

Breeding for biotic stress resistance in chickpea: progress and prospects

Haobing Li · Matthew Rodda · Annathurai Gnanasambandam · Mohammad Aftab · Robert Redden · Kristy Hobson · Garry Rosewarne · Michael Materne · Sukhjiwan Kaur · Anthony T. Slater

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Abstract Chickpea (*Cicer arietinum* L.) is the third most economically important food legume in the world. Its yield potential is often limited by various biotic stresses, including fungal and viral diseases, insects, nematodes and parasitic weeds. Incorporating genetic resistance into cultivars is the most effective and economical way of controlling biotic stresses and this is a major objective in many breeding programs. Extensive searches for resistances have been conducted by screening commercial varieties, landraces and closely related species. Resistances to disease such as Ascochyta blight and Fusarium wilt have been identified and molecular tools are being used to increase the efficiency of gene transfer from wild species into chickpea elite genotypes. Quantitative trait loci for resistance genes have been located on linkage maps and molecular markers associated with these loci can

potentially be used for efficient pyramiding of the traits. Significant chickpea genomic resources have been developed in order to investigate resistance genes. Such resources include an integrated genetic map, expressed sequence tag libraries, bacterial artificial chromosome libraries, microarrays and draft genome sequences. Although these resources have yet to be used to improve chickpea cultivars in the field, this is likely to change in the near future. These genomic resources, as well as high-resolution phenotyping tools and cutting-edge technologies such as next-generation sequencing, promise to increase efficiency as work to identify valuable candidate genes continues.

Keywords *Cicer arietinum* · Fungi · Virus · Insects · Nematodes · Molecular tools

H. Li (✉) · M. Rodda · A. Gnanasambandam · M. Aftab · R. Redden · G. Rosewarne · M. Materne
Victorian Department of Economic Development, Jobs, Transport and Resources, 110 Natimuk Road, Horsham, VIC 3401, Australia
e-mail: haobing.li@ecodev.vic.gov.au

Present Address:
A. Gnanasambandam
Plant Genetic Solutions Pty Ltd, Horsham, VIC 3400, Australia

K. Hobson
NSW Department of Primary Industries, 4 Marsden Park Road, Tamworth, NSW 2340, Australia

Present Address:
M. Materne
Global Grain Genetics Pty Ltd, Horsham, VIC 3400, Australia

S. Kaur · A. T. Slater
Victorian Department of Economic Development, Jobs, Transport and Resources, AgriBio, Centre for AgriBioscience, 5 Ring Road, Bundoora, VIC 3083, Australia

Introduction

Chickpea is the world's third most important food legume after peas (*Pisum sativum* L.) and beans (*Phaseolus vulgaris* L.) (Saxena 1990). It is cultivated in over 50 countries, with a total area of 12.14 million hectares and annual production of 11.30 million tons (FAOSTAT 2012). It is often grown in rotation with other crops as a disease break and helps maintain soil fertility by fixing atmospheric nitrogen (Singh 1997). Chickpea is a highly nutritious grain with its seeds containing 20–30 % protein, 40 % carbohydrate and 3–6 % oil (Gil et al. 1996). It provides a high-quality protein source for people in both developed and developing countries (Deb and Khaleque 2009). The stover of chickpea is also fed to some animals as a nutrient-rich supplement to their major cereal fodder in lean seasons (Deb and Khaleque 2009).

Global chickpea production is affected by major biotic stresses, including fungal, bacterial and viral diseases, insect pests, nematodes and parasitic weeds. Incorporating genetic resistance into the crop is the most economically efficient way of controlling biotic stresses (Rubiales and Fondevilla 2012). Many of the major chickpea biotic stresses have been overcome by developing enhanced resistance in elite cultivars. However, there are still a number of biotic stresses for which no resistance has been identified. This review focuses on the progress that has been made to breed resistance to major biotic stresses and the future prospects of using molecular tools to assist chickpea breeding.

Origin and genetic diversity

Chickpea is in the family Fabaceae (or Leguminosae) and the tribe Ciceraceae Alef (van der Maesen 1987) and is the only cultivated species of the *Cicer* genus. Domestication of chickpea, along with wheat, pea and lentils (Redden and Berger 2007), dates back 10,000–12,000 years in the Fertile Crescent of Iran, Turkey and Israel/Jordan. Three secondary centers of diversity are Ethiopia (plus the Mediterranean west from Greece/Crete), central Asia to the Indian sub-continent and Asia Minor to Iran and the Caucasus. Further distribution to the Americas and Australia occurred after European contact in these areas. The Desi type, with a small triangular seed, is the oldest

type, with the larger round “rams head” Kabuli type being domesticated later in the Mediterranean region. The Kabuli type has narrower genetic diversity, geographic distribution and morphological variation (Redden and Berger 2007).

The domestic gene pool of chickpea is narrower than that of wheat, pea or lentil due to (i) the limited adaptive genetic variation of the wild progenitor *Cicer reticulatum* (only found in southeast Turkey), (ii) the genetic bottleneck of domestication, in which only a limited range of variants were selected, and (iii) a further selection for spring habit with loss of vernalization. As a result, chickpea has little genetic diversity for disease resistance (Abbo et al. 2007). However, the wild relatives of chickpea can increase the genetic diversity of this crop by providing a wider range of ecotypes that contain sources of pest and disease resistance (Redden and Berger 2007).

The wild relatives of chickpea have a wide geographic distribution, ranging from sea level (*C. judiacum*) to 5000 m (*C. microphyllum*), and from central Asia and India to the Canary Islands (Abbo et al. 2007). *C. pinnatifidum* is an annual with the widest distribution, being found from Armenia to the eastern Mediterranean, while other annuals are restricted to smaller areas. For example, *C. judiacum* is only found in Israel-Palestine, *C. cuneatum* at medium–high elevation in Ethiopia, Egypt and Saudi Arabia and *C. yamashitae* being restricted to Afghanistan (Van der Maesen et al. 2007).

The perennial wild relatives grow in terrain ranging from rocky slopes to forests, with *C. anatolicum*, *C. incisum*, *C. microphyllum* and *C. montbrettii* being widely distributed variously from the Balkans, to the eastern Mediterranean region and eastwards to Asia (Abbo et al. 2007; Van der Maesen et al. 2007). Although the tertiary gene pools of the perennial and annual species are genetically equally separated from the domestic gene pool (Nguyen et al. 2004), the annual wild relatives have been more widely studied as potential sources of disease resistance genes in comparison with the perennials (Singh et al. 2007).

A genetic diversity study in *Cicer* based on crossability, karyotype, isozyme polymorphism, seed protein and RAPD analysis has demonstrated a close genetic relationship among *C. arietinum*, *C. reticulatum* and *C. echinospermum* which formed a primary crossability group (Ahmad 1999). This was supported by an analysis of the external transcribed sequence

(ETS) of 18s rRNA sequences (Fig. 1). The ETS data also indicated a close association of the cultivated *C. arietinum* to *C. bijugum*, *C. judaicum* and *C. pinnatifidum*, which may infer that these species also played a role in the evolution of the cultivated species. This conclusion contradicted the previous finding of AFLP analysis (Nguyen et al. 2004), but is in agreement with a more recent study by van der Maesen et al. (2007). There has been limited success in crossing *C. bijugum*, *C. judaicum* and *C. pinnatifidum* with species in the primary crossability group (Singh et al. 1994; ICARDA 1998), however, tissue culture methods such as embryo rescue techniques may provide the means to overcome crossability barriers

to produce wide and interspecific hybridizations in the future (Badami et al. 1997). Furthermore *C. judaicum*, *C. bijugum* and particularly *C. pinnatifidum* possess very high levels of genetic diversity and were reported as sources of resistance or tolerance to biotic and abiotic stresses (Singh et al. 1998a, b) and therefore offer great potential as sources of resistance for the future of chickpea breeding.

Genetic resources for resistance breeding

Most of the genetic resources for chickpea are in *ex situ* genebanks. The two main genebanks are the

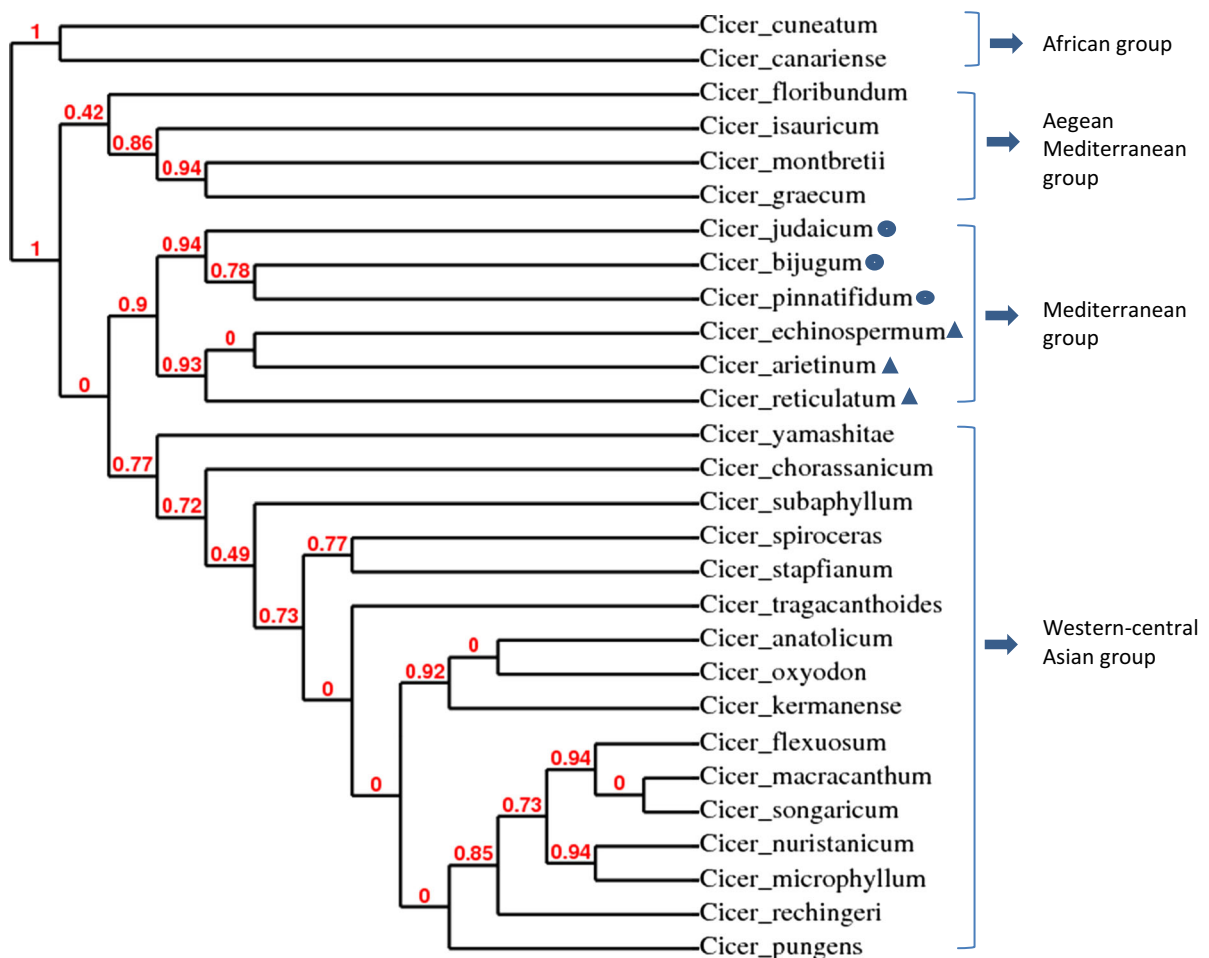


Fig. 1 Distribution and phylogeny of 28 cicer species based on the partial sequence of 18s rRNA gene. *Filled triangle* represents the *Cicer* species with least distance to cultivated chickpea and composed the primary crossability group; *filled circle* represents some annual species with close distance and

potential crossability to cultivated chickpea. The 18s rRNA sequences were sourced from NCBI data base and the dendrogram tree was generated using a robust phylogeny analysis method (Dereeper et al. 2008)

International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in India with over 20,000, mainly Desi, accessions, and the International Center for Agricultural Research in the Dry Areas (ICARDA) in Syria with 13,800, mainly Kabuli, accessions. These collections are mainly traditional landraces, seed-lots derived from material that has evolved over centuries of selection in farmers fields. In addition to these genebanks, there are other important collections in India (16,000), the US Department of Agriculture (6200), Iran (5600), the Aegean Agricultural Research Institute in Turkey (2000), the Vavilov Institute in St. Petersburg (2600), and the Australian Grains Genebank in Horsham, Australia (9300 accessions). In addition, other collections exceeding 1000 accessions are in the Ukraine, Spain, Portugal, Ethiopia and Hungary (Guarino 2008). The majority of these collections consist of over 50 % landraces. Many countries around the Fertile Crescent and in central Asia have small collections with limited representation of both landraces and wild relatives (Guarino 2008).

Wild relatives of *C. arietinum* are generally under-represented in the genebank collections, even though they are genetically rich in comparison to the landrace collections. The level of duplication between collections is unclear, since many accessions have been shared between collections. For example, the world collection of annual wild *Cicer* species only consists of 593 entries held in nine genebanks around the world, with 285 being known as separate accessions of 8 wild species (Berger et al. 2003; Ahmad et al. 2005).

Breeding for fungal disease resistance

Fungal diseases are the most important biotic stresses limiting grain production in chickpea. There are up to 172 pathogens that attack chickpea, of which 67 are fungal species. The most important diseases of chickpea are *Ascochyta* blight (AB), *Botrytis* grey mould (BGM), *Fusarium* wilt, *Phytophthora* root rot, dry root rot, *Sclerotinia* stem rot and rust (Singh et al. 2003a, b; Ahmad et al. 2005; Singh et al. 2007; Knights et al. 2008).

Ascochyta blight

AB, caused by *Ascochyta rabiei* (Pass.) Labr. (teleomorph, *Didymella rabiei* (Kov.) v. Arx), is a severe

disease in most chickpea-growing regions of the world. *A. rabiei* can infect all above-ground plant parts, and symptoms can appear any time after crop emergence. AB first appears as grey areas on the leaves, stems or pods that quickly turn into brown lesions with dark borders. As the disease progresses, small, circular, brown-black pycnidia develop in the center of the lesions. Concentric rings of pycnidia are the most diagnostic characteristic of the disease (Markell et al. 2008) (Fig. 2). Cool wet conditions (15–25 °C, 65–100 % RH) normally favour disease development and spread. The disease can significantly reduce seed quality and complete yield loss under heavy infection has been recorded (Davidson et al. 2004; Pande et al. 2005).

Considerable efforts have been made to develop screening methods to identify genetic resistance to AB in chickpea. Both controlled environment and field screening methods are being used to identify resistant genotypes. Temperature and relative humidity are critical factors in artificial disease establishment. A high level of relative humidity during the first 24 h post-inoculation is critical. Growth chambers where relative humidity can be controlled are useful, however additional steps, such as use of foggers or mist irrigation immediately after inoculation can help maintain relative humidity at high levels and ensure successful infection (Udupa and Baum 2003; Chen et al. 2005). Spore concentration in the inoculum is also a significant factor, with the ideal level being the lowest spore concentration that causes sufficient disease in a majority of host genotypes. This facilitates the greatest discrimination among the lines in a trial.

Field screening techniques for AB resistance in chickpea were initially developed by Singh et al. (1981). Screening was carried out in areas where the prevailing weather conditions were conducive to the development of disease and preferably where natural inoculum is abundant. The procedure consists of planting susceptible check plants every two or four tested entries, scattering infected plant debris collected in the previous season, maintaining high humidity through sprinkler irrigation, and, if needed, spraying the test entries with a spore suspension of a virulent isolate or mixture of isolates of *A. rabiei*. A resistant check was included in order to compare resistance of test entries with that of known resistant material.

Despite the availability of screening methods, variation in the reporting of races and pathotypes of



Fig. 2 Typical symptoms of some fungal diseases in chickpea. **a** *Ascochyta* blight. Note symptoms of leaf and pod infection (Image courtesy Hollaway et al. 2012); **b** *Botrytis* grey mould. Note fluffy, grey spore mass on the infected pod (Image courtesy Hollaway et al. 2012); **c** *Sclerotinia* stem rot. Note white mycelial growth starting to develop on infected stem (Image courtesy Hollaway et al. 2012); **d** Chickpea rust. Note the small, round, brown pustules on infected leaves (Image provided by Dr

Pedro Manjarrez-Sandoval from University of Arkansas); **e** *Fusarium* wilt. Note wilting of whole plant (Image courtesy Cunnington et al. 2007); **f** *Phytophthora* root rot. Note lack of lateral roots and discoloured root tissue (Image courtesy Hollaway et al. 2012); **g** Dry root rot. Note lack of lateral roots (Image provided by Professor Robert Harveson from University of Nebraska–Lincoln)

A. rabiei has made it difficult to compare results consistently across resistance studies (Vir and Grewal 1974; Qureshi and Alam 1984; Reddy and Kabbabeh 1985; Porta-Puglia et al. 1996; Udupa et al. 1998; Jamil et al. 2000; Chongo and Gossen 2003; Bayaa et al. 2004; Chongo et al. 2004). Classification of pathotypes is currently based on testing isolates against a set of host genotypes that have different

resistance to the aggressiveness of the pathogen. Reddy and Kabbabeh (1985) reported six races of *A. rabiei* from Syria and Lebanon using six chickpea differentials, while 13 chickpea genotypes were used to cluster the 41 *A. rabiei* isolates into 3 pathogenic groups (Porta-Puglia et al. 1996). By using ILC1929 (susceptible), ILC 482 (moderately resistant) and ILC 3279 (highly resistant), Udupa et al. (1998) classified

53 Syrian isolates into three pathotypes: pathotype I (least aggressive), pathotype II (aggressive) and pathotype III (most aggressive). Jamil et al. (2000) investigated the response of 130 isolates using a similar classification system. A differential set of chickpeas (Sanford, CDC Frontier, Amit, ILC 3856, ICC 4200, ICC 4475 and UC 27) was used by Chongo et al. (2004) who identified 14 different pathotypes based on their responses to the differential set. Chen et al. (2004) further suggested that these could also be assigned to two classes: pathotype I (less aggressive) and pathotype II (aggressive). In short, the attempts to classify virulence in *A. rabiei* have been inconclusive because of the variable number of categories proposed by different studies, the lack of reproducibility of disease phenotypes among laboratories and the lack of comparable standard check cultivars or pathotypes (Peever et al. 2012). In addition, the number of pathotypes identified may be an artefact of the pathogen mating system or sampling (Caten 1987), as two mating types have been reported that enable sexual recombination in *A. rabiei*. It has been difficult to correlate the mating types with different pathogenic groups, and it is unclear what the differences in pathogenicity between locations actually mean (Pande et al. 2005).

Evaluation of chickpea germplasm has shown that only 2 out of 6594 Kabuli chickpeas and 3 out of 12,749 Desi chickpeas were identified as resistant to *Ascochyta rabiei*, none of the 19,343 germplasm accessions evaluated were found immune or highly resistant (Reddy and Singh 1984, 1992). However, some accessions of the wild *Cicer* species such as *C. bijugum*, *C. echinospermum*, *C. pinnatifidum*, *C. reticulatum* were classified as resistant to AB, especially two *C. echinospermum* accessions, having good resistance (Collard et al. 2001) and being cross-compatible with *C. arietinum*, could provide valuable sources of resistance (Singh and Reddy 1993; Ahmad and Slinkard 2004). Tertiary wild accessions also contain sources of resistance with the *C. judiacum* accession ATC 46934 showing resistance to AB 21 days after inoculation (Nguyen et al. 2004). Four other *C. judiacum* accessions and one *C. pinnatifidum* were also resistant 14 days after inoculation in this study. Two of the *C. judiacum* accessions were also resistant in a study by Haware et al. (1992). Screening of wild accessions at ICRISAT revealed five accessions of *C. judiacum* that were resistant (Pande et al.

2006a, b). Some new sources of resistance to AB have been identified in chickpea breeding lines at ICRISAT (Pande et al. 2010). The feasibility of introgression from the tertiary to the domestic gene pool is a research focus at ICRISAT, and access to these novel sources of resistance (Table 1) is an important priority for chickpea breeders (Singh and Ocampo 1993; Mallikarjuna 1999).

Classic genetic studies of AB resistance have shown it to be governed by single dominant genes in Desi cultivars (Hafiz and Ashraf 1953; Vir et al. 1975; Eser 1976; Taleei et al. 2009). A resistant Kabuli genotype had resistance conferred through the combination of a recessive and a dominant gene (Singh and Reddy 1983). Other studies have reported incomplete host plant resistance to AB, with a single dominant gene plus recessive genes, complementary genes, and various quantitative genes according to pathotype and host genotype (Ahmad et al. 1952; Tewari and Pandey 1986; Kusmenoglu 1990; Dey and Singh 1993; Tekeoglu et al. 2000a; Millán et al. 2006; Singh et al. 2007; Bhardwaj et al. 2010; Rubiales and Fondevilla 2010). Varieties with improved AB resistance (Table 1) have been released and widely adopted by growers in India, Pakistan, Syria, the United States, Canada and Australia (Ahmad et al. 2005). However, genetic changes in pathogen populations (Vail and Banniza 2009) and reports of fungicide resistance in the pathogen (Chang et al. 2007) provide continuing challenges for breeders.

Botrytis grey mould

BGM, caused by *Botrytis cinerea* Pers., is the second most important disease of chickpea (Pande et al. 2006a, b) (Fig. 2). BGM can attack the chickpea plant at any stage of development (Hawthorne et al. 2012), but the disease usually appears around flowering time, when the canopy is fully developed and the weather is warm and humid (20–30 °C, 70–100 % RH). The flowers are more easily infected than other parts of the plant (Bakr and Ahmed 1992; Grewal et al. 1992; Haware and McDonald 1992; Haware 1998; Bakr et al. 2002; Pande et al. 2006a, b) and can subsequently abort. Botrytis can also infect pods and be carried into the next season through infected seed (Nene et al. 2012; Matthews et al. 2014). Relative humidity, leaf wetness and temperature are the most important factors for disease development (Tripathi and Rathi

Table 1 The most widely used resistant sources for the related individual diseases in chickpea

Diseases	Resistant sources	Level of resistance	References
Ascochyta blight	ILC72	Resistant	Singh et al. (1984)
	ILC191	Resistant	Singh et al. (1984)
	ILC3279	Resistant	Singh et al. (1984)
	ILC3856	Resistant	Singh et al. (1984)
	ICC4475	Resistant	Singh and Reddy (1993)
	ICC6328	Resistant	Singh and Reddy (1993)
	ICC12004	Resistant	Singh and Reddy (1993)
	ILC200	Resistant	Singh and Reddy (1993)
	ILC6482	Resistant	Singh and Reddy (1993)
	Sanford	Resistant	Muehlbauer et al. (1998a)
	Dwelley	Resistant	Muehlbauer et al. (1998b)
	Myles	Resistant	Muehlbauer et al. (1998c)
	Ambar	Resistant	http://www.heritage-seeds.com.au
	RIL58-ILC72/Cr5	Resistant	Rubio et al. (2006)
Botrytis grey mould	CH-2007-22	Resistant	Khan et al. (2010)
	ICC5035	Medium resistant	Rewal and Grewal (1989c)
	ICC1069	Medium resistant	Laha and Khatua (1988)
	GL84195	Resistant	Singh and Kaur (1989)
	GL84212	Resistant	Singh and Kaur (1989)
	GL86094	Medium resistant	Singh and Kaur (1989)
	ICCL97322	Resistant	Haware et al. (1997)
	<i>C. judaicum</i> 182	Highly resistant	Singh et al. (1998a, b)
	<i>C. judaicum</i> ILWC 19-2	Highly resistant	Singh et al. (1998a, b)
	<i>C. pinnatifidum</i> 188	Highly resistant	Singh et al. (1998a, b)
Fusarium wilt	ICCV2	Highly resistant	Ali et al. (2002)
	UC15	Highly resistant	Ali et al. (2002)
	FLIP85-20C	Highly resistant	Ali et al. (2002)
	FLIP85-29C	Highly resistant	Ali et al. (2002)
	FLIP85-30C	Highly resistant	Ali et al. (2002)
	ICC14194	Highly resistant	Gaur et al. (2006)
	ICC17109	Highly resistant	Gaur et al. (2006)
	WR315	Highly resistant	Gaur et al. (2006)
Sclerotinia stem rot	GL84012	Partial resistant	Singh et al. (2007)
	GL88223	Partial resistant	Singh et al. (2007)
	GLK8824	Partial resistant	Singh et al. (2007)
	GF89-75	Partial resistant	Singh et al. (2007)
Chickpea rust	RIL58-ILC72/Cr5	Resistant	Rubio et al. (2006)

1992; Butler 1993; Pande et al. 2002, 2006a, b). Chickpea genotypes with vigorous seedling growth, early canopy closure and early flowering are more likely to develop BGM than other cultivars (Nene et al. 2012; Matthews et al. 2014). Under favourable

conditions, BGM can develop rapidly, spread widely and cause complete yield loss (Reddy et al. 1988; Pande et al. 2002, 2006a, b).

The *B. cinerea* pathogen is reported to be variable and adaptable to a wide range of environmental

conditions (Pande et al. 2006a, b). *B. cinerea* isolates collected from India and Nepal have been differentiated based on their morphocultural characters and effects on different chickpea genotypes (Singh and Bhan 1986; Rewal and Grewal 1989a, b; Kishore 2005). Nine simple sequence repeat markers were used on *B. cinerea* (Fournier et al. 2002) to study population structure of a total of 51 alleles were amplified among 146 *B. cinerea* isolates of chickpea from Bangladesh, India and Nepal, which revealed a high amount of within-population and overall genetic diversity (Isenegger et al. 2005, 2008).

Different methods have been applied to screen germplasm for BGM resistance under in vitro, greenhouse and field conditions (Pande et al. 2002, 2006a, b; Gurha et al. 2003). The cut-twig technique (Singh et al. 1998a, b) allows for non-destructive sampling of the plants and is particularly useful in wide hybridization programs (Pande et al. 2006a, b). High levels of resistance have not been found in cultivated chickpeas (Haware and Nene 1982; Haware and McDonald 1993), however Kabuli type chickpeas appear to be more susceptible to BGM than Desi types (MacLeod et al. 2005). Extensive screening of germplasm for BGM resistance at different locations has identified 9 sources of resistance to BGM (Pande et al. 2002), however these lines were found resistant at one location but may become susceptible at other locations because of pathogen variability (Singh and Bhan 1986).

Moderate levels of resistance to BGM (Table 1) have been found by screening over 13,000 lines and transgressive segregation among progeny of moderately resistant crosses has identified higher level of resistance that may be useful in breeding (Singh et al. 1982). Some domestic landraces with an erect habit appear to be less affected by BGM and maintained their yield even under conditions that highly favour disease development (Haware and McDonald 1993). The screening of a core collection of chickpea landraces revealed two accessions (IG 70037 and IG 70038) were found to be resistant to both AB and BGM (Pande et al. 2006a, b) whilst a breeding line (CH-2007-22) with a high level of resistance was identified by Khan et al. (2010). High levels of resistance have also been reported in wild relatives, including accessions of *C. judiacum*, *C. pinnatifidum*, *C. bijugum* and *C. echinospermum* (Singh et al. 1991).

The limited reports available on the genetics of BGM resistance in chickpea suggest that a few major

genes control host resistance (Tewari et al. 1985; Rewal and Grewal 1989c; Chaturvedi et al. 1995; Pande et al. 2006a, b). Some of the resistant chickpea lines such as ICC1069, P349-2 and NEC2451 have been widely used in breeding (Haware et al. 1992; Chaturvedi et al. 1995) but higher levels of host resistance still need to be identified (Pande et al. 2005). Furthermore, these resistances are unlikely to hold in the longer term as pathogen diversity indicates likely breakdown of host resistance (Isenegger et al. 2008).

Fusarium wilt

Fusarium wilt, caused by *Fusarium oxysporum* f. sp. *ciceris* (Padwick) Synd. & Hans, can severely limit chickpea production in most chickpea-growing areas of the world. Annual chickpea yield losses from Fusarium wilt vary from 10 to 15 % (Jalali and Chand 1992; Trapero-Casas and Jiménez-Díaz 1985), but can also result in the total loss of the crop under specific conditions (Halila and Strange 1996; Cachinero et al. 2002).

The fungus enters the vascular system of the plant via the roots. Cell wall degrading enzymes produced by the pathogen break down the host cell walls to form gels that block the plant's transport systems and cause wilting. Chlorosis will first appear on old leaves and gradually extends to the young ones so that at a late stage of the disease, all leaves are yellow (Fig. 2). The infected seedlings will have shrunken stems both above and below ground, which lead to the seedlings' collapse and death (Haware et al. 1986; Brayford 1998; Leslie and Summerell 2006).

Effective field screening and laboratory procedures have been developed, and genetic sources of resistance to Fusarium wilt have been identified at ICRISAT (Nene and Haware 1980). A significant proportion of the resistant chickpea accessions were Desi types rather than Kabuli (Haware et al. 1992) with some of these resistance sources also having resistance to dry root rot, Sclerotinia stem rot and AB (Haware 1990).

Eight pathogen races of Fusarium wilt have been documented, with races 2, 3 and 4 found only in India, races 0, 1B/C, 5 and 6 found mainly in the Mediterranean and the United States and race 1A reported in India, the United States, and the Mediterranean (Landa et al. 2006). Resistance to Fusarium wilt is race-specific and controlled by major resistance genes (Sharma et al. 2004; Sharma and Muehlbauer 2007).

Genetic studies have revealed that resistance to race 1 is controlled by at least three independent loci (h1, h2, and H3) (Upadhyaya et al. 1983a, b; Singh et al. 1987) while three independent genes (a, b, and C) conferred resistance to race 2 (Gumber et al. 1995; Kumar 1998). Resistance to race 0 and race 4 has been shown to be controlled by two genes (Tullu et al. 1999; Rubio et al. 2003) with resistance to race 3 and race 5 being controlled by a single gene (Tekeoglu et al. 2000b; Sharma et al. 2004). The genetic basis of resistance to races 1B/C and 6 is unknown. Markers linked to the genes governing resistance to six races (0, 1A, 2, 3, 4 and 5) of the pathogen have been identified and their position on chickpea linkage maps located. These genes lie in two separate clusters on LG2 and LG5 (Winter et al. 2000; Sharma and Muehlbauer 2007).

Fusarium wilt resistance has been incorporated into high-yielding Desi and Kabuli backgrounds (Kraft et al. 1994) using donors that were identified as highly resistant in wilt infected plots at ICRISAT. In a cooperative research effort between ICRISAT and ICARDA, wilt-resistant chickpea lines were developed in Tunisia. These lines may be exploited for the development of resistant cultivars against wilt (Halila and Strange 1997). Several chickpea varieties with durable and stable resistance to Fusarium wilt (Table 1) have been released in India and a number of other countries. Recent advances in the understanding of the genetics of resistance are likely to result in successful pyramiding of resistance genes (Singh et al. 2008). In countries where Fusarium wilt is not a major problem, such as Australia, pre-emptive breeding is underway to minimize the impact of this disease if it becomes a major production constraint.

Chickpea rust

Chickpea rust, caused by *Uromyces cicerisarietini* (Grogon) Jacz. & Boyer, is a widespread and serious disease that causes considerable damage to this crop each year. It has been reported as a significant problem affecting chickpea production in the Mediterranean region, South Africa, Mexico, Australia, Italy and the United States (Ragazzi 1982; Jones 1983; Díaz-Franco and Pérez-García 1995; Sillero et al. 2006; Rubiales et al. 2011). Cool and moist weather conditions favour the build-up of rust. Symptoms first appear on the leaves as small, round or oval, cinnamon-brown, powdery pustules that tend to coalesce. Occasionally a

ring of small pustules can be seen around larger pustules, which occur on both leaf surfaces but more frequently on the underside. If the crop is severely infected, pustules can be seen on stems and plants may dry up prematurely (Fig. 2).

No sources of resistance to rust have been identified in cultivated chickpea (Madrid et al. 2008), but a certain degree of slow-rusting (Table 1) has been reported recently and this tends to be more frequent in wild *Cicer* relatives (Rubiales et al. 2001; Sillero et al. 2012). Conventional breeding methods have facilitated the introgression of resistance from wild relatives such as *C. reticulatum* and *C. echinospermum* into *C. arietinum* (Ladizinsky and Adler 1976; Madrid et al. 2008). However, no successful crosses have been reported between cultivated chickpea and other wild relatives such as *C. pinnatifidus*, *C. judaicum*, and *C. bijugum* (Ahmad and Slinkard 2004; Madrid et al. 2008).

Sclerotinia stem rot

Sclerotinia stem rot, caused mainly by *Sclerotinia sclerotiorum* (Lib.) de Bary, has been recorded as an important disease of chickpea in Australia (Bretag and Mebalds 1987; Fuhlbohm et al. 2003), Canada (Hilton 2000), Chile, India, Iran, Morocco, Syria (Haware, 1990), the United States (Matheron and Porchas, 2000; Chen et al. 2006) and elsewhere (Haware 1990; Boland and Hall 1994). *Sclerotinia minor* and *S. trifoliorum* have also been reported in chickpea fields in Australia (Bretag and Mebalds 1987; Fuhlbohm et al. 2003) and the United States (Matheron and Porchas 2000; Njambere et al. 2008).

This disease can occur at all stages of crop development and is favoured by excessive vegetative growth, high soil moisture, and cool weather (20 °C). Disease symptoms in the field include whitish or brownish mycelial strands on branches or inside the stem (Nene et al. 2012). Plants or branches turn yellow or droop while remaining green, then dry up and turn straw colored. Infections are typically not uniform within a field with chlorotic or drying branches or whole plants being scattered (Fig. 2). In order to screen for possible sources of resistance to Sclerotinia stem rot, Akem and Kabbabeh (1999) developed a detached shoot technique to determine the preliminary reaction of chickpea genotypes to *S. sclerotiorum*. By using this technique under controlled conditions in a

growth chamber, the authors identified five chickpea genotypes with some resistance to *Sclerotinia* stem rot. Resistance components included delayed initial infection, restricted lesion development and reduced sclerotial production (Akem and Kabbabeh 1999).

No complete resistance to *Sclerotinia* stem rot has been found in chickpea. However, some lines (GL84012, GL88223, GLK8824, and GF89-75) do show moderate resistance to the disease (Table 1). Some accessions in wild *Cicer* sp. (*C. reticulatum*, *C. pinnatifidus*, *C. judaicum*, and *C. yamashitae*) have shown good resistance to stem rot (Singh et al. 2007).

Phytophthora root rot

Phytophthora root rot is a disease of chickpea caused by the oomycete *Phytophthora medicaginis* (Irwin and Dale 1982). It is most commonly observed in chickpea crops following alfalfa in the United States but is not a major yield-limiting disease. It is widespread in Australia, especially in the cracking clay soils of northern New South Wales and southern Queensland. Infection by *P. medicaginis* can occur at any growth stage causing seed decay, pre- and post-emergence damping off, loss of lower leaves, and yellowing, wilting and death of older plants (Moore et al. 2011) (Fig. 2). Symptoms are sometimes delayed if temperatures are cool and the soil is moist. *P. medicaginis*, in favorable environments, can cause up to 85 % of yield loss in susceptible varieties (Moore et al. 2015).

Screening can be performed directly in the field, in the greenhouse or in the laboratory. Effective screening for disease resistance requires accurate simulation of natural environmental conditions where plants are exposed to the inoculum (Porta-Puglia and Aragona 1997; Infantino et al. 2006). Genotypic differences in resistance to *Phytophthora* root rot have been identified (Brinsmead et al. 1985; Dale and Irwin 1991a, b) and cultivars that are less susceptible to the disease have been developed. The levels of resistance available in cultivated species are low compared to levels in wild species (Knights et al. 2003, 2008).

Higher levels of resistance to *Phytophthora* were found in *C. judiacum*, *C. reticulatum*, *C. bijugum* and *C. echinospermum*, with resistance in accessions of the last species being confirmed in greenhouse tests (Knights et al. 2008). Selections from inter-specific crosses with *C. echinospermum* were as resistant as the

wild parent, indicating that these sources will be useful for breeders.

Dry root rot

Dry root rot of chickpea, caused by *Rhizoctonia bataticola* Taub (Butler), is a serious disease under dry hot summer conditions, particularly in the semi-arid tropics of Ethiopia and in most of the chickpea-growing regions in India (Ali and Kumar 2001; Chen 2011). Disease generally appears around the flowering and podding stage. The first symptom is yellowing and sudden drying of the plants. Drooping of petioles and leaflets is confined to the top of the plant. Sometimes when the rest of the plant is dry, the leaves are chlorotic. The taproots become dark brown and quite brittle in dry soil and show extensive rotting, resulting in the loss of lateral roots. The lower portion of the taproot is often left in the soil when the plant is uprooted (Fig. 2).

Rhizoctonia survives in the soil as mycelium and sclerotia on debris. High daytime temperatures (25–30 °C) and dry soil conditions at flowering and podding increase the severity of the disease (Gurha et al. 2003). Previous studies have reported high levels of pathogenic and genetic variation in *R. bataticola* from different parts of the world (Tripathi and Sharma 1983; Trivedi and Gurha 2006; Aghakhani and Dubey 2009). The inheritance of resistance to dry root rot of chickpea was reported to be a dominant monogenic trait (Ananda Rao and Haware 1987).

Both pot culture and field screening techniques have been developed to screen chickpea resistance to dry root rot, and several sources that show resistance to dry root rot and fusarium wilt have been identified. These resistant sources have been utilized in chickpea breeding to develop varieties that are resistant or tolerant to multiple diseases (Gurha et al. 2003). Moderate resistance to dry root rot has also been identified at ICRISAT in chickpea germplasm and breeding lines (Pundir et al. 1988), leading to the development of moderately resistant varieties (Dua et al. 2001).

Breeding for resistance to viruses

Viruses are a significant production constraint in chickpea (Bos et al. 1988; Kumar et al. 2008) and at

least 39 (Table 2) species of viruses are reported to infect this crop. On a worldwide scale, the major viruses affecting chickpea are *Alfalfa mosaic virus* (AMV), *Cucumber mosaic virus* (CMV), *Beet western yellows virus* (BWYV), *Bean leaf roll virus* (BLRV), *Chickpea chlorotic dwarf virus* (CpCDV), *Chickpea chlorotic stunt virus* (CpCSV) and *Faba bean necrotic yellows virus* (FBNYV). The viruses detected in Australian chickpea are AMV, CMV, BLRV and BWYV, with the latter being most important (van Leur et al. 2013). AMV and CMV are transmitted mechanically and non-persistently by aphids. The aphids carry the virus for only a few hours, but the virus can be transmitted in less than a minute of feeding. BLRV and BWYV are transmitted by aphids in a persistent manner, where the virus remains infective in the aphids for many weeks. None of the modern high-yielding chickpea varieties have adequate virus resistance. However, screening a wide range of chickpea germplasm for virus resistance revealed some potential sources of resistance that will be used in the Pulse Breeding Australia chickpea breeding program (van Leur et al. 2014).

BWYV (genus *Polerovirus*, family Luteoviridae) was first reported in North America (Duffus 1960) and has a global distribution with a wide host range. It is transmitted only by aphids and not through seed or mechanical means. It persists between seasons on alternative hosts such as perennial weeds. Infected Kabuli chickpea plants develop pale, chlorotic leaves and show stunting of the whole plant, while Desi chickpea plants develop purple leaves with mild stunting of the plant. In both types, plants that are infected early do not produce flowers and die. Common aphid species that spread this virus in chickpea include *Myzus persicae*, *Aphis craccivora*, *Acyrtosiphon kondoi* and *Acyrtosiphon pisum*. In recent years, BWYV has emerged as the most important virus of chickpea in Australia (Aftab and Freeman 2013). During late September 2012, unusually high BWYV incidence was observed in chickpea crops (88 %) in northern New South Wales (van Leur et al. 2013). In 2009, chickpea virus surveys were conducted in eastern Australia, and the percentage of plants infected by BWYV in individual chickpea paddocks ranged from 5–69, 1–19, 1–29 and 3–58 % in Victoria, South Australia, and northern and southern New South Wales, respectively (Aftab and Freeman 2013). Previous surveys in 2007 in Victoria and South

Australia showed an incidence of 18–61 and 8–25 %, respectively. The chickpea variety Gully was developed through mass selection from an Iranian germplasm accession under high virus pressure and is resistant to BWYV (van Leur et al. 2014).

CMV (genus *Cucumovirus*, family Bromoviridae) was first found in cucumbers (*Cucumis sativus*) (Price 1934). It has a large host range that includes over 1000 plant species (Douine et al. 1979). It can be transmitted from plant to plant both mechanically by sap and by aphids in a stylet-borne fashion. It can also be transmitted in seeds and by parasitic weeds. Symptoms of CMV in Desi chickpea are leaf chlorosis, reddening, off shoots, reduced internode length and stunting. Kabuli chickpea symptoms are leaf chlorosis, reduced internode length, off shoots and stunting. In Australia, CMV is the second most important virus after BWYV. Chickpea surveys conducted in 2007 in Victoria and South Australia found that CMV occurred in 1–10 % of the chickpea plants. In 2009, surveys conducted in Victoria, South Australia and northern and southern New South Wales revealed that the incidence of CMV ranged from 1–63, 2–9, 1–17, and 2–16 %, respectively (Aftab and Freeman 2011).

AMV (genus *Alfamovirus*, family Bromoviridae) was first described in alfalfa (*Medicago sativa* L.) (Weimer 1931). It has a host range of at least 700 species belonging to 71 families (Edwardson and Christie 1997) and is widely distributed throughout the world. Transmission of the virus occurs mainly by some aphids or by seeds. Desi chickpeas show the symptoms of tip necrosis combined with chlorosis and reddening of the leaf margin. Infected Kabuli chickpeas show yellowing and necrosis of tips and stunting of plants. In Australia, this is the third important chickpea virus after BWYV and CMV. Australian surveys have shown incidence rates of AMV of 1–9 % in Victoria in 2007 and 2009, between 9–25 % in South Australia in 2006 and between 1–18 % in New South Wales in 2009 (Aftab and Freeman 2011).

CpCDV (genus *Mastrevirus*, family Geminiviridae) was first identified in 1993 in India. Infected Kabuli chickpea plants show yellowing of foliage whereas Desi plants show reddening. Other symptoms include phloem browning (revealed by a shallow cut at the collar), stunting and premature death (Nene and Reddy 1987; Nene et al. 1991; Horn et al. 1993). The vectors of CpCDV are two leafhopper species, *Neolimnus aegyptiacus* and *Orosius albicinctus* (Horn

Table 2 Virus Diseases of Chickpeas

Virus species	Genus	Family	Natural spread	Distribution	References
<i>Alfalfa mosaic virus</i>	Alfamovirus	Bromoviridae	Aphids, seed	Worldwide	Edwardson and Christie (1991)
<i>Bean common mosaic virus</i>	Potyvirus	Potyviridae	Aphids	Worldwide	Brunt et al. (1996)
<i>Bean leafroll virus</i>	Luteovirus	Luteoviridae	Aphids	Worldwide	Edwardson and Christie (1991)
<i>Bean yellow mosaic virus</i>	Potyvirus	Potyviridae	Aphids, seed	Worldwide	Edwardson and Christie (1991)
<i>Beet curly top virus</i>	Curtovirus	Geminiviridae	Leaf hopper	Worldwide	Brunt et al. (1996)
<i>Beet western yellows virus</i>	Polerovirus	Luteoviridae	Aphids	Worldwide	Edwardson and Christie (1991)
<i>Broad bean mottle virus</i>	Bromovirus	Bromoviridae	Beetles	Africa, Europe	Edwardson and Christie (1991)
<i>Broad bean stain virus</i>	Comovirus	Secoviridae	Weevils, seed	Europe, Africa,	Edwardson and Christie (1991)
<i>Broad bean true mosaic virus</i>	Comovirus	Comoviridae	Weevils, seed	Africa, Asia	Edwardson and Christie (1991)
<i>Broad bean wilt virus</i>	Fabavirus	Comoviridae	Aphids	Worldwide	Edwardson and Christie (1991)
<i>Cassia yellow blotch virus</i>	Bromovirus	Bromoviridae	Unknown	Australia	Brunt et al. (1996)
<i>Chickpea bushy dwarf virus</i>	Potyvirus	Potyviridae	Unknown	India	Brunt et al. (1996)
<i>Chickpea chlorosis virus</i>	Masterovirus	Geminiviridae	Leaf hopper	Australia	Thomas et al. (2010)
<i>Chickpea chlorotic stunt virus</i>	Polerovirus	Luteoviridae	Aphids	Africa, Asia	Abraham et al. (2006)
<i>Chickpea chlorotic dwarf virus</i>	Masterovirus	Geminiviridae	Leaf hopper	Asia	Horn et al. (1993)
<i>Chickpea distortion mosaic virus</i>	Potyvirus	Potyviridae	Aphid	India	Edwardson and Christie (1991)
<i>Chickpea filiform virus</i>	Potyvirus	Potyviridae	Aphid	USA	Edwardson and Christie (1991)
<i>Chickpea redleaf virus</i>	Masterovirus	Geminiviridae	Leaf hopper	Australia	Thomas et al. (2010)
<i>Clitoria yellow vein virus</i>	Tymovirus	Tymoviridae	Unknown	Kenya	Brunt et al. (1996)
<i>Cucumber mosaic virus</i>	Cucumovirus	Bromoviridae	Aphids, seed	Worldwide	Edwardson and Christie (1991)
<i>Epirus cherry virus</i>	Ourmiavirus	Unassigned	Seed	Greece	Brunt et al. (1996)
<i>Fababean necrotic yellows virus</i>	Nanovirus	Nanoviridae	Aphids	Asia	Katul et al. (1993)
<i>Glycine mosaic virus</i>	Comovirus	Comoviridae	Unknown	Australia	Brunt et al. (1996)
<i>Lettuce mosaic virus</i>	Potyvirus	Potyviridae	Aphids, seed	Worldwide	Edwardson and Christie (1991)
<i>Lettuce necrotic yellows virus</i>	Cytorhabdovirus	Rhabdoviridae	Aphids	Australia, Europe	Edwardson and Christie (1991)
<i>Lucerne Australian latent virus</i>	Nepovirus	Secoviridae	Seed	Australia	Brunt et al. (1996)
<i>Lucerne transient streak virus</i>	Sobemovirus	Unassigned	Unknown	Australia	Brunt et al. (1996)
<i>Pea enation mosaic virus</i>	Enamovirus	Luteoviridae	Aphids	Europe, USA	Edwardson and Christie (1991)
<i>Pea mild mosaic virus</i>	Comovirus	Comoviridae	Seed	New Zealand	Brunt et al. (1996)
<i>Pea seed-borne mosaic virus</i>	Potyvirus	Potyviridae	Aphids, seed	Worldwide	Brunt et al. (1996)
<i>Pea streak virus</i>	Carlavirus	Betaflexiviridae	Aphids	Europe, USA	Edwardson and Christie (1991)

Table 2 continued

Virus species	Genus	Family	Natural spread	Distribution	References
<i>Peanut stunt virus</i>	Cucumovirus	Bromoviridae	Aphids, seed	USA, Japan	Brunt et al. (1996)
<i>Phasey bean virus</i>	Polerovirus	Luteoviridae	Aphids	Australia	Sharman et al. (2012)
<i>Soybean dwarf virus</i>	Luteovirus	Luteoviridae	Aphids	Worldwide	Edwardson and Christie (1991)
<i>Subterranean clover stunt virus</i>	Nanovirus	Nanoviridae	Aphids	Australia	Chu and Vetten (2003)
<i>Swordbean distortion mosaic virus</i>	Potyvirus	Potyviridae	Aphids	India	Brunt et al. (1996)
<i>Tomato spotted wilt virus</i>	Tospovirus	Bunyaviridae	Thrips	Australia	Thomas et al. (2004)
<i>Turnip mosaic virus</i>	Potyvirus	Potyviridae	Aphids	Worldwide	Brunt et al. (1996)
<i>Wisteria vein mosaic virus</i>	Potyvirus	Potyviridae	Aphids	Europe	Brunt et al. (1996)

et al. 1993; Kumari et al. 2004). Significant yield losses due to CpCDV, of 60–100 %, have been reported in Sudan and India (Horn et al. 1995).

CpCSV (genus *Polerovirus*, family Luteoviridae) is a recently described virus that infects cool-season food legumes (Abraham et al. 2006, 2009; Asaad et al. 2009) and is a phloem-limited virus that is present in very low concentration and transmitted by aphids (*Aphis craccivora* Koch. and *Aphis pisum* Harris) in a persistent manner (Abraham et al. 2006; Asaad et al. 2009). CpCSV symptoms cannot be distinguished from those caused by other yellowing viruses like BLRV or BWYV.

FBNYV (genus *Nanovirus*, family Nanoviridae) was first reported in Syria. It is the causal agent of a destructive disease of chickpea in some arid regions, including countries in north Africa, west Asia and southern Europe (Katul et al. 1993; Franz et al. 1996). FBNYV is known to infect more than 50 legume species. Characteristic symptoms in chickpea include leaf rolling, yellowing and stunting. FBNYV is transmitted in a persistent manner by several aphid species, including *Aphis craccivora*, *A. fabae* and *A. pisum*, but it is confined to phloem tissues in the infected plants, rendering it non-transmissible by sap and through seed and pollen. No cultivars of chickpea with resistance to FBNYV are commercially available.

BLRV (genus *Luteovirus*, family Luteoviridae; Katul 1992) is a luteovirus transmitted by aphids in a persistent manner (Ashby 1984), with *A. pisum*, *A. craccivora* and *M. persicae* being the main vectors. This virus is not transmitted through seed or

mechanically. Symptoms include phloem discoloration and foliage yellowing or reddening. This virus is limited to the Fabaceae family, and was first reported in Australia in 1999 (Schwinghamer et al. 1999). In Australia, this is the least important of the viruses affecting chickpea (data not shown).

Outside Australia other viruses infect chickpea and can cause significant yield loss. *Red clover vein mosaic virus* (RCVMV, genus *Carlavirus*, family Betaflexiviridae) causes mosaic symptoms, yellowing and bronzing of leaves, distortion of leaves, severe stunting and proliferation of auxiliary buds (rosetting). Yield loss can be 100 % if RCVMV infects chickpea at the pre-bloom stage (Larsen and Miklas 2001). *Pea streak virus* (PeSV, genus *Carlavirus*, family Betaflexiviridae) causes yellowing of foliage, wilting of the terminal tip, phloem discoloration and plant death, particularly when seedlings are infected. *Pea enation mosaic virus* (PEMV, genus *Enamovirus*, family Luteoviridae) causes a yellowing or reddening of the foliage, upward curling of the leaf margin, phloem discoloration, stunting and twisting of the seed pod.

Efforts have been made to identify sources of resistance and develop virus-resistant chickpea cultivars. For example, Chalam et al. (1986) identified two chickpea accessions that are resistant to CMV and nine that are resistant to BYMV. Kumar et al. (2005) found seven accessions that are resistant to CMV by screening 500 chickpea germplasm lines. In a recent study, 8 Desi type accessions were identified to be resistant to PEMV (Larsen and Porter 2010) and should make useful donors in virus resistance

breeding. A few chickpea varieties released in India have shown some level of resistance to viruses (Dua et al. 2001).

Breeding for resistance to insects

Worldwide, nearly 60 insect species are known to feed on chickpea. Of these, the most important insect pests are the pod borers (*Helicoverpa* spp.), leaf miners (*Liriomyza cicerina*), bruchid weevils (*Callosobruchus* spp.), cowpea aphid (*Aphis craccivora*), cutworms (*Agrotis* spp., etc.), and leaf-feeding caterpillars such as armyworms (*Spodoptera* spp.) (Sharma et al. 2007).

Pod borers

The pod borers *Helicoverpa armigera* and *H. punctigera* (the latter of which is an Australian migratory pest in early spring) are important insect pests of chickpea and are increasingly difficult to control (Sharma et al. 2007). The larvae feed directly on the seed pod, causing seed abortion and damage, thereby having the potential to cause major crop losses. Like field peas and faba beans, chickpeas are preferred by *Helicoverpa* over lupins, canola, Indian mustard and linseed (Sequeira et al. 2001). The spatial and temporal dynamics of this pest can be highly variable, so its control requires regular monitoring with the correct timing of chemical sprays (Evans et al. 2005). Host plant resistance has the potential to be a highly valuable part of an integrated pest management approach (Sharma et al. 2007).

Greenhouse and field-based screening methodologies have been used with conventional breeding techniques to select for *Helicoverpa* resistant cultivars (Sharma et al. 2005b). Open-field screening of 12,000 chickpea germplasm accessions at ICRISAT found some accessions had reduced susceptibility to *H. armigera* (Lateef 1985). Desi chickpeas appear to have variability in resistance to *H. armigera* (Cowgill and Lateef 1996).

Moderate resistance to *Helicoverpa* was found to be associated with increased acid exudate on the leaves, which can deter oviposition of moths and reduce larval damage on the plant (Lateef 1985). Oxalic acid production is important for *H. armigera* antibiosis, as this compound significantly inhibits the growth of

larvae (Yoshida et al. 1995). Malic acid has no effect on larval growth, but it stimulates the oviposition of *Helicoverpa* moths (Yoshida et al. 1997).

Even stronger resistance to *H. armigera*, with high levels of antibiosis, has been found in wild *Cicer* spp. such as *C. pinnatifidum* and *C. judaicum* and in some perennial *Cicer* spp. (Sharma et al. 2005a, 2006). Commercial chickpea lines with genetically engineered resistance to *Helicoverpa* based on the Bt toxin are under development (Sanyal et al. 2005; Lawo et al. 2008; Acharjee et al. 2010). These lines have not yet been released, but evidence from cotton suggests that host plant resistance using the Bt toxin, coupled with effective management, will enable them to be used without triggering the development of significant insect resistance to the toxin in the field (Mahon et al. 2007).

Partial resistance to the pod borer *H. armigera* was found in breeding lines in a comparison of protected (netted) versus unprotected plants in a field trial during a pest infestation, and in another comparison between endosulfan-sprayed replicates versus unsprayed plants (Yadav et al. 2006). Susceptibility was greater in spreading types and in the Kabuli type. At ICRISAT, wild relatives of chickpea have shown low susceptibility to *H. armigera*, and wide crosses with elite lines are being used to study the genetics of this resistance and for breeding with the aid of MAS (Sharma 2006; Sharma et al. 2007).

Leaf miners

The chickpea leaf miner (*Liriomyza cicerina*) is found throughout much of Europe, central and western Asia and north Africa (Naresh and Malik 1989; Kolesík and Pastucha 1992; CABI 2007; Martinez 2007). The larvae of this insect hatch from eggs oviposited under the leaf epidermis and feed inside the mesophyll, creating characteristic serpentine mines. Heavy infestations can cause leaf desiccation and premature leaf drop. In the Mediterranean region, leaf miners are the main insect pest of chickpea, causing up to 30 % yield loss (Weigand 1990). Spring-sown chickpea is more affected than winter-sown chickpea because of the insect's life cycle, which includes over-wintering diapause (El Bouhssini et al. 2008).

Chickpea germplasm with resistance to leaf miners, based on accessions of *C. echinospermum* and *C. reticulatum*, have been developed and released by

ICARDA for use in breeding programs (Singh and Weigand 1994, 1996). Leaf miner resistance is significantly correlated with leaf type and leaflet size, but not with leaf pigmentation. Genotypes with a large, simple leaf type were the most sensitive to leaf miner damage, whereas genotypes with multipinnate leaves composed of small/narrow leaflets were less sensitive (Toker et al. 2010).

Bruchid weevils

Beetles of the genus *Callosobruchus* are major storage pests of chickpea and cause considerable economic losses (Erler et al. 2009). They can attack seed both in the field but more damage occurs during storage. Erler et al. (2009) studied chickpea resistance to bruchid feeding and found that Desi chickpeas were more resistant to *C. maculatus* than Kabuli chickpeas and one genotype exhibited complete resistance. Unfortunately, the most resistant Desi types had a rough (wrinkled), thick, green seed coat, making the product unacceptable to most consumers (Erler et al. 2009). Previous screens for resistance to *Callosobruchus* in 3000 Kabuli accessions at ICARDA revealed no resistant germplasm (Reed et al. 1987). However, a chickpea landrace with resistance to the seed beetle *C. maculatus* F. has been identified (Erler et al. 2009).

Aphids

Although virus transmission by aphids is the major concern caused by this insect (Weigand 1990; Sharma et al. 2007), they can also cause direct damage to the plant through feeding. The main aphid pest in chickpeas is the cowpea aphid, *Aphis craccivora*, a species that is widely distributed, especially in the tropics (CABI 1983). However, due to the exudation of organic acids from granular hairs covering the surface of chickpeas, direct damage by aphids is generally of little concern (Popelka et al. 2004). Work against direct aphid damage was conducted by Chakraborti et al. (2009) to produce transgenic chickpea plants expressing an antifeed compound from garlic (*Allium sativum*). The mannose-binding lectin was expressed with a phloem-specific promoter and caused potent antibiosis that reduced aphid populations on the plant.

Breeding for resistance to nematodes and parasitic weeds

Root-knot nematodes

The root-knot nematodes (RKN) are one of the most important groups of plant parasitic nematodes. The three species of RKN known to infest chickpea differ in their climatic distribution: *Meloidogyne artiella* is the main species of importance in the Mediterranean region, whereas *M. incognita* and *M. javanica* are more common in the subtropics of Asia, Africa and South America (Thompson et al. 2000). RKN reproduction is known to be higher during warmer seasons, therefore spring-sown crops around the Mediterranean are more affected than those sown in winter (Di Vito and Greco 1988; Thompson et al. 2000). Compared with other cool-season food legumes, chickpea is grown in warmer climates or at warmer times of the year and is consequently more exposed to RKN. By comparison, common and durum wheat are significantly better hosts for *M. artiella* than chickpea and produce higher rates of RKN multiplication (Di Vito and Greco 1988; Hernández Fernández et al. 2005).

Parasitism by RKNs involves the establishment of permanent feeding sites in the plant roots where the nematodes stimulate the production of giant cells that act as sinks for plant photosynthates that the nematode preferentially access. Deformation and blockage of vascular tissues due to nematode feeding can limit translocation of water and nutrients, suppress plant growth and result in reduced seed yield. Affected plants are often stunted, with pale green to yellow leaves (Vovlas et al. 2005; Castillo et al. 2008).

A number of root-disease complexes are associated with RKN attack in plants. The fungal pathogens *Fusarium oxysporum* and *Macrophomina phaseolina* are known to cause root rot/wilt, which is exacerbated by the damage caused by RKN. Nematode attack can break down plant defenses and cause *Fusarium* wilt-resistant genotypes to become diseased (Siddiqui and Husain 1991; France and Abawi 1994; Maheshwari et al. 1995). In the Indian state of Karnataka, there was a 28 % incidence of wilt disease associated with the complex of *M. incognita* and *F. oxysporum* f. sp. *ciceri* in chickpea crops (Rao and Krishnappa 1995).

In screening more than 7000 accessions of chickpea and wild *Cicer* species, no resistance was found to *M.*

javanica (Ansari et al. 2004). However, some lines had good tolerance to RKN and achieve significantly greater yield and total dry matter in naturally infested fields (Sharma et al. 1993; Ansari et al. 2004). Resistance to *M. incognita* in chickpea is unknown, but there is some evidence that reduced susceptibility to RKN in some genotypes is associated with greater increases in root peroxidase activity in response to nematode infection (Siddiqui and Husain 1992). These peroxidases are associated with the initiation of the hypersensitive response, systemic defense mechanisms and lignification of cell walls, mechanisms that are commonly employed by plants in response to infection from a range of pathogens and parasites (Reuveni and Ferreira 1985; Bronner et al. 1991; Do et al. 2003; Montes et al. 2004; Choi et al. 2007; Oliveira et al. 2012).

Root lesion nematodes

Root lesion nematodes (*Pratylenchus* spp.) are a major constraint to chickpea production and rank second after RKN in their global impact (Castillo et al. 2008). As their name indicates, they cause root lesions, which results in reduced growth and yield. They can also increase *F. oxysporum* infection (Castillo et al. 1998). After wheat, chickpea is one of the most susceptible crops to *Pratylenchus thornei* in rain-fed cropping systems (Taylor et al. 2000). *P. neglectus*, *P. mediterraneus* and possibly *P. penetrans* also infest chickpea (Thompson et al. 2000).

Chickpea genotypes vary in both their resistance and tolerance to *P. thornei* (Castillo et al. 1998). Nevertheless, few modern chickpea varieties show sufficient resistance to *P. thornei* or *P. neglectus* (Thompson et al. 2008, 2011). Consequently nematode numbers build up in the soil when chickpea is grown, reducing the usefulness of chickpea in a cropping rotation with wheat. Recently, chickpea lines that are resistant to root-lesion nematodes have been produced from hybrids of Desi chickpea cultivars with resistant accessions of *C. reticulatum* and *C. echinospermum* (Thompson et al. 2011). Levels of resistance identified in wild relatives were far superior to the levels identified in *C. arietinum*. Although many backcrosses are required to produce progeny that possess acceptable agronomic and seed quality parameters for commercial chickpea production, the

quantum leap in resistance that is gained justifies the breeding effort.

Cyst nematodes

The cyst nematode *Heterodera ciceri* is an aggressive parasite of chickpea found in the eastern Mediterranean region, particularly Syria and Turkey (Thompson et al. 2000; Sikora et al. 2005). Chickpea plants infested with cyst nematodes are stunted and chlorotic with reduced flowers and pods, along with poorly developed roots and reduced number of *Rhizobium* nodules, all of which lead to lower seed protein content (Greco et al. 1988).

Breeding for resistance to cyst nematodes presents the best option for control of nematode populations and reduction of yield loss (Greco et al. 2003). However, the cultivated chickpea species *C. arietinum* showed no resistance to *H. ciceri* in 9257 lines tested (Singh and Ocampo 1997). Fortunately, the accession Ladiz of the wild relative *C. reticulatum* had good resistance, and chickpea varieties based on hybrids of this line with a widely adapted and high-yielding Kabuli cultivar have been released (Malhotra et al. 2002).

Parasitic weeds

Like other grain legumes, chickpeas are susceptible to parasitism by *Orobanch* spp. (broomrape) when they are grown in infested Mediterranean regions. Chickpea is a host of four different species of broomrape namely crenate broomrape (*Orobanch crenata* Forsk.), fetid broomrape (*O. foetida* Poir.), Egyptian broomrape (*Phelipanche aegyptiaca* Pers.) and *O. minor* (Rubiales et al. 2011). Among these *Orobanch* species, *O. crenata* is the most economically damaging parasitic plant on chickpea worldwide, while *O. minor*, *O. aegyptiaca* and *O. foetida* are only considered of importance in certain areas (Kharrat et al. 1992).

Fortunately, chickpea and wild *Cicer* relatives show good resistance to *Orobanch crenata* (Rubiales et al. 2003, 2004; Pérez-De-Luque et al. 2009). This resistance has been shown to lower broomrape seed germination and produce darker tissue at the site of radicle penetration, preventing parasite establishment or reducing development of established tubercles on the host roots (Rubiales et al. 2003, 2004). This

darkening host tissue is associated with the accumulation of secretions at the infection site that block neighbouring apoplastic vessels (xylem occlusions) in order to inhibit nutrient transfer to the parasite (Pérez-De-Luque et al. 2005).

Prospect of chickpea biotic resistance breeding in the genomic era

Modern plant breeding has the capacity to use molecular tools to assist in the identification and selection of desirable characteristics (Moose and Mumm 2008). The ongoing development and application of molecular tools to plant breeding is likely to increase efficiencies and make recombining multiple traits possible in the absence of phenotypic selection.

Molecular markers and marker assisted selection

DNA markers serve as powerful tools to improve the efficiency and precision of traditional plant breeding using marker-assisted selection (MAS). Marker loci tightly linked to major genes responsible for economically important traits such as disease resistance, male sterility, self-incompatibility and seed characteristics including shape, size, colour and texture, can be used for improving selection efficiently. Molecular research related to crop biotic stress has focused on locating and tagging genetic loci for resistance genes. As a result of the often simpler inheritance patterns, there has historically been a better understanding of the genetic basis of disease resistance, as compared to other traits such as insect and abiotic stress resistance. Therefore, the development and application of

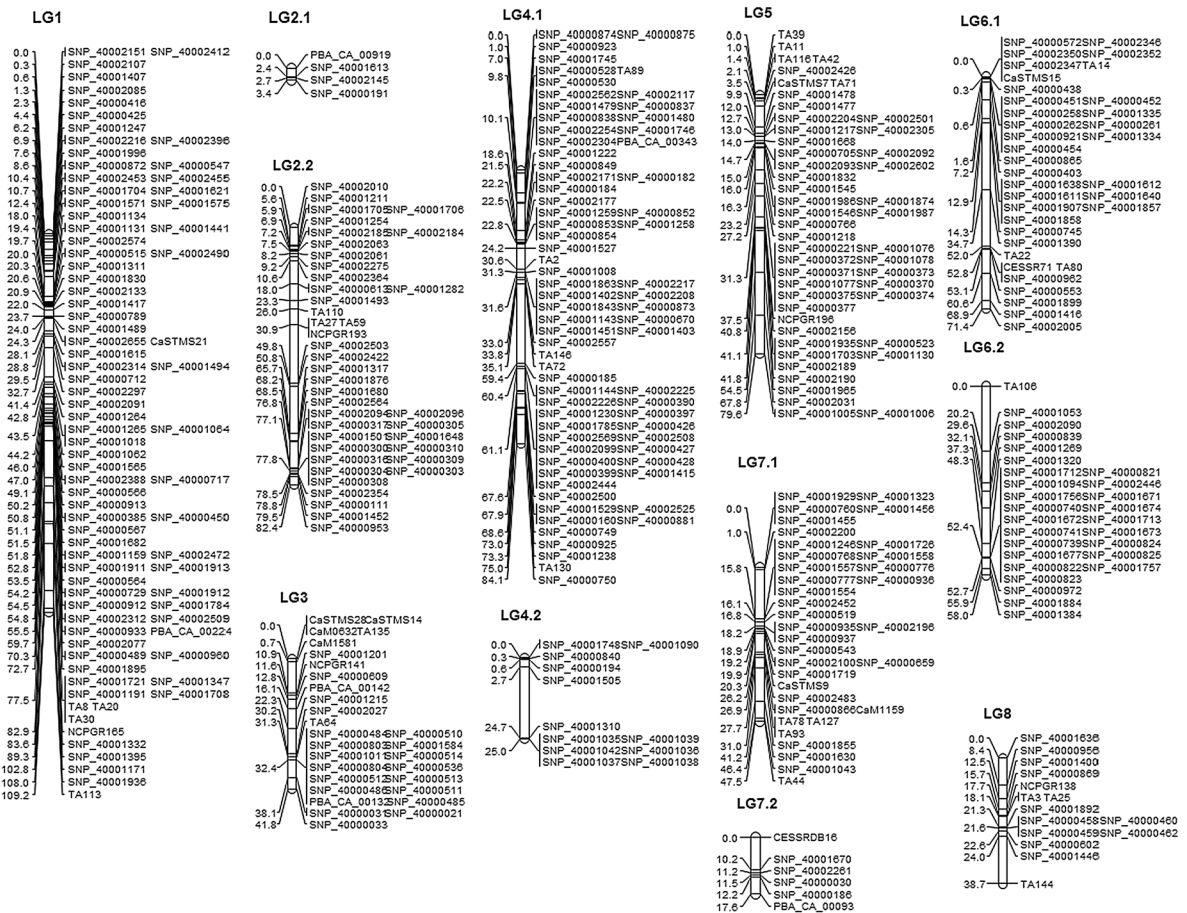


Fig. 3 A genetic linkage map of chickpea from Lasseter × ICC3996 RIL mapping population (Map generated by Dr Sukhjiwan Kaur, part of this map was published in Stephens et al. 2014)

markers for disease resistance is more advanced and the most successful applications of MAS in plant breeding are diseases for which major resistance genes have been backcrossed into elite cultivars (Torres et al. 2010; Varshney et al. 2014).

A large number of inter- and intra-specific linkage maps (Fig. 3) have been generated and published for chickpea using different types of DNA markers (Kazan et al. 1993; Simon and Muehlbauer 1997; Hüttel et al. 1999; Winter et al. 1999, 2000; Lichtenzweig et al. 2005; Sethy et al. 2003, 2006a, b; Choudhary et al. 2006; Nayak et al. 2010; Thudi et al. 2011; Gaur et al. 2011, 2012; Stephens et al. 2014). Through the use of these linkage maps, linked markers/quantitative trait loci (QTLs) for resistance to various diseases in chickpea have been identified (Table 3).

Ascochyta blight

Resistance to AB has been increasingly considered a quantitative trait and many QTLs have been identified in different genomic regions (Santra et al. 2000; Flandez-Galvez et al. 2003a; Udupa and Baum 2003; Pande et al. 2005; Taran et al. 2007; Kanouni et al. 2009, 2011). Linkage group (LG) 4 has been reported by several researchers to contain QTLs for AB resistance (Santra et al. 2000; Tekeoglu et al. 2002; Cho et al. 2004; Taran et al. 2007; Stephens et al. 2014), while other reports highlight LG2 (Udupa and Baum 2003; Cho et al. 2004) and LG8 (Lichtenzweig et al. 2006). In an effort to provide more durable resistance, emphasis has shifted to developing molecular tools to allow successful pyramiding of resistance sources (Millán et al. 2006). These tools have significantly enhanced the capacity to breed chickpea for AB resistance, however only a limited number of gene-based markers capable of efficient implementation within a breeding program have been described in close linkage to AB resistance determinants segregating within cultivated germplasm (Madrid et al. 2013).

Botrytis grey mould

A limited number of reports are available on markers associated with BGM resistance in chickpea. However, a recent study identified three QTLs for resistance to BGM in chickpea, and associated markers provide

an opportunity to pyramid different genes or QTLs to obtain higher levels of resistance (Anuradha et al. 2011). It is suggested that introgression of BGM resistance into elite material is practical, provided that donor parents with a high level of resistance are identified in the cultivated or cross-compatible wild species (Pande et al. 2006a, b).

Fusarium wilt

Molecular mapping studies have found that resistance genes to races 0, 1, 2, 3, 4, and 5 of the pathogen appear on LG2 of the chickpea map (Castro et al. 2010). The clustering of six resistance genes makes LG/2 a hotspot for fusarium wilt resistance (Millán et al. 2006; Sharma and Muehlbauer 2007). In order to apply MAS and better understand the molecular mechanism of resistance, closely linked markers have been identified for some of the genes and validated in different genetic backgrounds (Gowda et al. 2009; Ali et al. 2012). Near-isogenic lines have been developed for the resistance gene to race 5, which can be used for fine mapping and map-based cloning of this gene (Castro et al. 2010).

Rust

Recently, Madrid et al. (2008) identified a single dominant gene controlling resistance to chickpea rust in a recombinant inbred line population derived from an interspecific cross between *C. arietinum* (ILC72) × *C. reticulatum* (Cr5-10), the latter line being the resistance donor. This gene, *Ucal/ucal1*, was located in an interval of 3.9 cM on LG7 (Madrid et al. 2008). Flanking markers should be able to facilitate a MAS program to incorporate this resistance into cultivated chickpea.

Experience with MAS in other crops has shown that molecular markers are most likely to succeed for traits with monogenic inheritance, or those in which the inheritance is controlled by few genes with large effect (William et al. 2007). In contrast to cereals (Koeber and Summers. 2007; Gupta et al. 2010) and corn (Ragot and Lee 2007), there are very few reports of MAS in legumes (Ragagnin et al. 2009; Torres et al. 2010). Several factors that limit the application of MAS in legume breeding include lack of marker studies, the need to validate the effect of MAS in

Table 3 The QTLs or genes identified for chickpea host resistance to various biotic stresses

Trait	Name of population	Locations	Markers associated with genes or QTL(s)	Genetic effects	References
Ascochyta blight	FLIP84-92C × PI 599072	LG1, LG6	UBC733b, UBC181a, <i>Dia4</i>	50.3 and 45 %	Santra et al. (2000)
	Lasseter × ICC1 2004	LG1, LG2, LG3	TS45, TA146, TA130	76 %	Flandez-Galvez et al. (2003b)
	Lasseter × PI527930	LG4	CS5b650, GA2, OPB17c560	N/A	Collard et al. (2003)
	ILC 1272 × ILC 3279	LG2, LG4	Ta20, TA72, ar1	35.9 %	Udupa and Baum (2003)
	PI 359075 × FLIP84-92C	LG2, LG4, LG6	GA16, GA24, GAA47, Ta46	69.2 %	Cho et al. (2004)
	Cr5-10 × ILC72	LG2	OPAI09746, UBC881621	28.0 %	Cobos et al. (2006)
	LC3279 × WR315	LG4	TA194	55 %	Iruela et al. (2007)
	ICCV96029 × CDC Frontier	LG3, LG4, LG6	TA64, TS54, TA176	56 %	Taran et al. (2007)
	ICCV 96029/CDC Luna,	LG2, LG4	TR19, TS54	48 %	Anbessa et al. (2009)
	ICCV 96029/CDC Corinne,	LG4, LG8	TA132, TS45	38 %	Anbessa et al. (2009)
	ICCV 96029/Amit	LG3	TA64	14 %	Anbessa et al. (2009)
	ICC 12004 × Bivanij	LG3, LG4, LG6	TA125, TA72, GA26	46.5 %	Kanouni et al. (2009)
	C 214 × ILC 3279	LG4, LG5, LG6	STMS11, Ta106, CaM0244	41.6 %	Sabbavarapu et al. (2003)
	Lasseter × ICC3996	LG4	SNP_40000185	45 %	Stephens et al. (2014)
	S95362 × Howzat	LG4	TA146, TA72	59 %	Stephens et al. (2014)
Fusarium wilt	WR-315 × C-104	N/A	CS-27, UBC170	foc-1	Mayer et al. (1997)
	ICC-4958 × PI 498777	N/A	CS-27, UBC-855	foc-4	Ratnaparkhe et al. (1998)
	JG-62 × Surutato-77	N/A	CS-27	foc-1, foc-4	Tullu et al. (1999)
	ICC-4958 × PI 498777	LG2, LG3	CS-27, UBC-170	foc-0, foc-4, foc-5	Tekeoglu et al. (2000b)
	ICC-4958 × PI 498777	LG2	CS27, TA96, TA27	foc-1, foc-4, foc-5	Winter et al. (2000)
	CA2156 × JG62	LG3	OPJ 20600	foc-0 ₁ and foc-0 ₂	Rubio et al. (2003)
	WR-315 × C-104	LG2	TA96, CS27A	foc-1, foc-3, foc-4	Sharma et al. (2004)
	CA2139 × JG62	LG3	OPJ20(600), TR59	37.8 %	Cobos et al. (2005)
	JG62 × Vijay	LG2	TA110, TA96, H1B06y	foc-1, foc-2, foc-3	Gowda et al. (2009)
	C 214 × WR 315	LG6	CaM1402, CaM1125, TA22	29.2 %	Sabbavarapu et al. (2003)
Botrytis grey mould	JG62 × ICCV2	LG3, LG6	SA14, TA25, TA159	43.6 %	Anuradha et al. (2011)
Chickpea rust	ILC-72 × Cr5-10	LG7	TA18, TA180	31 %	Madrid et al. (2008)

RAPD Random Amplified Polymorphic DNA, *SSR* Simple Sequence Repeats, *ISSR* Inter simple sequence repeat, *SNP* Single Nucleotide Polymorphism, *SCAR* Sequence Characterized Amplified Region, *STMS* Sequence-tagged microsatellite site markers, *RGA* Resistance Gene Analogs, *ASAP* Allele Specific Associated Primers, *LG* Linkage Group

different genetic backgrounds, and high genotype \times environment interactions. However, a recent study by Varshney et al. (2014) reported successful introgression of Fusarium wilt and AB resistance into an elite cultivar of chickpea through the use of marker-assisted backcrossing. These success cases and some of the high-throughput marker technologies such as the SNP marker system may be able to accelerate the use of MAS in legume breeding.

Genetic transformation

The efficiency of conventional breeding methods are sometimes limited in enhancing resistance to biotic stresses due to a lack of highly resistant sources in the available gene pool (Haware and McDonald 1992). Developing an efficient genetic transformation system for chickpea could add value to conventional breeding strategies. Two different transformation methods have been established in chickpea: the biolistic transformation technique (Kar et al. 1997) and the *Agrobacterium*-mediated method (Fontana et al. 1993; Kar et al. 1996; Krishnamurthy et al. 2000; Tewari-Singh et al. 2004). Due to its cost-effective nature, the latter has been optimized and used more widely in chickpea (Senthil et al. 2004; Mehrotra et al. 2011a, b).

The high efficiency of *Agrobacterium*-mediated transformation protocols has made this method an alternative approach of improving stress tolerance in elite chickpea cultivars by genetically modifying a genome with a gene conferring the desired tolerance. Significant achievements have been made at ICRI-SAT, including the development of transgenic plants carrying the *cryIAC* and *P5CSF* genes (Jandhyala 2005; Sharma 2006). The *cryIAC* gene, derived from the bacterium *Bacillus thuringiensis*, produces a toxin that kills the economically important chickpea pod borer (Jandhyala 2005). The *P5CSF129A* gene for proline accumulation stabilizes degrading proteins under osmotic stress (Mitra 2001; Munns 2005). Non-chimeric transgenic progeny plants with a high expression level of Bt-Cry protein have been created recently using embryogenic callus (Mehrotra et al. 2011).

Future work such as deploying antifungal genes like chitinase and glucanase for effective control of biotrophic fungal diseases in transgenic crop plants

(Amian et al. 2011; Ceasar and Ignacimuthu 2012), or polygalacturonase-inhibitory proteins (PGIPs) to inhibit the activity of the fungal cell wall-degrading polygalacturonases and hence reduced disease symptoms due to necrotrophic pathogens like *B. cinerea* (Wally and Punja 2010) could make genetic transformation a potentially valuable and practical strategy for breeding resistance to biotic stresses in chickpea. A more efficient way of enhancing and broadening resistance of plants to different biotic stresses is to combine transgenes expressing several genes into a single line using different strategies such as crossing, single vector with multiple genes, co-transformation, sequential transformation and IRES elements. These genes or strategies should be utilized to develop more disease resistant plants and enhance chickpea breeding efficiency in future.

Genomic technologies

Development of new genomic technologies has increased during the last decade, allowing the use of new strategies in crop breeding. For example, the study of complex biological processes in legumes has been facilitated by comparative genome analysis using model plants, such as *Medicago truncatula* and *Lotus japonicus*. These models allow us to better understand plant development, responses to biotic stresses, and evolution. Synteny among legume genomes, and specifically among chickpea and other legume species, has been investigated during the last 20 years. Comparative mapping among chickpea, pea, lentil and *Medicago* has suggested a high degree of synteny among legume crop species (Aubert et al. 2006).

Medicago is taxonomically the closest model species to chickpea (Kalo et al. 2004; Choi et al. 2006), and the extent of synteny between chickpea and *M. truncatula* has been assessed on the basis of the sequence from 11 bacterial artificial chromosome clones (Rajesh et al. 2007b). Coram and Pang (2005a) showed that levels of similarity between chickpea expressed sequence tag (EST) sequences and those in *Medicago* and *Lotus* were marginally superior to those observed for *Arabidopsis*. These studies provide evidence for macro-synteny between chickpea and the model crop species, although relatively little micro-synteny exists (Coram and Pang 2005a; Rajesh et al. 2007b). Thus, the use of the model crops to study

chickpea on a gene sequence level needs further assessment (Coram et al. 2007).

As the chickpea genome is the smallest (750 Mbp) among cool season food legumes, it is an attractive target for the development of saturated genetic linkage maps employing transcriptome and genome sequence information to identify important genes of interest. To date, several transcriptome sequencing studies for cultivated and non-domesticated chickpea accessions have been completed. The first EST study in chickpea was reported in 2005 (Coram and Pang 2005a). More than 500 unigenes were identified from the assembled transcriptome isolated from the stems and leaves of an AB resistant chickpea genotype after pathogen inoculation. As a result, potential defense related unigenes were identified by microarrays that were constructed using only defense related ESTs (Coram and Pang 2005b, 2006, 2007). A transcriptomics approach was also used to characterize the molecular interactions between chickpea and race 1 of *F. oxysporum* f. sp. *ciceris* (Nimbalkar et al. 2006). Investigation of the transcription difference in the root infection of some resistant and susceptible genotypes uncovered 19 differentially expressed sequences that were potentially involved in a defense response. Some of these expressed sequences were similar to previously characterized defense related proteins, including two transcription factors and three nucleotide binding site leucine-rich repeat-type gene sequences (Nimbalkar et al. 2006). In recent years, deep sequencing of the chickpea transcriptome using next-generation technologies has enabled the identification of new candidate genes and the development of functional molecular markers (Hiremath et al. 2011; Garg et al. 2011; Agarwal et al. 2012; Jhanwar et al. 2012).

Recently, the draft genome sequence of the genotype CDC Frontier, a Kabuli chickpea variety with resistance to AB and pod borer, has been released and was estimated to contain 28,269 candidate genes. Resequencing and analysis of 90 cultivated and wild genotypes resulted in the identification of candidate genes responsible for traits of interest including 187 disease resistance gene homologs (Varshney et al. 2013). These resistance genes still need to be characterized to understand their functional annotations and can be employed in MAS in near future. Jain et al. (2013) generated the draft sequence of a Desi chickpea genome with the assembly covering 70 % of the genome length, and more than 80 % of the gene space

and predicted the presence of 27,571 genes. RNA-Seq analysis identified several tissue specific and stress responsive genes (Jain et al. 2013).

A series of reverse/forward genomic approaches to fully determine gene function, such as targeted induced local lesions in genomes (TILLING), insertional mutagenesis, and activation tagging have been applied in the model legumes (Coram et al. 2007). A chickpea TILLING mutant population has been constructed, and individuals carrying point mutations in the genes of interest can be phenotypically assessed to determine the function(s) of each gene (Rajesh et al. 2007a). This is a highly valuable chickpea genomic resource which may be used to screen for changes in the functions associated with previously identified candidate genes. Although these technologies have not yet directly led to the improvement of cultivars, the identification of candidate genes for stress resistance and tolerance will surely accelerate future breeding of elite chickpea cultivars.

Conclusions

A major aim of chickpea breeding is to develop cultivars with a high level of resistance to yield reducing biotic stresses. Extensive searches for resistance to various biotic stresses have been conducted by screening germplasm, including cultivated varieties, landraces, and wild species. Resistance to some biotic stresses, such as AB and fusarium wilt, have been found in the chickpea and breeding for resistance to these diseases is making progress by identifying new resistance genes. To speed up the process of introgressing genes into chickpea elite genotypes, molecular tools can be integrated with conventional breeding approaches. Molecular markers associated with major QTLs conferring resistance to some biotic stresses have been located on linkage maps, and these markers can be used for efficient pyramiding of the traits of interest.

In an attempt to uncover important genes that are involved in resistance to biotic stresses, significant achievements have been made in chickpea genomics. Valuable resources, such as an integrated genetic map (Millán et al. 2010; Zatloukalová et al. 2011), a high resolution physical map (Zhang et al. 2010), EST libraries (Coram and Pang 2005a), bacterial artificial chromosomes (BAC) libraries (Rajesh et al. 2004,

2007b) and draft genome sequences (Varshney et al. 2013; Jain et al. 2013) have been generated. Although candidate genes identified from genomics have not yet been used directly to improve chickpea cultivars in the field, they may be used in this way in the near future.

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