





Integrated breeding approaches for improving drought and heat adaptation in chickpea (*Cicer arietinum* L.)

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Abstract

Chickpea (*Cicer arietinum* L.) is a dry season food legume largely grown on residual soil moisture after the rainy season. The crop often experiences moisture stress towards end of the crop season (terminal drought). The crop may also face heat stress at the reproductive stage if sowing is delayed. The breeding approaches for improving adaptation to these stresses include the development of varieties with early maturity and enhanced abiotic stress tolerance. Several varieties with improved drought tolerance have been developed by selecting for grain yield under moisture stress conditions. Similarly, selection for pod set in the crop subjected to heat stress during reproductive stage has helped in the development of heat-tolerant varieties. A genomic region, called *QTL-hotspot*, controlling several drought tolerance-related traits has been introgressed into several popular cultivars using marker-assisted backcrossing (MABC), and introgression lines giving significantly higher yield than the popular cultivars have been identified. Multiparent advanced generation intercross (MAGIC) approach has been found promising in enhancing genetic recombination and developing lines with enhanced tolerance to terminal drought and heat stresses.

KEYWORDS

Cicer arietinum, climate change, early maturity, high temperature, moisture stress, molecular breeding

1 | INTRODUCTION

Chickpea (*Cicer arietinum* L.) is the second most important pulse crop globally, grown in an area of about 12.6 million ha across 55 countries (FAOSTAT, 2016). It is highly valued for its nutritional quality and health benefits and ability to improve soil fertility and sustainability of the cropping systems. Chickpea is an excellent source of protein, carbohydrate, dietary fibres, polyunsaturated fatty acids, minerals and vitamins (Jukanti, Gaur, Gowda, & Chibbar, 2012). It is also considered as a high energy and protein feed in animal diets (Bampidis & Christodoulou, 2011).

During the last decade (2004–06 to 2014–16), overall global chickpea production increased by 44% due to 23% increase in area and 17% increase in yield (FAOSTAT, 2016) (Table 1). Among the top 12 chickpea producing countries, remarkable increase in chickpea production occurred in Russian Federation (1189%), Australia (326%), Tanzania (222%), Ethiopia (141%), United States (141%), Myanmar (106%) and India (47%). Several of these countries, such as Ethiopia (2.0 t/ha), Canada (1.8 t/ha), Mexico (1.7 t/ha), Myanmar (1.5 t/ha), Australia (1.3 t/ha) and Turkey (1.2 t/ha), made impressive progress also in productivity of chickpea. India is the largest producer of chickpea with a share of about 69% in area and 68% in the production in the world. India continued to remain a major importer of desi chickpea (thick and coloured seed coat, mostly brown), but has emerged as a major exporter of kabuli chickpea (thin and cream coloured seed coat) during the past decade.

The chickpea crop is largely grown under rainfed conditions without irrigations. Thus, soil moisture deficit towards end of the crop season (terminal drought) is the most important abiotic stress in about two-thirds of the global chickpea area (Gaur, Krishnamurthy, & Kashiwagi, 2008). Varieties with improved drought avoidance (dehydration postponement) and/or drought tolerance (dehydration resistance) abilities are needed for improving grain yield under drought stress (Gaur, Krishnamurthy et al., 2008). Drought avoidance can be achieved by water uptake by the roots from deeper soil layers, by osmotic adjustment and by reducing water loss (stomata conductance or by reduction in leaf area), while drought tolerance comes from the ability of cells to continue metabolism at low leaf water status (Turner, 2003).

Chickpea being a cool season food legume suffers heavy yield losses when exposed to heat stress at reproductive (flowering and podding) stage (Devasirvatham, Gaur, Raju, Trethowan, & Tan, 2015; Devasirvatham, Tan, Gaur, Raju, & Trethowan, 2012; Devasirvatham, Gaur et al., 2012; Devasirvatham et al., 2013; Gaur, Jukanti et al., 2014; Gaur, Samineni, Krishnamurthy et al., 2015). The optimal temperatures for chickpea growth and reproductive phase range between 10°C and 30°C. High temperature during the reproductive stage causes a greater problem than at the seedling or vegetative phase. A few days of exposure to high temperatures ($\geq 32^{\circ}\text{C}$) during reproductive phase can cause heavy yield losses.

The frequency and severity of drought and heat stresses are further expected to increase due to increasing climatic variability and

overall impacts of climate change. Varieties with enhanced tolerance to drought and heat stresses are needed for increasing and stabilizing chickpea production in the country. Considerable progress has been made in breeding drought and heat-tolerant varieties and early maturing varieties that escape these stresses. This review provides an update on the research progress made in these areas.

2 | EARLY MATURITY FOR ESCAPING TERMINAL DROUGHT AND HEAT STRESSES

Early phenology (early flowering, early podding and early maturity) is the most important mechanism to escape terminal drought stress (Gaur, Krishnamurthy et al., 2008; Gaur, Kumar et al., 2008). Chickpea breeding at ICRISAT and in Indian national programme has placed high emphasis on the development of early maturing varieties for enhancing adaptation of chickpea to environments prone to predictable terminal drought stress. There is a wide variability for time to flowering in chickpea germplasm (Figure 1), which provides opportunity for developing chickpea cultivars with desired earliness. Four genes for early flowering (*efl*) have been reported in chickpea. These are *efl-1* from ICCV 2 and ICCV 96029 (Gaur, Samineni, Tripathi, Varshney, & Gowda, 2015; Hegde, 2010; Kumar & van Rheenen, 2000), *ppd* or *efl-2* from ICC 5810 (Hegde, 2010; Or, Hovav, & Abbo, 1999), *efl-3* from BGD 132 (Gaur, Samineni, Tripathi et al., 2015; Hegde, 2010) and *efl-4* from ICC 16641 and ICC 16644 (Gaur, Samineni, Tripathi et al., 2015). Studies on allelic relationships of flowering time genes indicated that these four early flowering genes (*efl-1*, *efl-2*, *efl-3* and *efl-4*) are nonallelic (Gaur, Samineni, Tripathi et al., 2015). The results of these studies 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 (Gaur, Samineni, Tripathi et al., 2015).

A study was conducted on molecular mapping of genes/QTLs controlling flowering time in chickpea using F_2 populations from four biparental crosses. The crosses involved four early flowering lines, ICCV 96029, ICC 5810, BGD 132 and ICC 16641, which flower in 25 to 29 days at Patancheru, Telangana, India (17°53' N latitude, 78°27' E longitude and 545 m altitude). Figure 1 shows differences in the podding of the early flowering line ICCV 96029 as compared to late flowering lines. The four early flowering lines were used as female parents and crossed with a common male parent 'CDC Frontier', a Canadian kabuli chickpea variety (Warkentin, Banniza, & Vandenberg, 2005) which is very late in flowering (takes about 65 days to flower at Patancheru). A consensus map spanning 363.8 cM with 109 loci was constructed by integrating four genetic maps. Genetic studies revealed monogenic control of flowering time in the crosses ICCV 96029 \times 'CDC Frontier', BGD 132 \times 'CDC Frontier' and ICC 16641 \times 'CDC Frontier', while digenic control with complementary gene action in ICC 5810 \times 'CDC Frontier'. Three major QTLs, Qefl1-

TABLE 1 Change in area, production and yield of chickpea during 2002–04 to 2014–16 in the world, different continents and major chickpea producing countries (FAOSTAT 2016)

	Average area (1,000 ha)		Share in global area during 2014–16 (%)	Change in area during 2004–06 to 2014–16 (%)	Average production (1,000 MT)		Share in global production during 2014–16 (%)	Change in production from 2004–06 to 2014–16 (%)	Average yield (kg/ha)		Change in yield from 2004–06 to 2014–16 (%)
	2004 –06	2014 –16			2004 –06	2014 –16			2004 –06	2014 –16	
<i>World and different continents</i>											
World	10,403	12,824		23.3	8,464	12,176		43.9	814	949	16.7
Asia	9,455	11,137	86.8	17.8	7,574	10,053	82.6	32.7	801	903	12.7
Oceania	147	537	4.2	264.0	161	686	5.6	325.7	1,094	1,279	16.9
Africa	496	614	4.8	23.8	365	759	6.2	107.9	735	1,235	68.0
Americas	219	282	2.2	28.7	298	429	3.5	44.2	1,356	1,520	12.1
Europe	85	254	2.0	198.7	67	249	2.0	273.2	786	982	24.9
<i>Major chickpea producing countries^a</i>											
India	6,886	8,837	68.9	28.3	5,587	8,226	67.6	47.2	811	931	14.7
Australia	147	537	4.2	264.0	161	686	5.6	325.7	1,094	1,279	16.9
Myanmar	232	371	2.9	59.9	275	567	4.7	106.2	1,184	1,527	29.0
Ethiopia	198	241	1.9	21.9	197	475	3.9	141.2	995	1,967	97.8
Turkey	561	366	2.9	–34.8	591	455	3.7	–23.0	1,052	1,244	18.2
Pakistan	1,035	966	7.5	–6.7	653	432	3.5	–33.9	631	447	–29.1
Iran	571	475	3.7	–16.8	292	213	1.8	–27.1	512	449	–12.3
Russian Federation	14	189	1.5	1,286.3	14	180	1.5	1,188.6	1,024	952	–7.0
Mexico	95	84	0.7	–11.2	134	144	1.2	7.3	1,410	1,703	20.7
USA	35	80	0.6	124.8	48	116	1.0	141.2	1,363	1,462	7.3
Canada	80	57	0.4	–27.8	106	104	0.9	–1.5	1,333	1,819	36.5
Tanzania	70	118	0.9	68.3	32	102	0.8	222.1	450	862	91.4

^aContribute to 96% of the global area and production of chickpea.



FIGURE 1 Chickpea breeding lines exhibiting wide variation in phenology. The middle line is the super early line ICCV 96029, which flowers in 28–30 days and matures in 75–85 days at Patancheru, India

2, Qefl3-3 and Qefl4-1, corresponding to flowering time genes *efl-1* from ICCV 96029, *efl-3* from BGD 132 and *efl-4* from ICC 16641 were mapped on CaLG04, CaLG08 and CaLG06, respectively

(Mallikarjuna et al., 2017). Four major QTLs, Qefl2-1, Qefl2-2, Qefl2-3 and Qefl2-4, for flowering time were identified in the cross ICC 5810 × ‘CDC Frontier’ on CaLG01, CaLG03, CaLG04 and CaLG08, respectively. Thus, it was not clear which of these QTLs corresponded to *efl-4* (Mallikarjuna et al., 2017).

Several early maturing high-yielding cultivars have been developed in chickpea. Under Tropical Legumes-II project, a large number of farmer-participatory varietal selection (FPVS) trials were conducted on short-duration varieties/elite lines to identify well-adapted farmers’ preferred varieties. In Andhra Pradesh state of India, JG 11 and JAKI 9218 were the most preferred varieties by farmers. Adoption of these varieties was enhanced through knowledge empowerment of farmers and enhancing availability of seed of these varieties. According to a survey conducted on the extent of adoption of chickpea varieties, the short-duration chickpea variety JG 11 covered about 82% of the chickpea area in Andhra Pradesh (Bantilan, Kumara, Gaur, Shyam, & Jeff, 2014). Improved chickpea varieties led to a more than six-fold increase in area cultivated with the crop. The productivity has doubled, rising by an average 38 kg/ha per year between 1996 and 97 and 2009 and 10 in Andhra Pradesh (Figure 2), compared with an average annual increase of 5 kg/ha for the

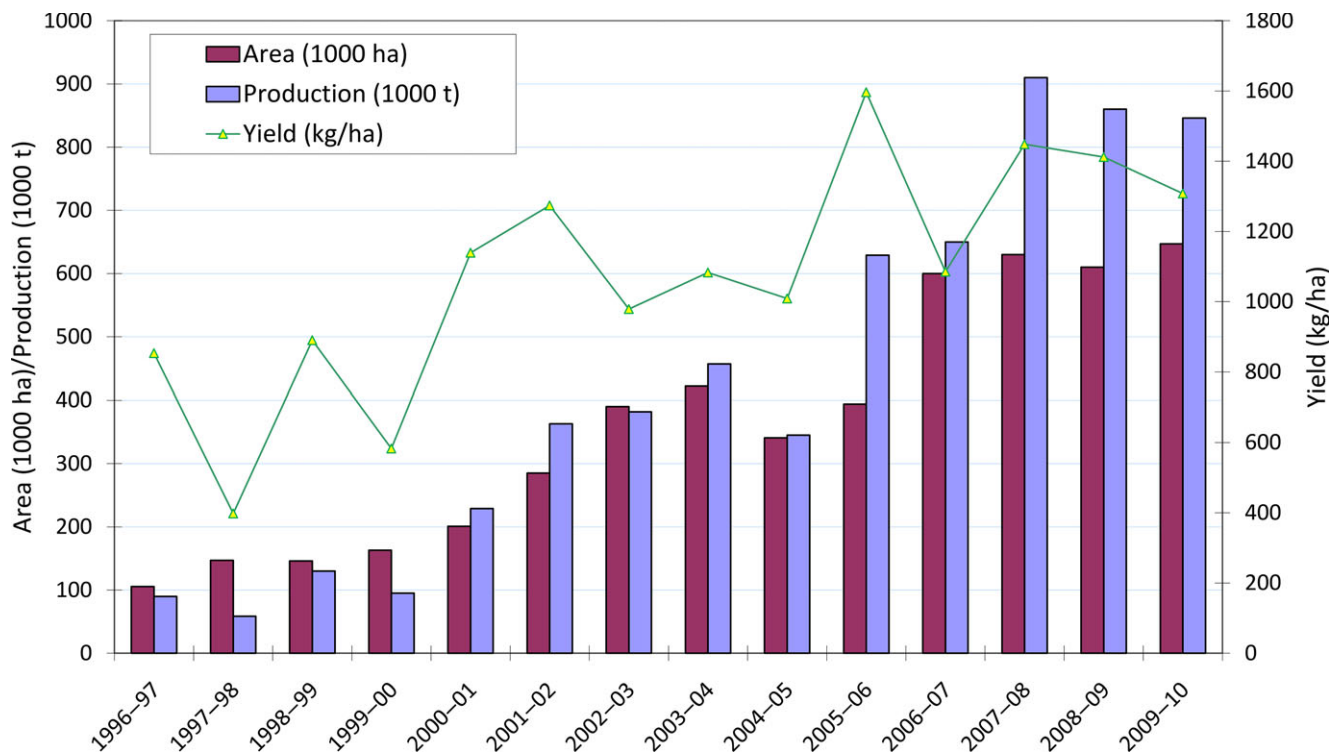


FIGURE 2 Increase in area, production and yield of chickpea in Andhra Pradesh state of India during 1996-97 to 2009-10

country as a whole. Further, this study indicated that the direct welfare benefits accrued to Andhra Pradesh due to adoption of short-duration chickpea cultivars were estimated at \$358.9 million. The new short-duration cultivars produced yields about 37% higher than the previous cultivar ('Annigeri'). The introduction of new cultivars reduced the unit cost of production to farmers by 22%, which was calculated at \$144 per ton (Bantilan et al., 2014).

FPVS trials conducted in Kenya, Tanzania and Ethiopia under Tropical Legumes-II project accelerated the process of the release of varieties in these countries. Several short-duration high-yielding varieties were released in these countries during 2009 to 2017. These include LTD 065 (ICCV 00108), LTD 068 (ICCV 00305), Chania desi 1 (ICCV 97105), Saina K1 (ICCV 95423), Chania desi 2 (ICCV 92944), Chania desi 3 (ICCV 97126), Mwea 1 (ICCV 97406), Ahero 1 (ICCV 97128) and Haraka (ICCV 970110) in Kenya; Ukiriguru 1 (ICCV 97105), Mwanza 1 (ICCV 00108), Mwanza 2 (ICCV 00305) and Mwangaza (ICCV 92318) in Tanzania; and Minjar (ICCV 03107), Akuri (ICCV 03402), Kobo (ICCV 01308) and Dalota (selection from ICCX-940002) in Ethiopia. During 2006 to 2016, the chickpea production has doubled in Ethiopia (Figure 3) and tripled in Tanzania (Figure 4) and both these countries showed an impressive growth rate of over 6% in the yield (FAOSTAT, 2016).

3 | DROUGHT TOLERANCE

Most breeding programmes use grain yield under moisture stress for selection of genotypes with enhanced drought avoidance/tolerance.

In most cases, the breeding material is exposed to terminal drought by growing the crop under rainfed conditions or under rainout shelters. Grain yield is a complex trait controlled by many genes and highly influenced by the environment. Thus, early generation selection solely for grain yield is not effective because of low heritability (Kumar & Bahl, 1992). The lack of uniform spread of soil moisture/drought stress in the field further reduces efficiency of selection. Hence, advanced breeding lines are evaluated at multiple locations and over the years.

Several phenotyping techniques have been suggested for elucidating genetic variations among chickpea accessions for drought tolerance (Upadhyaya et al., 2012). Saxena (1987) identified two drought-tolerant lines, ICC 4958 and ICC 10488, through screening of large number of germplasm accessions under irrigated and nonirrigated conditions. It was found that partitioning coefficient provides an effective selection criterion for grain yield under terminal drought conditions (Krishnamurthy et al., 2013). Several studies conducted at ICRISAT demonstrated that a prolific root system contributes positively to grain yield under terminal drought conditions (Kashiwagi et al., 2013, 2015). Despite well-recognized importance of rooting traits in terminal drought tolerance, limited efforts have been made to breed for improved root traits because the screening for root traits is a destructive and labour-intensive process and difficult to use in large segregating populations. Some breeding programmes have used genotypes with deep and prolific root system, such as ICC 4958, as one of the parents in crosses, but selection of breeding lines was based invariably for higher seed yield under water-stress conditions rather than on root traits.

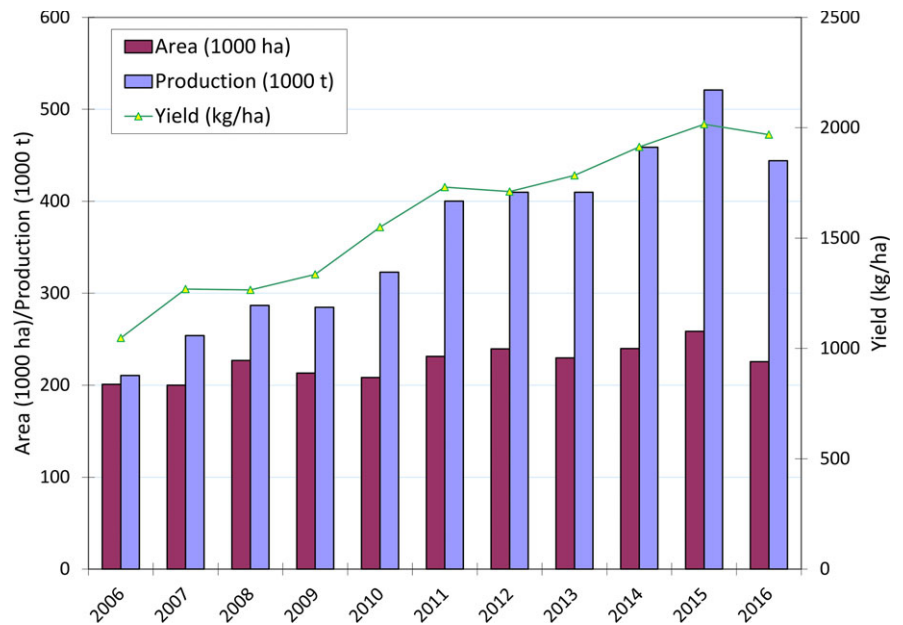


FIGURE 3 Increase in area, production and yield of chickpea in Ethiopia during 2006–2016

The identification of molecular markers linked to major genes controlling root traits can facilitate marker-assisted breeding (MAB) for root traits. Thudi, Upadhyaya et al. (2014) used genome-wide and candidate gene-based association mapping approaches to identify markers associated with drought and heat tolerance in chickpea. The reference set (300 accessions) of chickpea was phenotyped for drought tolerance-related root traits, heat tolerance, yield and yield components in India and Africa. For establishing marker–trait associations (MTAs), both genome-wide and candidate gene-sequencing-based association mapping approaches were conducted using 1,872 markers (1,072 DArTs, 651 SNPs, 113 gene-based SNPs and 36 SSRs). A total of 312 significant MTAs were identified. The association analysis identified 15 markers significantly associated with five rooting traits (root dry weight, root length density, root surface area, root volume and rooting depth) with PVE ranging from 8.25% to

22.41%. Among them, seven markers showed significant relation with a single trait (rooting depth) and two markers (NCPGR7 and DR_237) with more than one trait. Thus, these two markers were associated with colocalized/pleiotropic QTLs. A total of 18 SNPs from five genes (ERECTA, ASR, DREB, CAP2 promoter and AMDH) were significantly associated with different traits. A total of 10 candidate drought-responsive genes were amplified on the reference set. Of these, five genes (abscisic acid stress and ripening, CAP2 gene, ERECTA, sucrose synthase and sucrose phosphate synthase) were amplified on the reference set.

There has been considerable progress in the development of molecular markers and expansion of genome map of chickpea in recent years (Gaur, Jukanti, & Varshney, 2012; Gaur, Thudi, Samineni, & Varshney, 2014). A genomic region called QTL-hotspot carrying several quantitative trait loci (QTLs) that are associated with

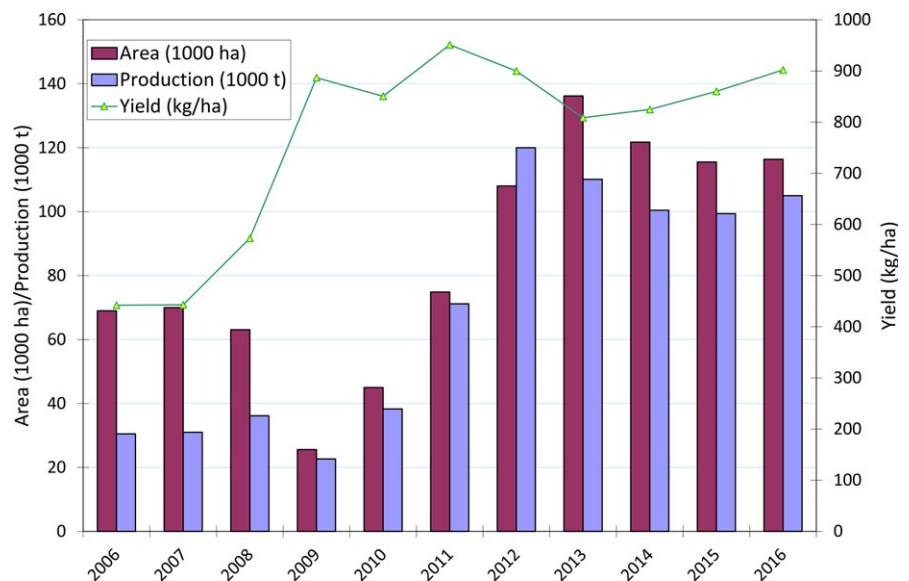


FIGURE 4 Increase in area, production and yield of chickpea in Tanzania during 2006–2016

several drought tolerance-related traits including some root traits was located on CaLG04 from the recombinant inbred lines (RILs) of ICC 4958 × ICC 1882 and ICC 283 × ICC 8261 crosses (Varshney et al., 2014). RILs of the cross ICC 4958 × ICC 1882 have been further studied for identifying genomic regions for plant vigour (growth and canopy size) and canopy conductance traits (Sivasakthi et al., 2018). The RILs were evaluated at vegetative stage under well-watered conditions using a high-throughput phenotyping platform (LeasyScan). The phenotypic traits measured included canopy traits measured by LeasyScan (projected leaf area, projected leaf area growth rate, 3D leaf area, 3D leaf area growth rate, leaf area index, plant height, plant height growth rate and plant vigour score), transpiration traits measured by gravimetric balance system (residual from 3D and projected leaf area, evapotranspiration, evapotranspiration rate, transpiration and transpiration rate) and biomass traits (shoot dry weight, specific leaf area and specific leaf weight). A total of 13 major QTLs for plant vigour traits were identified on CaLG04, most of these comapped with the *QTL-hotspot* region on CaLG04 (Varshney et al., 2014). The favourable alleles for plant vigour were contributed by the high vigour parent ICC 4958. Thus, it was suggested that the earlier reported drought tolerance *QTL-hotspot* is a seedling vigour locus. In the study of Sivasakthi et al. (2018), QTLs for canopy conductance traits, which are important determinant of plant water use, were mapped on CaLG03. Thus, this genomic region of CaLG03 may also be considered in breeding for drought tolerance.

This *QTL-hotspot* was introgressed in desi chickpea cultivar JG 11 from ICC 4958 (desi type) using marker-assisted backcrossing (MABC) (Varshney, Gaur et al., 2013). A set of 20 BC₃F₄ lines generated from the cross involving JG 11 as recurrent parent was evaluated at three locations in India and one each in Kenya and Ethiopia. Several BC₃F₄ lines giving significantly higher yield than the cultivar JG 11 were identified at each location (Gaur et al., 2013). Now, this genomic region has been introgressed in several other cultivars, including ICCV 10 (Figure 5). The initial results from the evaluation of MABC lines are encouraging, and several introgression lines are



FIGURE 5 The popular chickpea cultivar ICCV 10 (right) and one of the *QTL-hotspot* introgression lines of ICCV 10 developed through 3 cycles of marker-assisted backcrossing (MABC). This introgression line gave about 10% higher yield than ICCV 10

being evaluated under the trials of All India Coordinated Research Project (AICRP) on chickpea.

4 | HEAT TOLERANCE

A simple and effective field screening technique for reproductive stage heat tolerance in chickpea has been developed (Gaur, Jukanti, Samineni, & Gowda, 2012; Gaur, Jukanti et al., 2014). It involves delaying of sowing to coincide with high temperatures (>35°C) during the reproductive phase (Figure 6). For example, at ICRISAT, Patancheru (latitude 17° 36' 10" N, longitude 78° 20' 39" E) in southern India, the sowing for heat tolerance screening is carried out during the first fortnight of February. Although the normal sown crop (October-sown) can be grown on residual moisture without any supplementary irrigation, the February-sown crop has to be irrigated frequently (at 10- to 15-day interval). The other weather parameters which differ during the reproductive phase in normal and late-sown conditions are bright sunshine hours (8.1–8.7 hr in normal sown and 9.0–9.6 hr in late sown) and relative humidity 37.6%–44.3% in normal sown and 29.6%–36.4% in late sown). However, the major difference under two growing conditions is in temperatures (heat stress). It was found that number of filled pods per plant in late-sown crop (Figure 7) could be considered as a selection criterion for reproductive stage heat tolerance (Gaur, Jukanti et al., 2014).

The recent studies on screening of chickpea genotypes for heat tolerance indicate existence of large genotypic variation for reproductive stage heat tolerance in chickpea (Gaur, Samineni, & Varshney, 2014; Gaur, Jukanti et al., 2014; Gaur, Samineni, Krishnamurthy et al., 2015; Krishnamurthy et al., 2011). Several heat-tolerant genotypes have been identified which include landraces (e.g., ICC 1205, ICC 1356, ICC 4958, ICC 6279 and ICC 15614), breeding lines (e.g., ICCV 07104, ICCV 07105, ICCV 07108, ICCV 07109, ICCV 07110, ICCV 07115, ICCV 07117, ICCV 07118 and ICCV 98902) and cultivars (e.g., JG 14, IPC 2006-77, JG 16, GG 2, JG 130, JAKI 9218, JGK 2 and KAK 2).

The availability of effective, efficient and robust field screening technique for heat tolerance greatly facilitates chickpea breeding for heat tolerance. The general breeding scheme includes growing of segregating populations (F₄ or F₅) under late-sown conditions for selecting heat-tolerant plants based on the number of filled pods per plant. Then, single plant progenies are developed from the selected heat-tolerant plants and evaluated further for grain yield and other desired traits (resistance to key diseases, seed traits, etc.) under normal and heat-stress conditions.

A heat-tolerant breeding line ICCV 92944 has been released for cultivation in Myanmar (as Yezin 6), India (as JG 14), Kenya (as Chania Desi 2) and Bangladesh (as BARI Chola 10). JG 14 is becoming popular for sowing under late-sown conditions (e.g., rice fallows) in India. The variety JG 14 was evaluated along with local check on farmers' fields under late-sown conditions in Uttar Pradesh and Madhya Pradesh states of India. In Uttar Pradesh, JG 14 gave 24%–40% higher yield than the local check when planted late in

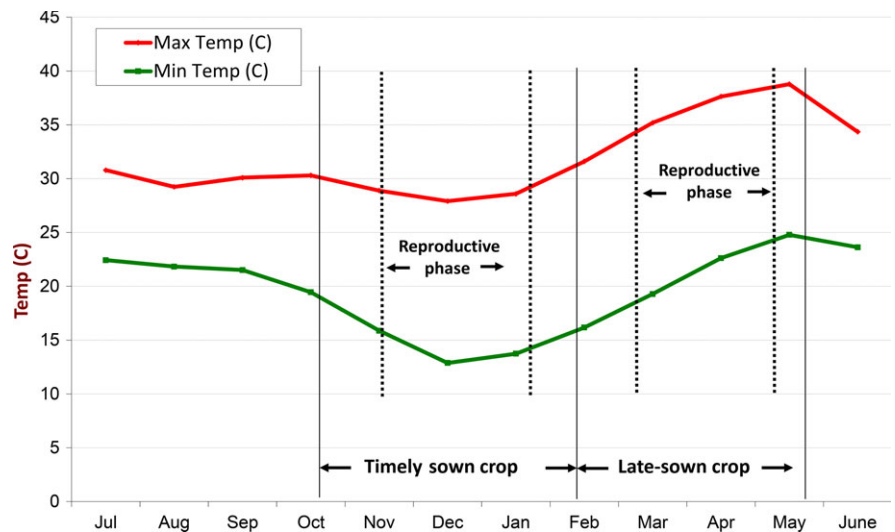


FIGURE 6 Average minimum and maximum temperatures during reproductive phase of timely sown and late-sown (for heat tolerance screening) crop of chickpea at ICRISAT, Patancheru, India

December. Similarly, in Madhya Pradesh, JG 14 gave 20%–48% higher yield than the local cultivar in demonstrations conducted under late-sown (heat-stress) conditions. Variety JG 14 has become very popular in several states of India, such as Eastern Uttar Pradesh, Bihar, Jharkhand, Odisha and Chhattisgarh. In Myanmar, area under heat-tolerant variety Yezin 6 increased from 1,700 ha in 2005–06 to 46,000 ha in 2011–12 (Win, Shwe, & Gaur, 2014).

Marker-assisted selection for heat tolerance can further accelerate breeding process and facilitate combining different desired traits. The study by Thudi et al. (2014) on genome-wide association mapping using the reference set (300 accessions) of chickpea did not find any significant MTA for heat tolerance index (HTI). RILs developed from the cross ICC 4567 (heat sensitive) × ICC 15614 (heat tolerant) have been used to identify molecular markers linked to QTLs related to heat tolerance traits. Phenotyping of RILs was undertaken for two heat stress (late sown) and one nonstress (normal sown) environments. The traits measured included days to 50% flowering, visual score on podding behaviour, number of filled pods, % pod setting, total number of seeds, grain yield, harvest index,

biomass and 100-seed weight. A two-fold variation for number of filled pods, total number of seeds, harvest index, per cent pod setting and grain yield was observed in the RILs under heat-stress environments compared to nonstress environment (Paul et al., 2018a). A genetic map spanning 529.11 cM and comprising of 271 genotyping by sequencing (GBS) based SNP markers was constructed. Composite interval mapping (CIM) analysis revealed two consistent genomic regions harbouring four QTLs each on CaLG05 and CaLG06. Four major QTLs for heat tolerance-related traits (number of filled pods per plant, total number of seeds per plant, grain yield and % pod setting), having cumulative phenotypic variation of above 50%, were identified on CaLG05 (Paul et al., 2018b). These QTLs, after validation, can be introgressed through marker-assisted breeding for improving heat tolerance.

5 | COMBINED DROUGHT AND HEAT TOLERANCE

The chickpea breeding programme of ICRISAT screens all promising lines targeted for the semi-arid tropical environments for heat tolerance. The lines which perform well under both nonstress and heat-stress environments are selected for evaluation in multilocation environments through International Chickpea Varietal Trials (ICVTs). Thus, concerted efforts are now being made to develop varieties with improved heat tolerance. It is anticipated that several new heat-tolerant cultivars of chickpea will be released in the coming years and provide greater choice to the farmers.

The rainfed crop of chickpea often experiences drought and heat stresses simultaneously towards end of the growing season, particularly under late-sown condition. Thus, it is important to develop varieties with combined tolerance to drought and heat stresses. Tolerance to both drought and heat stress in maize was genetically distinct from tolerance to individual stresses, and tolerance to either stress alone did not confer tolerance to combined drought and heat stress (Cairns et al., 2013).



FIGURE 7 A heat-tolerant line (right) and a heat sensitive line (left) grown under late-sown (heat-stress) conditions at ICRISAT, Patancheru, India. Number of filled pods per plant is being used as a key trait in assessing heat tolerance

Efforts have been made to screen chickpea genotypes simultaneously for drought and heat tolerance to identify genotypes with combined drought and heat tolerance. Canci and Toker (2009) evaluated 377 chickpea accessions of chickpea for tolerance to combined drought and heat stresses by planting two months later than normal for the Antalya region (Turkey) to increase their exposure to drought and high-temperature conditions. One drought-tolerant (ICC 4958) and two drought-susceptible (ILC 3279 and ILC 8617) genotypes were used as checks. In general, the desi chickpea genotypes showed higher levels of drought and heat tolerance than the kabuli genotypes. Two desi chickpea genotypes, ACC 316 and ACC 317, showed high levels of drought and heat (>40°C) tolerance.

The genetic loci underlying tolerance to the combined stress are likely to differ from those for drought or heat-stress tolerance alone (Tricker, ElHabti, Schmidt, & Fleury, 2018). Studies in other crops have identified specific regulatory transcripts, combinations of metabolites and proteins, and physiological responses that are unique to combined drought and heat stresses (Zandalinas, Mittler, Balfagón, Arbona, & Gómez-Cadenas, 2017). Therefore, efforts should be made in chickpea to identify and deploy genes that control combined drought and heat tolerance.

6 | APPROACHES FOR IMPROVING EFFICIENCY OF CHICKPEA BREEDING PROGRAMMES FOR DEVELOPING DROUGHT- AND HEAT-TOLERANT CULTIVARS

The application of novel methods and tools is needed in breeding programmes to improve efficiency and effectiveness so that higher genetic gains can be achieved and the time required for the development of a variety can be reduced. Higher emphasis should be given on integrating approaches for broadening the genetic base, improving precision in phenotyping, enhancing efficiency in selections, reducing the time required to develop breeding lines and establishing an efficient breeding data management system. The breeding programmes should be able to develop varieties in the shortest possible time as per need of farmers, consumers and the industries.

6.1 | Broadening genetic base

There is a need to utilize greater genetic variability in the breeding programmes to develop varieties with enhanced tolerance to abiotic stresses. Wild *Cicer* species are known to have traits which help these species to survive in challenging environments. The barriers to interspecific hybridization have restricted utilization of wild species to only two species, *C. reticulatum* and *C. echinospermum*, which can be crossed easily with the cultigen (Gaur et al., 2010). These species and some of the segregants from interspecific crosses are very late in some growing environments. Vernalization treatment (exposure to low temperatures) will induce early flowering in the wild species and interspecific crosses. The wild species were found to be more

responsive to vernalization than the cultivated chickpea (Abbo, Lev-Yadun, & Galwey, 2002; Berger, Buck, Henzell, & Turner, 2005). Recently, a major QTL contributing 55% of phenotypic variation for vernalization response trait was identified on CaLG03 at LOD score of 27 from a RIL population developed from a cross ICC 4958 (*C. arietinum*) × PI 489777 (*C. reticulatum*). Markers linked to this QTL can help in selection against vernalization response gene in inter-specific populations (Samineni, Kamatam, Thudi, Varshney, & Gaur, 2015).

There has been extensive use of the germplasm of cultivated species available in ICRISAT Genebank by ICRISAT and other research institutes globally. The ICRISAT Genebank conserves 20,602 chickpea accessions from 60 countries. ICRISAT has so far distributed over 350,000 seed samples to scientists in 88 countries. In addition, over 190,000 seed samples were supplied internally to ICRISAT scientists. The chickpea breeding programme of ICRISAT made more than 20,000 crosses during the past 44 years. The parents of these crosses included at least 2,000 accessions from ICRISAT Genebank. Thus, chickpea breeding programme of ICRISAT has successfully used about 10% of germplasm available in ICRISAT Genebank.

Novel breeding approaches, such as the development of multi-parent advanced generation intercross (MAGIC) populations/lines, can be used to combine favourable genes for tolerance to abiotic stresses and other desired traits (Bandillo et al., 2013; Huang et al., 2015). The large number of accumulated recombination events in MAGIC populations increases novel rearrangements of alleles and brings about greater genetic diversity. A MAGIC population in desi chickpea has been developed at ICRISAT using eight parents, which include the drought-tolerant germplasm line ICC 4958, five well-known cultivars from India (ICCV 10, JAKI 9218, JG 11, JG 130 and JG 16) and two cultivars from Africa (ICCV 97105 and ICCV 00108). Twenty-eight-two-way, 14 four-way and seven-eight-way crosses were made to develop this MAGIC population. The MAGIC lines constitute a valuable genetic resource for trait mapping and gene discovery. In addition, these lines also provided breeding materials for direct use in breeding programmes. ICRISAT has shared F₄ seed from four-way and eight-way crosses with several institutes in South Asia and sub-Saharan Africa. The plant breeders have selected promising plants adapted to their locations and developed progenies for further evaluations. Several drought- and heat-tolerant progenies have been developed from MAGIC population at ICRISAT.

6.2 | High-throughput and precision phenotyping

Accurate, relevant and high-throughput phenotyping would play an important role in breeding for abiotic stress tolerance. Identification of molecular markers linked to QTLs associated with stress tolerance traits would also depend on accuracy of phenotyping. Controlled environmental facilities (e.g., rainout shelters, greenhouses and growth chambers) and other experimental practices (e.g., irrigated trials in dry regions; delayed planting for exposing crop to heat stress) can be utilized for improving efficiency of phenotyping. Adoption of high-throughput platforms will improve cost-effectiveness of

phenotyping and allow efficient collection of phenotypic data. Remote sensing via near-infrared spectroscopy has been found useful in high-throughput phenotyping platforms (Montes, Melchinger, & Reif, 2007).

The lysimeter facility available at ICRISAT uses long (1.2 m and 2.0 m) PVC tubes filled with soil to measure plant water use. These long PVC tubes give the plants the soil depth and aerial spacing similar to field conditions. The lysimeter approach provides a bridge between field-based and laboratory-based research and enables the collection of precise data on plant water use (quantities, timing).

ICRISAT has recently established a LeasyScan Phenotyping Platform, which is a high-throughput phenotyping platform to assess canopy traits affecting water use (leaf area, leaf area index, transpiration). LeasyScan is based on a novel 3D scanning technique to capture leaf area development continuously, a scanner-to-plant concept to increase imaging throughput and analytical scales to combine gravimetric transpiration measurements. This new platform has the potential to accelerate precise phenotyping for traits controlling plant water use at a high rate and precision and would facilitate studies on trait discovery and breeding for drought tolerance (Vadez et al., 2015).

6.3 | Genomics-assisted breeding

Rapid advances have been made in the development of genomic resources of chickpea during the past decade. A draft genome sequence has been published for the Canadian chickpea variety CDC Frontier (Varshney, Song et al., 2013) and the drought-tolerant breeding line ICC 4958 (Parween et al., 2015). Later on, several germplasm lines have been resequenced which led to identification of several millions of genome-wide variations (Thudi, Chitkineni et al., 2016; Thudi, Khan et al., 2016). In addition, large-scale genomic resources, including several thousand simple sequence repeats (SSR, Nayak et al., 2010; Gujaria et al., 2011; Thudi et al., 2011) and several million single-nucleotide polymorphisms (SNPs, Hiremath et al., 2011, 2012), high-density diversity array technology (Thudi et al., 2011), and Illumina GoldenGate assay genotyping platforms (Hiremath et al., 2011), Affymetrix SNP arrays “Axiom[®]CicerSNP array” (Roorkiwal et al., 2017), high-density genetic maps (Thudi et al., 2011) and transcriptome assemblies (Kudapa et al., 2014), have been developed. Molecular markers have been identified for QTLs/genes associated with a large number of traits (reviewed by Gaur, Thudi et al., 2014; Thudi, Gaur et al., 2014). The integration of genomics technologies in chickpea breeding will greatly improve the precision and efficiency of breeding programmes.

6.4 | Rapid generation turnover

The chickpea breeding programmes need to take two or more crop generations per year so that duration required to develop a variety can be reduced. A rapid generation advancement method was developed at ICRISAT (Gaur, Samineni, Gowda, & Rao, 2007). This has been further refined and now ICRISAT is taking three

successive generations per year in the field since 2010. Two generations are taken in field at Patancheru and one at Hiriyr (latitude 13° 56' 37" N, longitude 76° 36' 57" E). At Patancheru, the first crop is grown during the main crop season (Oct-Feb) and the second crop during the summer (Feb-Apr). The summer crop is exposed to high temperatures during reproductive stage, providing opportunity for heat tolerance screening at reproductive stage. The third off-season crop is grown at Hiriyr during June to September. Selection of breeding materials in different environments provides opportunity for developing varieties adapted to different environments. Taking three generations in one year significantly reduces the time required in the development of varieties, thus enhancing the genetic gain.

ICRISAT has recently standardized protocol for taking six generations per year in greenhouse. The plants are provided 24-hr light from emergence till flowering to induce early flowering. The immature seeds (fully developed green seeds removed from pods before drying) are used for planting next generation, thus, further reducing time.

6.5 | Establishing an efficient breeding data management system

The breeding programmes need to use an efficient data management system to make use of the information available from various sources about germplasm characterization, evaluation of breeding lines, pedigree information, phenotyping and genotyping data, and sequencing data. There is a need to link phenotypic information to genotyping and sequence information available for functional genomics and allele mining. One such data management system is International Crop Information System (ICIS) developed by the Consultative Group for International Agricultural Research (CGIAR) in partnership with several Advanced Research Institutions (ARIs) and the National Agricultural Research Systems (NARS). ICIS can be used for wide range of crops (Fox & Skovmand, 1996). The International Rice Information System (IRIS) developed by the International Rice Research Institute (IRRI) is an adaptation of the ICIS for rice (Bruskiewich et al., 2003; McLaren, Bruskiewich, Portugal, & Cosico, 2005). Similarly, The International Maize and Wheat Improvement Center (CIMMYT) has adopted ICIS to develop International Maize Information System (IMIS) and International Wheat Information System (IWIS).

In order to facilitate access to the data held within and/or across the databases, the Generation Challenge Programme (GCP, <http://www.generationcp.org/>) initiated development of Crop Ontology by the crop community of practice to facilitate the harmonization of the data across programmes. The crop ontologies (<http://www.cropontology.org/>) are now available for many crops, including chickpea, pigeon pea, groundnut, sorghum, pearl millet, wheat, rice, maize, barley, soybean, cowpea, lentil, banana, cassava, sweet potato and yam crops. The Crop Ontology will facilitate bridging the phenotypic and genetic data useful for integrated breeding (Rosemary et al., 2012). The Crop Ontology is a global public good, available to be used freely by all.

Breeding Management System (BMS) developed by the Integrated Breeding Platform (<https://www.integratedbreeding.net/breeding-management-system>) is another popular breeding data management system. It is being used by the crop breeding programmes of several CGIAR institutes, including ICRISAT, and other public and private sector organizations. The BMS provides various applications to help manage all activities of breeding programmes, including management of germplasm, crossing, nurseries and trials. BMS has an Integrated Breeding Field Book and can perform statistical analysis through visual and easy-to-use analytical pipelines with quality insurance measures. For integrating molecular breeding, the useful components of BMS include Genotypic Data Management System (GDMS), Integrated Breeding Planner, Integrated SNP Mining and Utilisation Pipeline (ISMU), Molecular Breeding Design Tool (MBDT) and OptiMAS. Thus, BMS can be used to manage the breeding data across all phases of the crop improvement cycle. It helps in managing trials, nurseries and seed inventory; runs statistical analyses; and supports in integrating molecular breeding.

7 | CONCLUDING REMARKS

Abiotic stresses such as terminal drought and heat stresses are major constraints to chickpea production worldwide, and these are expected to increase due to climate variability and climate change. Concerted efforts are needed to enhance efficiency of breeding programmes for rapid development of varieties with improved adaptation to abiotic and biotic stresses and other desired traits such as high yield, suitable maturity duration, nutrient use efficiency, suitability to machine harvesting, herbicide tolerance, market-preferred grain quality and improved nutritional quality. The recent advances made in genomics, high throughput and precision phenotyping, breeding methods and rapid generation turnover techniques are very encouraging. Integrated breeding, which involves these novel tools and techniques, is expected to provide needed pace, precision and efficiency to the chickpea breeding for improving adaptation to drought and heat stresses.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interests.

AUTHOR CONTRIBUTIONS

PMG conceived the idea and prepared the structure of the review. All authors contributed equally to the preparation of the manuscript and all authors read and approved the manuscript.

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