australia, Canada, Mexico, Turkey, Ethiopia, etc., to cater the need of ever-growing population. Similarly, Spain also needs to import approximately double than the Spanish chickpea production (FAO 2010). This is because of low productivity (<1 tons per hectare) as a result of exposure of the crop to a number of abiotic stresses such as drought, salinity, and biotic stresses (e.g., Fusarium wilt (FW) and Ascochyta blight (AB)).

9.2 Need for Draft Genome Sequence

Increasing and stabilizing the seed yield while minimizing inputs is the major aim of chickpea breeding. This goal can be achieved by developing cultivars better adapted to stresses in local environments. The recent developments in high-throughput or next-generation sequencing (NGS) technologies are opening up a wealth of possibilities for pulse breeding. A reference chickpea genome sequence provides a foundational resource for this important crop which also possesses a relatively modest genome size (~740 Mb). Availability of genome sequence information will dramatically accelerate complete identification of genomic variations as it is easy to generate re-sequence data from different genotypes which can be aligned with the reference genome and then be linked with phenotypes, to obtain biological insights as well as for breeding applications. In addition, the reference genome will aid in elucidation of complex genetic interactions in chickpea, which in turn facilitates pulse geneticists and breeders to develop a full understanding of the variations found in each genotype. Analyses beyond sequencing include finding candidate gene(s), variation for traits related to nutritional quality, bioactive compounds and bioavailable micronutrients in chickpea, will enable integration of these outputs into the applied pulse breeding activities like (a) selection of parents for crossing, (b) screening the early generations for the desired genotypes that contain all (or the majority of) favorable alleles, and (c) integration of the selected lines into elite cultivar development.

This chapter summarizes the background history of two independent efforts to generate draft genome sequence of kabuli and desi chickpea genomes. International Chickpea Genome Sequencing Consortium (ICGSC) was led by ICRISAT to decode the draft genome of kabuli genotype CDC Frontier, while The Next Generation Challenge Programme on Chickpea Genomics (NGCPCG) unraveled the genome sequence of desi genotype ICC 4958.

9.3 ICGSC Efforts to Unravel Draft Genome Sequence of CDC Frontier Genotype

Discussions initiated during the 5th International Conference on Legume Genetics and Genomics (ICLGG), held during July 8–10, 2010 in Asilomar, USA, led to the development of one consortium named as "International Chickpea Genome Sequencing Consortium (ICGSC)" co-led by ICRISAT, UC-Davis and BGI-Shenzhen, with the main objective of decoding the genome sequence information and making it available to chickpea research community. ICGSC comprised of seven leading research institutes of the world that have extensive expertise in both basic as well as applied genomics of chickpea.

CDC Frontier, a high yielding medium seeded kabuli chickpea variety was selected for developing the genome sequence. This variety was developed at University of Saskatchewan, Canada from the cross FLIP 91-22C × ICC 14912 in 1993. While FLIP91-22C was developed by the International Center for Agricultural Research in the Dry Areas (ICARDA), in Aleppo, Syria, and ICC 14912 was developed by the ICRISAT, India.

9.4 Consortium Partners and Strengths

ICRISAT with a global mandate to improve chickpea crop has lead the efforts of unraveling the draft genome of chickpea. For >40 years, ICRISAT has been engaged in pre-breeding research and has been sharing the breeding lines with national partners for their evaluation and release of the varieties in the targeted zones/countries. ICRISAT, in collaboration with its partners developed significant amount of genetic and genomic resources as given in Tables 9.1 and 9.2. For instance, large-scale SSR markers, SNP markers, DArT markers, several inter- and intra-specific genetic maps and QTL maps have been developed. ICRISAT has developed genome-wide physical map of chickpea in collaboration with UC-Davis and National Institute of Plant Genome Research (NIPGR), India (Varshney et al. 2013). The ICRISAT genebank has the largest collection of 20,267 accessions in genus *Cicer* from 60 distinct countries across five continents (Asia, Africa, Americas, Europe, and Oceania-pacific) including 308 accessions of 18 (eight annual and ten perennial) wild *Cicer* species.

University of California, Davis, USA—The research group led by Douglas Cook, possessed extensive expertise in the areas of comparative and structural genomics of the legume family and transcriptional profiling. They have a special focus to understand the molecular and genetic basis of symbiotic nitrogen fixation and legume–pathogen interactions. Apart from this, UC-Davis in collaboration with ICRISAT under Phase I of Tropical Legumes I, funded by Bill and Melinda Gates Foundation contributed to develop numerous SNPs (based on Sanger, 454 and Solexa re-sequencing, as well as an Illumina SNP GoldenGate platform); large collections (∼2800) of SSRs; bacterial artificial chromosome (BAC) libraries and >30 Mbp of BAC-end sequence information at NCBI; a comprehensive inventory of >400 NBS-LRR disease resistance genes.

BGI-Shenzhen, China is a premier genomics research organization, with a goal for developing projects and platforms that are on the cutting edge of research and technologies. Further, they focus on developing all kinds of applications, including de novo sequencing and assembly of plant and animal genomes, large-scale genome re-sequencing, genetic association studies, gene expression profiling, whole transcriptome assembly, miRNA detection, ChIP-Seq studies, DNA methylation characterization and metagenomics.

University of Saskatchewan, Canada—The Crop Development Centre (CDC) at University of Saskatchewan developed more than 15 kabuli and desi varieties that have been released in Canada. In addition, several cultivars of specific market classes such as green and black desi and green cotyledon kabuli have been released. University of Saskatchewan has a breeding program that focuses on enhancing yield, resistance to AB, earliness, grain visual, and processing qualities. Steady gains in yield potential together with the improvement in resistance to AB have been achieved over the past decade. Many recently released cultivars yield up to 20% or more than those that were released in mid-1990s. Molecular breeding efforts to develop improved genotypes for AB are underway (Tar'an et al. 2007a, b). Seed qualities like seed size, shape, and seed coat color were main focus and have been working in collaboration with ICRISAT, France and Australia for developing inter-specific hybrids in chickpea. In terms of genomics research, identified several SNPs from 454 sequencing of various tissues of CDC Frontier. The CDC chickpea breeding program has developed a number of populations to facilitate studying of AB blight disease resistance and others in chickpea (Table 9.3).

Table 1 Genetic resources developed at ICRISAT

Cross	Generation	No. of RILs	Segregating traits/significance
Mapping populations			
ICC 4958 × ICC 1882	F_{10+}	264	Root traits
ICC 283 × ICC 8261	F_{10+}	281	Root traits
Annigeri × ICC 4958	F_{10+}	257	Root traits
ICCV 2 × JG 11	F_3	290	Salinity tolerance
ICC 6263 × ICC 1431	F_6	286	Salinity tolerance
ICC 506-EB × Vijay	F_9	328	*Helicoverpa* resistance
ICC 3137 × IG 72953	F_5	244	*Helicoverpa* resistance
ICC 3137 × IG 72933			*Helicoverpa* resistance
ICCV 2 × JG 62	F_{10+}	573	Fusarium wilt resistance, Botrytis gray mold resistance, *Helicoverpa* resistance and salinity tolerance
WR 315 × C104	F_{10+}	84	Fusarium wilt resistance
ICCV 2 × ICC 1496	F_8	249	Botrytis gray mold resistance
ICCV 10 × ICC 1496	F_8	250	Botrytis gray mold resistance
Pb 7 × ICCV 04516	F_4	281	Ascochyta blight resistance
ICC 995 × ICC 5912	F_6	246	Protein content
MABC populations			
JG 11 × ICC 4958	BC_3F_2		For enhancing drought tolerance
ICC 92318 × ICC 8261	BC_3F_2		For enhancing drought tolerance
KAK 2 × ICC 8261	BC_3F_2		For enhancing drought tolerance
MARS populations			
JG 11 × ICCV 04112	F_5	188	For accumulation of favorable alleles for drought tolerance
JG 130 × ICCV05107	F_5	188	For accumulation of favorable alleles for drought tolerance

Table 2 Genomic resources developed by ICRISAT and its partners

Marker resources			Transcriptomic resources
SSRs	SNPs	DArT	
311 from SSR-enriched library (in collaboration with University of Frankfurt, Germany); 1344 from BAC-end sequences (in collaboration with UC-Davis, USA)	9,000 identified and 768 on GoldenGate assay (in collaboration with UC-Davis, USA, NCGR, USA)	Ca. 5,000 extended array with 15,360 (in collaboration with DArT Pty Ltd, Australia)	20,665 Sanger ESTs; 435,018 454/FLX reads; 103,215 TUSs; and ~118 million Solexa reads (in collaboration with NCGR, USA and UC-Davis, USA)

Table 3 RIL populations and polymorphic traits available at University of Saskatchewan

Cross	Polymorphic traits/markers[a]	Reference
ILC 72 × Cr 5-10	Blight, *B/b*, *Tt*, *Hg*, Isoenz, cross-genome markers, ISSR, RAPD, STMS	Cobos et al. (2006)
ICCL 81001 × Cr 5-9	*B/b*, *Fs*, FOC5, *Hg, Rt, Df,* ISSR, RAPD, STMS	Cobos et al. (2009)
ILC 3279 × WR315; WR 315 × ILC 3279	*Blight, B, FOC5, RAPD, SCAR, STMS*	Iruela et al. (2006, 2007)
CA 2139 × JG 62	*B/b, Tt, Sfl, FOC0, ISSR, RAPD, STMS*	Cobos et al. (2005, 2007) Halila et al. (2009)
CA2156 × JG62	*B/b, Tt, Sfl, FOC0, ISSR, RAPD, STMS*	Cobos et al. (2005)

[a]*FOC* Fusarium wilt resistance genes; *B* flower color (*pink/white); f* days to flower
g 100 seed weight; *Gh* Growth habit; *LS* length of the seed; *SC* seed color; *Sfl* and *s*: single/double pod; *STC* stem color; *Tt* testa thickness

CSIRO/University of Western Australia/ Curtin University, Australia—Dr. Karam Singh's group had world leading expertise on biotic stresses in legumes and highly relevant expertise on crop and patho-genomics. The Australian group has made excellent use of the model legume *Medicago truncatula* to progress legume disease and pest research. Of high relevance to this effort is their expertise on the major fungal pathogens of chickpea worldwide namely *Ascochyta rabiei* and *Fusarium oxysporum*. In the case of *A. rabiei,* they have generated a genome sequence using NGS technology involving Illumina 75 bp paired-ends reads at ~23X coverage and have identified ~12,000 protein encoding genes. In the case of *F. oxysporum,* they have generated the sequence of a medic isolate again using NGS technology. This group also has excellent expertise on another economically important soil-borne fungal pathogen, *Rhizoctonia solani*, which is an important problem for chickpea. They identified key transcriptional regulators in *M. truncatula* that can give high levels of resistance to *R. solani* when overexpressed in the roots of composite plants without any deleterious effects on plant growth (Anderson et al. 2010).

University of Córdoba/IFAPA, Spain—The research group in Córdoba (IFAPA and Univ. of Córdoba, Spain) has been running plant breeding programmes focused in obtaining new cultivars, better adapted to Mediterranean conditions together with the quality required in Spanish market. Integration of marker-assisted selection (MAS) in traditional breeding programs accelerates the achievement of productive cultivars. Involved in chickpea map development (Millán et al. 2010) but still it is necessary to target some agronomic traits or saturate genomic areas in order to have useful makers for MAS. Development of trait-specific germplasm for instance, recent development of near isogenic lines (NILs) differing in resistance for FW could facilitate the identification of different genes (Castro et al. 2010) and race-specific resistance to *F. oxysporum*. The most significant QTLs involved in AB resistance are two genomic regions in LG4 enclose two clearly differentiated QTLs (QTL1 and QTL2) more than 30 cM apart. Efforts to find candidate genes for QTL1 and QTL2 have been attempted (Iruela et al. 2009). Other traits like bushy growth habit and double-podded mutation also have a positive effect on yield and yield stability in chickpea crop under Mediterranean conditions (Rubio et al. 1998, 2004). Both traits are controlled by a single gene: simple/double pod (*S/s* or *Sfl/sfl*) and erect/bushy habit (*Gh/gh*) (Muehlbauer and Singh 1987).

National Centre for Genome Resources (NCGR), Santa Fe, USA has a worldwide

reputation for sequencing and the development of custom bioinformatic resources for research communities. The NCGR Sequencing Center undertakes massively parallel sequencing services using Illumina® (Solexa) Genome Analyzer and ABI SOLiD4 instruments and also provides genotyping, the gold standard for high-throughput SNP screening, and supplies software tools and services for analysis of genome and transcriptome projects worldwide. NCGR contributed to informatics and data analysis of chickpea genome sequences data.

Above-mentioned institutes were the part of ICGSGC (http://ceg.icrisat.org/gt-bt/ICGGC/ICGSC.htm). The key scientists from each institute leveraged resources from various funding organization including the CGIAR Generation Challenge Programme (GCP), US National Science Foundation (NSF), Saskatchewan Pulse Growers (Canada), Grains Research & Development Corporation (Australia), Indo-German Science Technology Corporation (Germany and India), National Institute for Agricultural and Food Research and Technology (Spain), National Research Initiative of US Department of Agriculture's National Institute of Food and Agriculture (USA), Ministry of Education, Youth and Sports of the Czech Republic and the European Regional Development Fund, University of Cordoba, ICAR (India), BGI (China) and ICRISAT for decoding the genome sequence of chickpea.

9.5 Efforts of NGCPCG to Unravel the Genome Sequence of ICC 4958 a *Desi* Genotype

NGCPCG was initiated by a group of nine NIPGR scientists, with three main objectives: (1) Chickpea genome sequence analysis and its alignment to genetic map; (2) Functional genomics of stress tolerance in chickpea; (3) Functional genomics of chickpea seed development and nutrition. The NGCPCG is purely the work of scientists belonging to just one Indian institute, the NIPGR. The NGCPCG, apart from deciphering the genes, had also worked on finding markers distributed all over the genome which could be used by plant breeders for creation of better variety of chickpea. Complexity of the genome is very high, and it reflects on the nature of biological evolution that there has been more than one line of evolution. The chickpea cultivar ICC4958 was used for generating the draft genome.

9.6 Announcement of Chickpea Genome

Chickpea draft genome sequence decoded was published on January 27, 2013, in a high impact factor Journal "Nature Biotechnology." This was the result of global research partnership led by ICRISAT, involving 49 scientists from 23 organizations in 10 countries. This genome sequence breakthrough was announced by Mr. Ashish Bahuguna, the then Secretary, Department of Agriculture & Cooperation, Dr. Swapan Datta, the then Deputy Director General, Crop Science, ICAR, Dr. William Dar, the then Director General, ICRISAT, and Dr. Rajeev K. Varshney, Coordinator, ICGSC on January 28, 2013 in Krishi Bhawan, New Delhi (Fig. 9.1).

During the press conference announcing the decoding of the chickpea genome sequence at Krishi Bhavan, New Delhi, the then Director General Dr. Dar said, "In the face of growing global hunger and poverty amid the threat of climate change, the chickpea genome sequence will facilitate the development of superior varieties that will generate more income and help extricate vulnerable dryland communities out of poverty and hunger for good, particularly those in the drylands of Asia and sub-Africa for whom ICRISAT and our partners are working." In addition Mr. Ashish Bahuguna, the then Secretary, Ministry of Agriculture, Government of India, recognizing the efforts of the global research team, said, "Decoding of the chickpea genome would facilitate the development of

Fig. 1 (Left–Right) Dr. Swapan Datta, the then DDG (Crop Science), ICAR; Mr. Ashish Bahuguna, the then Secretary, Ministry of Agriculture, Government of India; Dr. William Dar, the then Director General, ICRISAT; and Dr. Rajeev K. Varshney, coordinator of ICGSC and Director—Center of Excellence in Genomics, ICRISAT during the press conference announcing the decoding of the chickpea genome sequence at Krishi Bhavan, New Delhi

improved varieties with higher yields and greater tolerance to biotic and abiotic stresses. This would help chickpea farmers to increase productivity, reduce cost of inputs, and realize higher incomes." He added: "This development is of great importance to India, the largest producer and consumer of chickpea." Dr. Swapan Datta, the then Deputy Director General—Crop Science, Indian Council of Agricultural Research (ICAR), highlighted that "The chickpea genome sequence is expected to help in the development of superior varieties with enhanced tolerance to drought and resistance to several biotic stresses. India will benefit most from this genome sequence, our country being the largest producer of chickpea. This, in my opinion, is by far the most significant collaboration between ICAR, ICRISAT, and the global genomics community." While addressing the addressing the media during the press conference Dr. Rajeev K. Varshney, mentioned that "Genetic diversity, an important prerequisite for crop improvement, is very limited and has been a serious constraint for chickpea improvement. This study will provide not only access to "good genes" to speed up breeding but also to genomic regions that will bring genetic diversity back from landraces or wild species to breeding lines. Currently, it takes 4–8 years to breed a new chickpea variety. This genome sequence could reduce by half the time to breed for a new variety with market-preferred traits." Prof. MS Swaminathan, Member of Indian Parliament and renowned agricultural scientist said, "I would like to compliment the excellent scientific work done by Rajeev K. Varshney of ICRISAT and his colleagues in developing a high-quality genome sequence of chickpea. I am confident that the knowledge provided by this study will help accelerate the improvement of this crop through marker-assisted breeding."

9.7 A Road Map for Chickpea Improvement

Genome sequence will play a crucial role in speeding up the development of improved varieties that will ensure the food and nutritional security and enhance the income for small holder farmers. In addition, genome sequence also provides the basis for a wide range of studies, from the important goal of accelerated breeding to identifying the molecular basis of key agronomic traits, in addition to understanding the basic legume biology. In addition to developing superior varieties tolerant to drought, heat, *Fusarium* wilt and *Ascochyta* blight, genome sequence can also be used to develop early maturing varieties as well as varieties amenable for mechanical harvesting so that chickpea varieties can be introduced to new niches and drudgery of women can also be reduced. This would help chickpea farmers to increase productivity, reduce cost of inputs and realize higher incomes. Based on the discussions with higher officials and extensive consultations with stakeholders, a road map was developed for enhancing chickpea productivity in India.

For utilizing the genome sequence information of chickpea, Department of Agriculture and Cooperation, Ministry of Agriculture, Government of India funded a project entitled "Utilizing chickpea genome sequence for crop improvement" to a consortium of leading chickpea breeders and genomics scientists from different institutes like ICRISAT, ICARDA—New Delhi, Indian Institute of Pulses Research (IIPR)—Kanpur, Rajmata Vijayaraje Scindia Krishi Vishwa Vidyalaya (RVSKVV), RAK College of Agriculture (RAKCA), Sehore, MP, India, and Rajasthan Agricultural Research Institute (RARI)—Durgapura, Junagadh Agricultural University (JAU)—Junagadh. This project had a major emphasis on (i) identification of superior lines, (ii) integrate genomic selection (GS) approach in chickpea breeding, (iii) identification of molecular markers associated with trait of interest for chickpea using nested association mapping (NAM) and linkage mapping approach, and (iv) mapping of targeted traits and harnessing the germplasm diversity using genome-wide association study (GWAS) approach. Similarly, Indo-Australian Biotechnology Fund (IABF) and Department of Biotechnology, Government of India jointly funded a project entitled "Improving Chickpea Adaptation to Environmental Challenges in Australia and India." This proposal is a collaboration between ICRISAT, Indian Agricultural Research Institute (IARI), India, South Australian Research and Development Institute, Australia, and The University of Western Australia, Australia. The project has a major focus on identification and delivering genetic improvements in chickpea that will support breeding for enhanced abiotic and biotic stress.

9.8 Conclusion

In the year 2010, ICGSGC came into existence with main objective of decoding the chickpea genome sequence, and as a result of efforts of the consortium, the genome sequence was made public in 2013. Ever since the genome sequence information is available to chickpea research community, there have been efforts to utilize this information for crop improvement. For instance, the funding organizations like Department of Agriculture and Cooperation, Ministry of Agriculture, Government of India, Indo-Australian Strategic Research Fund have already encouraged research groups that are making use of chickpea genome sequence and re-sequence information for developing the climate resilient chickpeas.

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