



GENETICS AND GENOMICS APPROACHES TO ENHANCE ADAPTATION AND YIELD OF CHICKPEA (*Cicer arietinum* L.) IN SEMI-ARID ENVIRONMENTS

V.S. HEGDE^{1*}, S. TRIPATHI¹, C. BHARADWAJ¹, P.K. AGRAWAL² and A.K. CHOUDHARY³

¹Genetics Division, ICAR-Indian Agricultural Research Institute, New Delhi 110 012, India

²Indian Council of Agricultural Research, New Delhi 110 012, India

³ICAR Research Complex for Eastern Region, Patna 800 014, India

*Corresponding author email: vshegdeiari@gmail.com

Email addresses of co-authors: shaitri@rediffmail.com, drchbharadwaj@gmail.com, pawankagrawal@hotmail.com, akicar1968@gmail.com

SUMMARY

Chickpea is an important component of food security and hence to meet the increasing demand for food requirements, it is necessary to develop varieties with better adaptation and higher grain yield. Efforts to improve the yield potential through conventional breeding approaches have resulted in only a marginal increase in productivity during the last 50 years. Chickpea is predominantly cultivated under less productive rainfed environments characterized by terminal drought stress because of its indeterminate growth habit and poor response to high fertility and irrigation. Development of varieties for better agronomic management requires genetic reconstruction of the existing plant types in favour of increased harvest index. The change of plant type from indeterminate to determinate/semi-determinate stem growth habit, lodging resistance, modified phenology, and responsiveness to better agronomic managements is required to achieve a breakthrough in its productivity. Although, the past breeding efforts both at national and international levels have been successful in enhancing the yield marginally, a significant breakthrough in its productivity has not been possible so far. The approaches that integrates the use of genetics and genomic tools in breeding have the potential to generate superior genotypes with improved adaptation and enhanced grain yield in chickpea.

Key words: Chickpea, phenology, drought, QTL-hot spot, major diseases, stem growth habit, marker assisted selection, genomics

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INTRODUCTION

Chickpea belongs to the family *Leguminosae*, the sub-family *Papilionoideae*, the tribe *Cicereae* Alef., and the genus *Cicer* L. The genus *Cicer* consists of 9 annual and 35 perennial species (van der Maesen *et al.*, 2007). *Cicer arietinum* L. is the only species cultivated on a large scale and *C. reticulatum* L. is considered as its wild progenitor (Ladizinsky and Adler, 1976). The first cultivated form of chickpea probably originated in the Anatolian Plateau in Turkey (van der Maesen, 1984). Turkey and India are the two major centers of diversity of chickpea. It is a highly self-pollinated crop with a very low level of out-crossing due to cleistogamous nature of flowers (Toker *et al.*, 2006). The cultivated chickpea is an annual diploid species with $2n = 16$ chromosomes and a genome size of ~738Mb (Varshney *et al.*, 2013a).

The cultivated species of chickpea has two main types, desi and kabuli, representing two genetically diverse groups (Moreno and Cubero, 1978; van der Maesen, 1987). The first domesticated type was the desi chickpea and the newer kabuli type might have been derived from the older desi type through mutation followed by conscious selection (Ramanujam, 1976). The desi types are mainly cultivated in the Indian sub-continent and Ethiopia, whereas the kabuli types generally in the Mediterranean region and Latin America (Singh and Malhotra, 1984). Desi chickpeas are characterized by angular seed shape, dark seed coat, pink flowers, anthocyanin pigmentation of stem, bushier growth habit, more secondary branches, more pods per plant, more seeds per pod, and greater tolerance to drought and

heat. Whereas, kabuli types generally have owl-head shaped beige seeds, greater range in seed size and primary branches, white flowers, smooth seed surface, lack of anthocyanin pigmentation on stem, greater cold tolerance, a more upright and in some cases taller growth habit, and greater resistance to chlorosis (Hawtin and Singh, 1980; Pundir *et al.*, 1985). The desi chickpea accounts for 85-90% of its cultivation, while kabuli types occupy the remaining 10-15% area.

Chickpea is important because it provides food for humans, as well as feeds for livestock. It is a good source of energy, protein, minerals, vitamins, fiber, and contains potentially health beneficial phytochemicals (Wood and Grusak, 2007). The protein concentration of chickpea seed ranges from 15-16% to about 30% and is commonly 2-3 times higher than cereal grains. The amino acid composition of chickpea is well balanced apart from the limited sulphur-containing amino acids (methionine and cysteine) and is high in lysine which makes it an ideal companion to cereals. It is also rich in several minerals essential for human health such as phosphorus, calcium, magnesium, iron, and zinc. The calcium content is about 100 to 200 mg/100 g of grains compared to 35-70 mg/100 g in case of dry peas and lentils. It is a rich source of carotenoids that are primarily responsible for yellow color of its cotyledons. Abbo *et al.* (2005) found that chickpea seeds contain a higher concentration of β -carotene than the engineered golden-rice. Chickpea contains up to 49 μ g/100 g β -carotene present in both the cotyledons and seed coat (Atienza *et al.*, 1998). Chickpea is considered a cholesterol reducer due to its high fiber and

unsaturated fatty acid content. It is unique in moderating the rise in plasma glucose after meals and is used to help control diabetes in eastern Asia.

Chickpea is an important food legume crop of the semi-arid tropics (SAT), particularly in the Indian subcontinent, the Mediterranean region, the West Asia and North Africa (WANA) region, Eastern Africa, and Latin America. It is the second most important food legume crop in the world, after dry bean grown on 12.65 million hectares of land worldwide with a total production of 12.09 million tons (FAO, 2016). The world chickpea area is increased by about 40% in the last three and a half decades while its total production more than doubled during the same period. Growing interest in chickpea consumption, coupled with increased preference for vegetable-based protein has led to an increase in the global demand for chickpea (Gaur *et al.*, 2012). At present, it is cultivated in 65 countries in the world (FAO, 2016). It is a major food legume crop in Asia and Africa, which together account for about 90% of global chickpea production. South Asia is by far the largest producer of chickpea, which contribute to about 74% of world production with a share of 82% of area harvested. Also, its production and productivity fluctuated in many of the chickpea producing countries globally. Several biotic and abiotic stresses contribute to such low yield and year-to-year fluctuations in yield (Choudhary *et al.*, 2013). *Fusarium* wilt, *ascochyta* blight, *botrytis* gray mold, dry root rot, nematodes, pod borer, and leaf miner among the biotic stresses and drought and high and low temperature among the abiotic stresses, are the major constraints of higher yield in chickpea.

Among these stresses, drought alone causes 40-50 % reduction in chickpea yield globally (Ahmad *et al.*, 2005). Terminal drought is the major constraint limiting productivity of chickpea since the crop is predominantly cultivated under residual and receding soil moisture conditions of rainfed environments. In designing improved plant types for terminal drought stress environments, an agronomist's view point may be to better match crop phenology to the expected soil moisture availability or to incorporate traits that impart improved tolerance to minimize the risks of drought. Therefore, breeding for short duration (drought escape) and drought avoidance root traits are considered as the most important strategies in alleviating terminal drought stress for achieving high and stable grain yields in chickpea (Gaur *et al.*, 2008; Choudhary *et al.*, 2017). Other constraints to chickpea productivity also include problems of lodging susceptibility, indeterminate stem growth habit, and sensitivity to cold. In a crop like chickpea which is predominantly cultivated under rainfed residual soil moisture conditions, grain yield can be increased by accumulation of genes for modified phenology, resistance to major biotic and abiotic stresses for maximum expression of yield potential, and those traits that increase biomass and harvest index.

BREEDING FOR MODIFIED PHENOLOGY

Drought is the most important yield constraint in chickpea, accounting for about 50% yield reduction globally. It generally occurs at the terminal stage as the crop is mostly raised on conserved soil moisture under rain-fed

conditions. One of the ways of enhancing productivity of a crop in each environment is by improving its adaptation to the agro-climatic constraints. Turner (1986) suggested drought escape as an important strategy of matching phenological development with the period of soil moisture availability to minimize the impact of drought stress on crop production in environments where the growing season is short and terminal drought stress predominates. In developing cultivars more resistant to soil moisture and temperature stress, phenology must be modified first so that pre-anthesis growth and flowering will avoid the most severe stress periods (Buddenhagen and Richards, 1988). The shortening of crop duration along with fast initial growth has also been suggested as one of the ways of enhancing yield and yield stability in such stress environments (Subbarao *et al.*, 1995). Breeding for earliness has also been proposed as a major approach to increase yield under water-limited conditions, particularly terminal drought environments (Berger *et al.*, 2004). Early flowering is an important component of adaptation and productivity of chickpea in semi-arid environments characterized by terminal drought and heat stress. However, it is observed that the short duration chickpea genotypes are generally poor in their biomass and grain yield potential and hence, farmers may not accept them unless they are genetically improved to increase their yield potential similar or superior to locally adopted cultivars. In a study involving evaluation of large number of genotypes under residual soil moisture conditions (Hegde *et al.*, 2016) short duration types which flowered in about 35 days and matured in about 80

days, produced about 1.5 t ha⁻¹ grain yield, whereas the super-early genotypes that flowered in 30 days and matured in 75 days produced grain yield of only about 1 t ha⁻¹. Under similar growing conditions, the genotypes that flowered in 40-45 days and matured in 90-95 days produced high biomass (5.25 t ha⁻¹) and grain yield (2.37 t ha⁻¹) showing that it was possible to combine high biomass and grain yield in a relatively early maturing chickpea variety even in a warmer short duration rainfed environment. The most popular variety commercially cultivated in Peninsular India, JG 11, produced about 2 t ha⁻¹ of grain yield. The low yield of super-early and short duration types may be because earliness reduces the potential yield of the crop by reducing dry matter at flowering and the number of sites for post-flowering grain filling. Hence, the selection should be for genotypes that flower in about 40-45 days so that there is adequate dry matter at anthesis and number of sites for post-flowering grain filling. In contrast, Soltani and Sinclair (2012) observed that early maturity due to 20% shorter vegetative period from emergence to flowering and 20% longer grain filling period resulted in significantly increased chickpea yields under a water-limited environment in Iran. Therefore, the breeding programme to improve adaptation and grain yield should aim at optimizing chickpea phenology by modifying the duration of either vegetative or reproductive phase particularly the grain filling period or rate of grain filling depending on the target environment and available soil moisture. The flowering time in chickpea is governed by duplicate dominant genes with cumulative but

unequal effects on flowering time (Hegde, 2010) and so far, four early flowering loci, *Efl1* to *Efl4*, have been reported (Gaur *et al.*, 2015). In addition, six flowering time QTLs (quantitative trait loci) have been defined in LG1, 2, 3, 4 and 8 (Cho *et al.*, 2002; Vadez *et al.*, 2012; Jamalabadi *et al.*, 2013). A major QTL between markers TA117 and STMS22 has been identified (Jamalabadi *et al.*, 2013). Major QTLs 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). The QTLs and linked markers identified in these studies can be used in marker-assisted breeding for developing early maturing chickpea. Further identification of markers closely linked to all the flowering time alleles would facilitate marker assisted selection and pyramiding of *Early flowering* genes to improve adaptation and to understand their individual as well as combined effect on yield potential of chickpea in different environments.

BREEDING FOR ROOT TRAITS

Terminal drought stress is the major constraint of chickpea productivity and stability of yield in the major chickpea growing environments (Krishnamurthy *et al.*, 2010). Root traits such as root depth and root proliferation are found to be important in chickpea for improving tolerance to terminal drought stress as they help in extracting available soil moisture from deeper soil layers. Roots are also important for nutrient uptake, anchoring, and mechanical support (Smith and Smet, 2012). Roots serve as the major interface between the

plant and various biotic and abiotic factors in the soil environment, by both sensing and responding to environmental cues, enabling plants to overcome the challenges posed by their sessile status. Plants have the ability to alter their root architecture to optimize growth in a large variety of environmental and soil nutrient conditions. A deeper root system was also found to be associated with better harvest index and seed yields in chickpea (Kashiwagi *et al.*, 2006). A large amount of genetic variation was observed for root length density (RLD), root dry weight (RDW), rooting depth (RDp), and root to total plant weight ratio (R/T) among the accessions of the mini-core collection of chickpea (Kashiwagi *et al.*, 2005). They have identified two genotypes, ICC 4958 and ICC 8261, as good sources of genes for large and prolific root system in chickpea. Trait specific germplasm for these drought avoidance root traits have also been identified among 300 reference set of chickpea (Lalitha *et al.*, 2015). These germplasm with desirable root characteristics have the potential for utilization in breeding of chickpea ideotypes for improved plant yield under terminal drought prone rainfed environments. The modification of root system may enable plants to make more efficient use of existing soil nutrients, increase stress tolerance, and improving yields. The study on the genetics of root traits showed that the additive gene effect and additive x additive gene interaction play major roles in the inheritance of root length density and root dry weight (Kashiwagi *et al.*, 2008). Thus, the predominant role of additive gene action for root traits indicates that these important traits can be improved through direct selection for

their higher values in segregating generations of a cross.

The root traits are complex in nature and it is very difficult to extract them intact from the soil under field conditions. Therefore, the marker assisted selection (MAS) using linked molecular markers is an alternate approach to efficient selection for root traits in chickpea. The availability of closely linked molecular markers is an important pre-requisite for the marker assisted selection. The chickpea genomic regions with "QTL-hot spots" containing QTLs for several drought tolerance traits including root traits have been identified (Varshney *et al.*, 2014). This "QTL-hotspot" region has been successfully introgressed into the genetic background of elite and leading cultivars, JG 11 (Varshney *et al.*, 2013b), KAK 2, and Chefe. The introgression lines developed from JG11/ICC 4958 were found to possess higher root length density, root dry weight, and rooting depth compared to both the donor and recipient parents (Varshney *et al.*, 2013c). The phenotypic evaluation of these lines in India (Patancheru, Dharwad, Nandyal, Durgapura, and Gulbarga), Kenya, and Ethiopia produced >10% increased yield under rainfed conditions and about 20% higher yield under irrigated conditions. Efforts are being made by other research institutes like IIPR and IARI in India; Egerton University, Kenya and the Ethiopian Institute of Agricultural Research (Ethiopia) in sub-Saharan Africa for introgressing this region into genetic backgrounds of high yielding cultivars in their regions to improve their adaptation to terminal drought stress environments. Marker-assisted backcross breeding (MABB) approach was successfully used at IARI, New Delhi to introgress the 'QTL-hotspot'

into an elite chickpea cultivar Pusa 362. The Pusa 362 is an elite chickpea cultivar developed at IARI, New Delhi, India and was released in 1995. The introgression lines (BC₂F₄) were developed through MABB from the cross Pusa 362/ICC 4958 and evaluated for root traits and grain yield components (Seema, 2017). Fifty polymorphic SSR markers were used to genotype the introgression lines in the backcross generations for recovery of recurrent parent genome and NCPGR21 and NCPGR127 markers used for foreground selection. Introgression of this region into Pusa 362 enhanced its grain yield under terminal drought stress condition.

BREEDING FOR LODGING RESISTANCE AND RESPONSE TO BETTER AGRONOMY

Lodging is a major agronomic problem in many of the important crops including chickpea. Almost all the chickpea cultivars currently cultivated in India are susceptible to lodging. Severe plant lodging is known to result in reduction of both quantity and quality of seed yield, increased disease pressure, and reduced harvest efficiency (McPhee and Muehlbauer, 1999). In the case of a lodged plant population, the normal canopy structure is destroyed, resulting in reduced photosynthetic ability, dry matter production, and ultimately yield (Chen *et al.*, 2011). The extent of loss depends on the timing and the severity of the lodging which is a highly complex trait influenced by both the genotype and the environment. Therefore, improvement in lodging resistance will ultimately increase the yield potential as well as the quality of the produce, particularly when crop is grown under high fertility

and high moisture conditions that favour lodging. Lodging resistance in field pea has been improved by selection of plants that exhibit stiff stem trait (McPhee and Muehlbauer, 1999). Plant traits associated with lodging resistance that are not significantly affected by the environment have been found in soybean (Mancuso and Caviness, 1991). The introduction of semi-leafless trait (afila leaf morphology) and a dwarfing gene (*le*) into pea cultivars has contributed to improved lodging resistance (Ta'an *et al.*, 2003). The selection for short statured semi-dwarf cereals such as rice, wheat, and sorghum resulted in doubling of their yield potential, mainly because of their increased responsiveness to nitrogenous fertilizers, lodging resistance, and better partitioning of photosynthates (Khush, 2013). However, in case of chickpea, plant height is found to have a positive effect on the total biomass (Omar and Singh, 1997; Hegde and Kumar, 2015). Therefore, reducing height may result in decreased biomass and ultimately, grain yield in chickpea. It is also observed that in case of chickpea, lodging or stem bending occurs irrespective of the plant height of genotypes. Therefore, increasing the stem strength of the tall plant types will be a very promising strategy to breed high yielding chickpea varieties with lodging resistance. Increased stem strength allow the plants to withstand the heavy vegetative loads of the above ground canopy without reducing plant height (Ball *et al.*, 2006). Stem strength is found to be one of the major factors influencing lodging in soybean (Mancuso and Caviness, 1991), pea (Beeck *et al.*, 2006), and many other crops thus playing an

important role in breeding for lodging resistance. There is a need to enhance the structural characteristics of chickpea plants to ensure that grain yield potential is not sacrificed because of lodging. Genetic variability for resistance to lodging is observed in chickpea germplasm (VSH, personal observation) and identification of genes and transfer of genes for resistance to lodging into commercial cultivars make them more responsive to better agronomic management conditions such as irrigation water and chemical fertilizers thereby, increasing the yield potential of chickpea.

BREEDING FOR LOW TEMPERATURE TOLERANCE

Early flowering and ability to set pods early are desirable traits of chickpea in the cool long season environments of the semi-arid tropics. Early flowering cultivars are advantageous in this region since they escape end of season drought and heat stress as they are likely to mature early. However, early flowering has no advantage unless they can set pods early at low temperatures. The prevalence of low temperature during early flowering is a major cause of low yield of chickpea in sub-tropical regions of South Asia (Saxena, 1980). Both Freezing (mean daily temperature $< -1.5^{\circ}\text{C}$) and chilling temperatures (mean daily temperature between -1.5°C to 15°C) are known to affect chickpea at various stages of development from germination to maturation (Croser *et al.*, 2003). The reproductive period is a vital phase in the life cycle of all annual flowering plants, and metabolism during this phase ultimately determines crop yield (Thakur *et al.*, 2010). Plants exposed

to cold temperatures during the reproductive stage show decreased metabolic rates resulting in poor yields. The early formed flowers fail to set pods where temperature during early flowering phase of chickpea ranges from 5-20 °C. Low temperature (less than 15 °C) at flowering affects both the vegetative development and function of reproductive structures in the chickpea flower (Clarke and Siddique, 2004). It induces flower abscission or abortion (Srinivasan *et al.*, 1999; Nayyar *et al.*, 2005a) and has a deleterious effect on pollen germination and tube growth leading to poor pod or seed set and unstable grain yield (Savitri *et al.*, 1980). During chilling stress, reproductive tissues such as the tapetum, style, and endosperm suffer nutrient deficiency as the mobilization of solutes from source to sink is reduced (Nayyar *et al.*, 2007). Srinivasan *et al.* (1999), demonstrated that the ovule viability is compromised by callose deposition under low temperature regimes resulting in slowing of ovule maturation, decreasing ovule size by 10-28%, increasing embryo abortion and reduced proportion of fertilized ovules in all cultivars, and in case of few cultivars with late opened flowers the embryo sac was missing entirely. They also observed that cold stress reduced the size of the ovary and style, increased the distance between anther and stigma, reduced anther dehiscence, and therefore pollen load on the stigma resulting in reduced pollen transfer to stigma and limited fertilization. The cold stress decreased the rate and duration of seed filling, and increased seed and pod abortion producing smaller sized seeds (Kaur *et al.*, 2008; Nayyar *et al.*, 2007). In chilling stressed chickpea, increased electrolyte leakage, decreased

chlorophyll concentration and photosynthetic activity, and a reduction in the supply of photo-assimilates to sink tissues were observed (Nayyar *et al.*, 2005b). Kaur *et al.* (2008) observed increased rate of respiration, ion leakage, decreased photosynthetic activity, and carbohydrate metabolism at chilling temperatures. The chilling tolerant chickpea genotypes having the ability to set pods and seeds are available in the world germplasm collection. Besides having the ability to set pods and seeds during cold spells, cold tolerant genotypes are likely to have other advantages such as reduction of excessive vegetative growth leading to less lodging, reduced incidence of pests and diseases, and greater harvest index (Saxena *et al.*, 1988; Saxena and Johansen, 1990). All these advantages of cold tolerance lead to higher harvest index in chickpea varieties to achieve increased productivity and yield stability. Such varieties are also suitable for introduction of chickpea in new cropping systems like chickpea-sugarcane in the North Western India (Srinivasan *et al.*, 1998). Winter-sown chickpea in West Asia and North Africa (WANA) region often experiences freezing temperatures during the seedling and early vegetative stages and chilling temperatures at the early reproductive stage. Freezing temperature reduces growth vigour and vegetative biomass, whereas chilling temperature at flowering causes flower and pod abortion. Therefore, cultivars for winter sowing in WANA need to have cold tolerance both at seedling and flowering stages. Screening of germplasm has identified several cold tolerant genotypes from the cultivated (Singh *et al.*, 1989; 1995) and wild species (Robertson *et*

al., 1995). The inheritance of freezing tolerance indicated the presence of both additive and dominance gene effects, additive being the more important in chickpea (Malhotra and Singh, 1990; 1991). Malhotra and Singh (1991) suggested that early generation selection should be effective to improve freezing tolerance due to high heritability and the limited number of genes involved in the inheritance of this trait in chickpea. A pollen selection method was applied to transfer chilling tolerance from ICCV 88516 to chilling sensitive cultivars, leading to development and release of chilling tolerant cultivars Sonali and Rupali (Clarke *et al.*, 2004). RFLP markers for chilling tolerance were identified and subsequently converted to SCAR markers. These were used successfully to select chilling tolerant progeny from a cross between Amethyst and ICCV 88516 but were ineffective in other crosses (Millan *et al.*, 2006). A cDNA microarray approach was applied to previously identified stress responsive genes from chickpea to identify potential candidate genes for improving cold, salinity, and drought tolerance in chickpea (Mantri *et al.*, 2007). Dinari *et al.* (2013) using the cDNA-AFLP approach studied the expression pattern of chickpea genes under low temperature stress and identified genes that could facilitate breeding to improve the cold tolerance in the chickpea plant.

BREEDING FOR RESISTANCE TO MAJOR DISEASES

Fusarium wilt

Fusarium wilt caused by *Fusarium oxysporum* (Schlechtend.: Fr) f. sp. *ciceri* (Padwick) is the most

devastating disease of chickpea prevalent in the semi-arid tropic (SAT) regions of Asia, Africa, and South America where the chickpea growing season is dry and warm (Nene *et al.*, 1996). Yield loss up to more than 90% has been reported in susceptible cultivars. Eight physiological races (0, 1A, 1B/C, 2, 3, 4, 5, and 6) of the wilt pathogen with distinct geographical distribution have been identified by their differential reactions on chickpea lines (Haware and Nene, 1982; Jimenez-Diaz *et al.*, 1993; Halila and Strange, 1996). Effective field, greenhouse, and laboratory techniques for resistance screening have been developed (Nene *et al.*, 1981). Several sources of absolute resistance have been identified in the germplasm collection of chickpea. Germplasm lines and cultivars with resistance to more than one race of wilt pathogen are also available. For example, WR 315 is resistant to all races except race 3, while JG 74 is resistant to race 0, 1A, 3, 4, and 6 (Haware, 1998). The studies on the genetics of resistance to six races (0, 1A, 2, 3, 4, and 5) of the wilt pathogen revealed that resistance to each of these races is governed by 1 to 3 genes. Molecular markers have been identified for at least one resistance gene for each of these six races (Table 1). These resistance genes form two clusters on two different linkage groups (Sharma and Muehlbauer, 2007). Molecular breeding strategy has been deployed to introgress resistance gene (s) into elite chickpea cultivars. Pratap *et al.*, (2017) developed 5 highly resistant lines with *Foc* 2 gene in the background of an elite cultivar, Pusa 256, using marker-assisted backcrossing (MABC). Another desi chickpea cultivar, Vijay, was used as a

donor to introgress resistance to race 2 into Pusa 256 using two SSR markers (TA 37 and TA110). Varshney *et al.* (2014a) used MABC breeding method to develop 3 introgression lines with resistance to race 1 of Fusarium wilt in background of C 214. In the future, molecular markers closely linked to genes conferring resistance to different races of wilt can

help in pyramiding wilt resistance genes in a single cultivar. Several desi and kabuli chickpea cultivars developed through conventional breeding methods with durable and stable resistance to Fusarium wilt have also been released in several countries including India (Choudhary *et al.*, 2013).

Table 1. Genes identified for Fusarium wilt resistance in chickpea.

Resistance gene (s)	CaLG	Marker (s)	Marker type	Reference
<i>foc 0, foc 4 and foc 5</i>	2, 3	CS-27, UBC-170	RAPD	Tekeoglu <i>et al.</i> (2000)
<i>foc 2</i>	2	TA37	STMS	Winter <i>et al.</i> (1999)
<i>foc 2</i>	2	TS47	STMS	Winter <i>et al.</i> (1999)
<i>foc 1, foc 4 and foc 5</i>	2	CS27, TA96, TA27	STMS	Winter <i>et al.</i> (2000)
<i>foc 1, foc 3 and foc 4</i>	2	TA96, CS27A	STMS	Sharma <i>et al.</i> (2004)
<i>foc 2</i>	2	H3A12	SSR	Lichtenzveig <i>et al.</i> (2005)
<i>foc 3</i>	2	TA96, TA 27, CS27A	STMS, SCAR	Sharma <i>et al.</i> (2004)
<i>foc 1 and foc 3</i>	2	GA16	STMS	Milan <i>et al.</i> (2006)
<i>foc 1 and foc 3</i>	2	TAA60	STMS	Milan <i>et al.</i> (2006)
<i>foc 1 and foc 3</i>	2	TA 194	STMS	Milan <i>et al.</i> (2006)
<i>foc 1 and foc 3</i>	2	TS82	STMS	Milan <i>et al.</i> (2006)
<i>foc 1 and foc 3</i>	2	TA110	STMS	Milan <i>et al.</i> (2006)
<i>foc 1, foc 2 and foc 3</i>	2	TA110, TA96, H1B06y	STMS	Gowda <i>et al.</i> (2009)

Ascochyta blight

Ascochyta blight caused by *Ascochyta rabiei* (Pass.) Labr., is a highly devastating foliar disease in West and Central Asia, North Africa, North America, and Australia. In the Indian subcontinent, it is prevalent in North-west India and Pakistan. Cool, cloudy, and humid weather during the flowering to podding stage favours the onset of the disease. Nene and Reddy

(1987) reported the occurrence of 5 pathotypes while Udupa *et al.* (1998) have reported only 3 pathotypes (I, II, and III). Based on aggressiveness of the pathogen, Chen *et al.* (2004) classified the pathotypes into two broad groups: pathotype I (less aggressive) and pathotype II (aggressive). Screening of more than 13,000 germplasm accessions at ICARDA has identified 11 kabuli (ILC 72, ILC 196, ILC 201, ILC 202, ILC

2506, ILC 2956, ILC 3274, ILC 3279, ILC 3346, ILC 3956, and ILC 4421) and 6 desi (ICC 3634, ICC 4200, ICC 4248, ICC 4368, ICC 5124, and ICC 6981) accessions as resistant (Reddy and Singh, 1984). Singh and Reddy (1993) reported that 3 desi accessions (ICC 4475, ICC 6328, and ICC 12004) and 2 kabuli accessions (ILC 200 and ILC 6482) showed resistance to six pathotypes of the blight pathogen. Some of these resistant genotypes such as ILC 72, ILC 195, ILC 482, and ILC 3279, have been directly released as varieties in different countries.

The national breeding programmes of many countries have developed chickpea cultivars with improved resistance to ascochyta blight. They are Pusa 261, PBG 1, GNG 469, and Gaurav in India; Dasht, NIFA 88, CM 72, CM 88, CM 98, and CM 2000 in Pakistan; Dwelley, Sanford, Myles, Evans, and Sierra in USA; CDC Frontier, CDC Anna, CDC Cabri, CDC Desiray, CDC Nika, and Amit in Canada; and Sonali, Rupali, Genesis 508, Genesis 090, Genesis 836, Yorker, Flipper, Nafice, and Almez in Australia. Milan *et al.* (2006) reviewed the progress made in identification of markers for ascochyta blight resistance QTLs. QTLs governing resistance to ascochyta blight at the seedling or adult plant stages were reported in either inter- or intraspecific populations of chickpea (Anbessa *et al.*, 2009; Collard *et al.*, 2003; Flandez-Galvez *et al.*, 2003; Udupa and Baum 2003) (Table 2). Daba *et al.* (2016) identified 8 QTLs for ascochyta blight resistance that explained 10% to 19% of phenotypic variation. These QTLs were present on all chromosomes except chromosome 5. Previously, QTLs for ascochyta blight resistance were reported on LG1 and LG3 by Flandez-Galvez *et al.*,

(2003), and on LG2 and LG4 by Udupa and Baum (2003). QTLs on LG3, LG4, and LG6 were identified for ascochyta blight resistance in an F₂ population derived from ICCV 96029/CDC Frontier (Anbessa *et al.*, 2009). A linkage map of chickpea with 84 markers (82 SSRs and 2 ESTs) was constructed using F₂ and F_{2:3} population of an intra-specific cross between ICCV 04516 (resistant) and Pb 7 (susceptible). Three AB resistant QTLs were mapped, one on LG3 and QTL 2, and 3 on LG4 (Ramakuri, 2005).

Botrytis gray mould

Botrytis gray mould (BGM) caused by *Botrytis cineria* Pres is an important foliar disease of chickpea in northern India, Nepal, Bangladesh, Pakistan and Australia (Haware and McDonald, 1992; Corbin, 1975). The BGM fungus is necrotrophic and has extreme host range, high variability, and wide adaptability. More than 12,000 germplasm accessions and breeding lines were screened at ICRISAT for resistance to BGM, but none was found to be highly resistant (Pande *et al.*, 2002). However, moderate resistance has been observed in some genotypes like ICC 14344 which was released in India as Avarodhi. The genetics of resistance to BGM reveals that it is under the control of a single dominant gene (Rewal and Grewal, 1989) or due to complementary action of dominant genes (Rahul *et al.*, 1995). Anuradha *et al.* (2011) identified 3 QTLs which together accounted for 43.6% of the variation for BGM resistance and mapped on two linkage groups LG 3 and LG 6. QTL1 explained about 12.8% of the phenotypic variation for BGM resistance and was mapped on LG 6A.

QTL2 and QTL3 accounted for 9.5% and 48% of the phenotypic variation

for BGM resistance, respectively, and were mapped on LG 3.

Table 2. QTLs identified for *Ascochyta* blight resistance in chickpea.

CaLG	Marker(s)	Marker type	Genetic effects	Reference
LG 1 and LG 6	UBC733b, UBC181a, <i>Dia4</i>	RAPD	50.3 and 45%	Santra <i>et al.</i> (2000)
LG 1, 2 and 3	TS45, TA146, TA130	STMS	76%	Flandez-Galvez <i>et al.</i> (2003)
LG 4	CS5b650, OPB17c560	GA2, STMS, RAPD	N/A	Collard <i>et al.</i> (2003)
LG 2 and 4	Aa20, TA72, ar1	STMS	35.9%	Udupa and Baum (2003)
LG 2, 4 and 6	GA16, GA24, GAA47, Ta46	STMS	69.2%	Cho <i>et al.</i> (2004)
LG 2	OPA109746, UBC881621	RAPD	28%	Cobos <i>et al.</i> (2006)
LG 4	TA194	STMS	55%	Iruela <i>et al.</i> (2007)
LG 3, 4 and 6	TA64, TS54, TA176	STMS	56%	Taran <i>et al.</i> (2007)
LG 2, 4 and 8	TR19, TS54, TA132, TS45	STMS	14-38%	Anbessa <i>et al.</i> (2009)
LG 3, 4 and 6	TA125, TA72, GA26	STMS	46.5%	Kanouni <i>et al.</i> (2009)
LG 3, 4 and 6	STMS11, TA130, CaM2049, H4G11	STMS/SSR	31.9%	Sabbavarapu <i>et al.</i> (2013)
LG 4	TA146, TA72	STMS	59%	Stephens <i>et al.</i> (2014)

Some chickpea accessions such as ICCL 87322 and ICCV 88510 with erect plant type were found to be less affected by the disease possibly because of the erect plant type which allows air circulation thereby reducing build-up of humidity and spread of disease. Recent breeding efforts have resulted in lines with good agronomic characters and moderate level of resistance against BGM (ICCV 98502, 98503, 98505). Higher level of resistance has been identified in accessions of wild chickpea species. Screening of 36 germplasm accessions belonging to seven annual wild *Cicer* species for reaction to BGM in a controlled environment growth room, identified three accessions of *C. bijugum* (ICCW 41, 42, and 91) to

possess good level of resistance (Haware *et al.*, 1992), but this resistance has yet to be incorporated in cultivated species.

Development of multiple disease-resistant varieties through conventional breeding approaches is a tedious and long-term process due to difficulties in selecting plants with desired combination of genes in the segregating generations. Marker assisted selection can prove to be an effective and efficient breeding tool for detecting, tracking, and pyramiding stress-resistant genes in the segregating generations to improve yield potential in chickpea.

BREEDING FOR ALTERNATE PLANT TYPES IN CHICKPEA

In flowering plants, genotypes are morphologically classified as indeterminate or determinate depending on whether the terminal meristems are vegetative or reproductive. In indeterminate genotypes, the terminal meristems at the branch and stem apices remains in a vegetative state during which it controls the production of new nodes with leaves, produce an inflorescence meristem that only generates axillary floral meristems and hence continues to grow in stem length, flower and set pods if temperature and moisture permit (Bradley *et al.*, 1997; Tiana *et al.*, 2010). In determinate genotypes, the terminal meristems have eventually converted from a vegetative to a reproductive state, resulting in the production of a terminal flower and as a result, the vegetative growth ceases at flowering or continues for a short period thereafter (Bernard, 1972; Bradley *et al.*, 1997). Thus, the stem growth habit plays an important role in deciding the plant type or architecture, which is of major agronomic importance as it determines adaptability of plant to cultivation and potential grain yield (Reinhardt and Kuhlemeier, 2002). Chickpea (*Cicer arietinum* L.) is an indeterminate plant and continues to produce vegetative growth whenever soil moisture, temperature, and other environmental factors are favorable (Williams and Saxena, 1991). Because of its indeterminate growth habit, excess water triggers vegetative growth that acts as a competitive sink for developing pods thereby reducing fruit set (Khanna-Chopra and Sinha, 1990). The indeterminacy lead to

excessive vegetative growth due to prolonged growth cycle and a strong within plant competition between the reproductive and vegetative growth for the assimilate partitioning (Huyghe, 1998). Indeterminate growth habit is also reported to be disadvantageous under Western Canadian conditions, where it continues to flower and set new pods under declining temperatures and often wet conditions resulting in delayed maturity and increased risk of frost damage (Anbessa *et al.*, 2007). The determinacy is useful both under conditions of excessive vegetative growth and severe drought (van Rheenen, 1996). The stem growth habit in chickpea is governed by two non-allelic genes with dominance epistasis (Hegde, 2011). The two epistatic genes for stem growth habit are designated as *Dt1/dt1* and *Dt2/dt2* with *Dt1* epistatic to *Dt2* and *dt2*. The *Dt1* allele either in homozygous (*Dt1Dt1Dt2-* and *Dt1Dt1dt2dt2*) or heterozygous (*Dt1dt1Dt2-* and *Dt1dt1dt2dt2*) condition produced indeterminate growth habit. The *Dt2* allele either in homozygous (*dt1dt1Dt2Dt2*) or heterozygous (*dt1dt1Dt2dt2*) condition produced semi-determinate growth habit, but only in the absence of *Dt1*. The presence of recessive alleles at both loci in homozygous (*dt1dt1dt2dt2*) condition produced a determinate phenotype. Genes for determinate and semi-determinate growth habits have contributed to greater seed yields in soybean due to reduced lodging and reduced vegetative-reproductive competition for photosynthates in the more determinate types (Green *et al.*, 1977). The determinate growth habit has also been exploited in soybean breeding to accelerate flowering and shorten the flowering period (Cober

and Tanner, 1995). Like the 'green revolution' semi-dwarf cereals, semi-determinate soybean varieties are lodging resistant and particularly suitable for planting in high fertility and irrigated environments (Liu *et al.*, 2016). Determinate genotype was better adapted to cool and wet conditions resulting in early maturity and produced higher and stable yields than indeterminate type in white lupin (Julier *et al.*, 1993). In chickpea, a semi-determinate mutant was more responsive to supplemental N as compared to its indeterminate parent (Shamsuzzaman *et al.*, 2002). Hegde (2011) also reported that it was possible to combine determinate to semi-determinate growth habit and other economically important traits such as early flowering and maturity, plant height, seed size, and yield in chickpea. Therefore, utilization of genes for determinate to semi-determinate stem growth in the genetic restructuring of plant type is expected to result in a chickpea cultivar better adapted to cool climate and better agronomy, particularly high fertility and irrigated conditions, thereby increasing and stabilizing chickpea yields in cooler long-season sub-tropical environments of semi-arid tropics.

GENETIC DIVERSITY, GERMPLASM ENHANCEMENT, AND YIELD POTENTIAL

Yield potential is defined as the yield of a cultivar when grown in environments to which it is adapted, with nutrients and water non-limiting, and with pests, diseases, weeds, lodging, and other stresses effectively controlled (Evans, 1993). Average yields of chickpea in its major growing regions are only about 956 kg per ha

(FAO, 2016) and continue to be low when compared to its competing crops. When the various biotic and abiotic stress factors are minimized chickpea yield in the range of 3-4 tons per ha can be recorded (Saxena and Johansen, 1990). Exceptionally high yields of 6.2 tons per ha has been reported from Israel (FAO, 2013), but such a case is very rare. Although, the intensive breeding efforts both at national and international levels has been successful in enhancing the productivity marginally, reducing crop duration, improving resistance to biotic stresses particularly Fusarium wilt, a significant breakthrough in its productivity has not been possible so far. In fact, the increase in cereal production and productivity in recent decades has been achieved mostly from irrigated land through the diffusion of improved varieties and better agronomic practices suitable for specific ecosystems (Araus *et al.*, 2008). Therefore, expanding the cultivation of chickpea under irrigated high fertility conditions could be considered as another option to achieve breakthrough in its productivity.

Grain yield of chickpea is a function of biomass and harvest index in any environment. Therefore, grain yield can be increased either by increasing the biomass or harvest index or both. For maximum yields to be attained, a pulse crop should have high biomass coupled with high harvest index (Jain, 1986). It has been demonstrated in wheat that crossing between parents with high expression of biomass (source) and harvest index (sink) and other yield components can boost genetic gains (Reynolds *et al.*, 2017). Results have shown that selection of tall types with more number of secondary

branches/plant and seeds/plant and seeds of large size would be highly rewarding in increasing biomass and grain yield of chickpea in different environments (Omar and Singh, 1997; Singh *et al.*, 1990; Hegde and Kumar, 2015). The high harvest index, early flowering, and maturity are the important traits contributing to higher yield under terminal drought stress (Rehman *et al.*, 2011). Genetic diversity for characters of economic importance is a prerequisite for any crop improvement programme and to assure its continued genetic up-gradation or enhancement. Use of more diverse genotypes and utilization of desirable alleles in right combination(s) are expected to contribute to the development of cultivars with high and stable grain yield. With the development of ideotype concept by Donald (1968), attempts are made also in chickpea to hypothesize and develop an ideal plant ideotype for improved adaptation to specific environments and grain yield. Therefore, information on the extent of genetic diversity and utilization of genetically diverse genotypes as base material for target traits are vital for the successful breeding of an ideal plant ideotype in chickpea. But the attempts in chickpea crop are limited mainly to yield and its component traits (Bahl and Jain, 1977; Mani and Bahl, 1990). With the greater awareness of the role of earliness, root traits, lodging resistance, cold tolerance, and determinate to semi-determinate stem growth in the chickpea yield formation, the inclusion of diverse genotypes for these parameters in deriving an ideal plant ideotype is now being increasingly felt. The extent of genetic diversity for plant type traits in association with yield components forms the

prerequisite for planning an efficient breeding strategy for designing an ideal plant type in chickpea for better agronomy. The sources of genes for earliness (Hegde, 2010), root traits (Kashiwagi *et al.*, 2008), chilling tolerance (Singh *et al.*, 1989), lodging resistance (Ali and Kumar, 2005), and stem growth habit (Hegde, 2011) are already available in chickpea. A large amount of phenotypic diversity for agronomic traits is found in the world chickpea collection (Pundir *et al.*, 1988), chickpea core (Upadhyaya *et al.*, 2001) mini-core (Upadhyaya and Ortiz, 2001), and rich allelic diversity in the reference set (Upadhyaya *et al.*, 2008) that can be effectively utilized in the development of an efficient plant ideotype. Mining allelic variation in the mini-core collection and reference set will facilitate identification of diverse germplasm with beneficial traits for enhancing the genetic potential of chickpea globally and broaden the genetic base of cultivars (Upadhyaya *et al.* 2011). Chickpea is a highly self-pollinated crop and hence breeding methods commonly employed for the genetic improvement of agronomic traits in such crops are also applicable in chickpea breeding. Indirect selection for yield via pod number and seed weight was found to be more efficient than direct selection for yield in chickpea yield improvement (Kumar and Bahl, 1992). The seed size and pod number (seed number) per plant are the two important components of harvest index (sink size) in chickpea (Hegde and Kumar, 2015). The use of available molecular markers linked to genomic regions controlling time of flowering (Cobos *et al.*, 2009), root traits (Varshney *et al.*, 2014), disease resistance (Li *et al.*, 2015), and major components of grain yield (Cobos *et*

al., 2009) in the marker assisted selection (MAS) would increase the efficiency of chickpea breeding of a new plant type for better agronomy and adaptation to diverse growing environments. The genomic approaches that integrates the use of genomic tools in breeding has the potential to generate superior genotypes with improved adaptation and enhanced grain yield in chickpea.

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