Dry Root Rot in Chickpea: A Perspective on Disease Resistance Breeding Strategies

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Abstract

Chickpea is an essential crop nutritionally rich in protein and grown around the world, generally in rain-fed condition. Dry root rot (DRR) is an emerging and economically devastating disease caused by the chickpea-specific strain *Macrophomina phaseolina*. Environmental conditions such as drought and high temperature aggravate DRR causing significant crop loss. The control of *M. phaseolina* is challenging due to the broad host range of this fungus. Genetic resistance of enhancement of resistance to DRR through breeding is a potential way to prevent crop loss due to the disease. In this chapter, we highlight the importance of breeding strategies for rapidly developing DRR disease-resistant varieties of chickpeas. We also provide a brief overview of the role of next-generation sequencing (NGS) technology and high-throughput phenotyping (HTP) in the next-generation breeding strategy against DRR disease. We suggest that the advancement of sequencing technology and the availability of the high-quality reference genome of chickpeas can facilitate genotyping and mining of the allelic variation among the diverse chickpea population. We also discuss the potential of genome editing integrated with speed breeding to reduce the generation time significantly. Thus, we suggest the combination of genome-wide association study (GWAS) and speed breeding with genome editing can take DRR resistance breeding in chickpea to the next level and have the potential to provide precisely edited chickpeas in a short duration of time.

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U. C. Jha et al. (eds.), *Diseases in Legume Crops*,
https://doi.org/10.1007/978-981-99-3358-7_4

Keywords

Chickpea · Dry root rot · Resistance breeding · High-throughput phenotyping · Genome-wide association study · Speed breeding

4.1 Introduction

Macrophomina phaseolina (Tassi.) Goid is a soil-inhabitant, plant-pathogenic fungus that belongs to the Botryosphaeriaceae family of *Ascomycetes*. This fungus acts as a causal agent of several diseases in more than 500 wild and cultivated plant species (Gupta et al. 2012). These diseases affect the yield of economically important legume crops such as chickpeas, soybean, green gram, and cowpea. *M. phaseolina* causes dry root rot (DRR) disease in chickpea (*Cicer arietinum* L.). It has been reported that specific abiotic stresses, such as drought and heat, aggravate DRR disease symptoms in chickpea (Sinha et al. 2021). Under favorable environmental conditions, up to 100% yield loss can be observed in susceptible cultivars. This pathogen generally attacks the chickpea root system and leads to root architecture damage that can lead to severe yield losses. DRR is an emerging chickpea disease widely spread in major chickpea cultivation regions across the globe (Rai et al. 2022). Further, the changing environmental conditions will favor the geographical spread of the disease (Pandey and Basandrai 2021; Mirchandani et al. 2023).

The control of this fungus is difficult due to its broad host range and prolonged survival in the field. The development of DRR-resistant cultivars of chickpea is one of the important methods to prevent yield loss caused by the disease. DRR phenotyping in the available germplasm is significantly less explored to date. Exploration of chickpea germplasm with high efficiency and accuracy is the minimal requirement for DRR resistance breeding. Efficient utilization of phenomic and genomic tools will be essential in identifying resistant cultivars in the germplasm and developing new cultivars with DRR resistance. Further, techniques such as speed breeding can rapidly advance the generations and significantly reduce the standard breeding period (Samineni et al. 2020). This book chapter aims to highlight the use of HTP and NGS information in identifying associated DRR resistance loci in the chickpea genome and their use in the next-generation breeding strategy to develop DRR disease-resistant varieties.

4.2 DRR Disease Distribution

The disease is particularly prevalent in arid and semiarid agroclimatic conditions worldwide. The total chickpea cultivation area is 13 million hectares (ha), and the total production ranges from approximately 15–16 million tonnes annually. The DRR disease is reported worldwide in major chickpea-growing regions such as Africa, Spain, South Asia, Turkey, the Mediterranean region, and several North

Table 4.1 Examples of chickpea genotypes with contrasting response to DRR

S. No	Genotype name	Disease reaction	Reference
1	JG 62, ICC 1715, JGK 18	Highly susceptible	Chilakala et al. (2022), Talekar et al. (2017)
2	BG212, ICCV 07107, ICCV 07306	Susceptible	Karadi et al. (2021), Talekar et al. (2021)
3	ICCV 08315, ICC 11550, ICC 14395	Moderately susceptible	Talekar et al. (2021)
4	ICC2867, ICC 9023, ICC 14307	Moderately resistance	Talekar et al. (2021)
5	PG 06102, BG 2094	Resistance	Talekar et al. (2021)

American countries. In India, the chickpea area under cultivation is 6.3 million ha, and 85% of the area is under rainfed conditions (FAOSTAT 2019). In mild infection, yield loss can range between 5 and 10%, while in moderate infection, it can be between 30 and 50%, and in severe disease infection, it can be up to 80% (Rai et al. 2022). Changing climatic conditions such as low rainfall and high temperature can elevate the risk of economic yield loss due to DRR. A survey conducted in the chickpea cultivating area of Rajasthan showed that DRR is the major problem in the Churu, Jodhpur, Bikaner, and Jaisalmer districts of Rajasthan. The average disease incidence observed is 9.15% in Rajasthan (Partap and Godara 2022). In contrast, some other regions of the country show higher disease incidence, such as Niwadi (31.5%), middle Gujarat (26%), Kalburgi, and Raichur (30–35%) of Madhya Pradesh, Gujarat, and Karnataka, respectively, (Mirchandani et al. 2023). The disease occurrence varies with soil type or edaphic factors, environmental factors, and cultivated varieties. Table 4.1 represents the name of some reported genotypes against DRR resistance or susceptibility. Figure 4.1 shows the image of DRR infestation in the chickpea field.

4.3 DRR Causal Agent and Disease Cycle

Based on the sequence information of 28s rDNA, *M. phaseolina* is classified under the *Ascomycota* division (Crous et al. 2006). The hyphae are thin-walled, dark to light brown, hyaline, branched, and septate. Branches arise from the parent hyphae, generally at right angles with a constriction at the base. Microsclerotium, a compact mass of fungal mycelium, is light brown (early stage) to dark brown (aging) in color with an oval or spherical shape (Sharma et al. 2015). The fungus reproduces by fragmentation (Sharma and Pande 2013; Ghosh et al. 2013).

The general symptoms associated with DRR disease in chickpea plants are root necrosis, lateral root shedding, yellowing of leaves, and premature drying. The characteristic feature of a DRR-affected field is the presence of irregular dried patches of straw-colored plants. The below-ground symptoms include brownish to black necrotic lesions on lateral and tap roots (Sharma and Pande 2013). Gradual progression of necrosis leads to the complete loss of lateral roots during the later

Fig. 4.1 Dry root rot disease infestation in chickpea field. The arrows represent DRR-infected plants in the field. The photo was taken from a field location at Guntur (India) during rabi 2021

stages of the disease. The taproot may remain intact with plants, but they generally become brittle. Thus, infected plants can be easily uprooted without much force. The premature drying occurs due to blocking in stele by fungal mycelium and microsclerotia growth that reduces the water and nutrient transport to the shoot. Gradual yellowing of leaves from base to top during the vegetative to flowering stage transition period marks the onset of aboveground symptoms. DRR-affected plants remain upright with straw-colored leaves and stem. Healthy chickpea plants become dry only after physiological maturity (90–120 days after sowing (DAS), while DRR-affected plants show premature drying at the reproductive stage (60–80 DAS) (Rai et al. 2022).

DRR disease incidence in the field depends on initial inoculum load, host plant susceptibility, high temperature, and moisture stress in soil. Microsclerotia are present in the soil or on plant debris from the previous cultivated season and act as a source of primary inoculum. The microsclerotia remain dormant but viable in the soil or on plant debris for several years. High soil moisture reduces the survival of microsclerotia, but it can stay in the quiescent stage and be viable for up to 15 years in the soil (Gupta et al. 2012). At the seedling stage (1–10 DAS), microsclerotia can attach to the root and begin epidermal necrosis. Necrotic lesions increase with incubation time and show asymptomatic foliage at the vegetative stage (20–40 DAS). Most pathogen-infected plant tap and lateral roots start to rot, and root loss begins at the reproductive stage (40–60 DAS). The development of symptoms is accelerated under moderate drought stress conditions. The infection period after

symptoms appear on foliage is called the active infection period (40–90 DAS) (Rai et al. 2022). However, the abundance of primary inoculum and favorable environmental condition in the field is mainly responsible for the severity of the disease.

4.4 Effect of Abiotic Stresses

Generally, chickpea growth season in India is between November to April. Thus, it encounters terminal drought and heat, i.e., at the reproductive stages of chickpeas (Sharma and Pande 2013; Sinha et al. 2019, 2021) due to rainfed cultivation. In field experiments, Sinha et al. (2019) reported that DRR incidence varied with the severity of drought stress. Higher incidence (40–60%) occurred in severely drought-stressed plots, while pathogen treatment plots with appropriate irrigation had significantly lower disease incidence (0–20%). Under controlled conditions, it was shown that DRR incidence and severity levels increased under drought stress (Sharma and Pande 2013; Sinha et al. 2019). In addition, reduced root water potential caused a rise in the DRR pathogen's lytic enzymatic activity, intensifying the disease (Rai et al. 2022).

In high temperatures, soil-borne necrotrophic pathogens could reproduce, spread widely, and adapt to high-temperature stress better than the host. Studies showing more significant necrosis and colonization in plants at high temperatures indicate a competitive advantage for the pathogen (Desaint et al. 2021). In addition, specific secondary metabolites and enzymes can accumulate in more significant quantities in warm environmental conditions (Rai et al. 2022). The DRR pathogen requires cellulolytic enzymes to lyse the host's cell walls. At temperatures between 15 and 35 °C, the soybean-specific *M. phaseolina* produced the most cellulolytic enzymes in the carboxymethyl cellulose broth medium and less at temperatures lower than 15 °C and higher than 35 °C (Gawade et al. 2018). These studies indicate that infection and colonization of fungus significantly increase with an increase in temperature (Sharath Chandran et al. 2021; Sharma and Pande 2013).

4.5 DRR Resistance Breeding

DRR phenotyping studies have revealed very few resistant genotypes of chickpea. Talekar et al. (2021) screened more than 500 chickpea genotypes in controlled conditions and reported only three resistant and 21 moderately resistant genotypes, while most of the screened genotypes were susceptible. Figure 4.2 depicts the normal distribution curve of a small set of phenotypic data. The data indicates that the distribution is skewed towards susceptibility, i.e., a higher percentage of the genotypes are susceptible. The proportion of resistant genotypes is low at 1.15%, indicating that more germplasm lines should be disease phenotyped and the resistant lines should be explored. The prerequisite for resistance breeding is the availability of resistant pre-breeding material for introgression into elite chickpea cultivars.

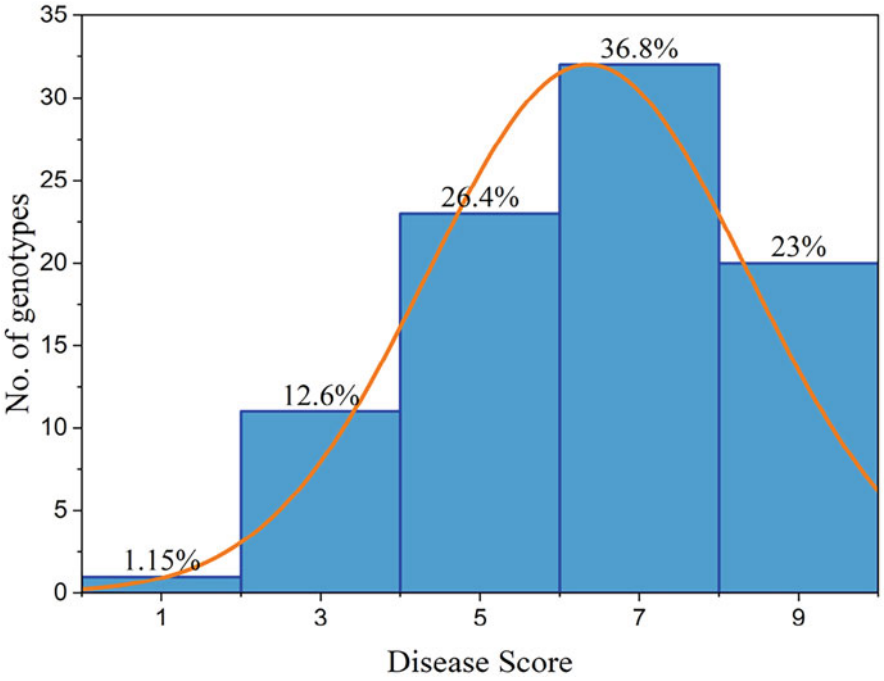

Fig. 4.2 Normal distribution curve of the DRR disease score of a few screened genotypes. The phenotypic data of 88 genotypes (Talekar et al. 2021) is represented here. The percent values indicate the proportion of genotypes with the corresponding disease score in the set of data. The orange line represents the normal distribution curve

Thus, exploring the available large chickpea germplasm is required to discover novel resistant genotypes and for subsequent breeding programs.

Towards DRR resistance breeding, two independent mapping populations have been developed by crossing two contrasting genotypes of chickpeas for DRR. The first mapping population was developed by Talekar et al. (2017). They crossed the highly susceptible genotype L550 and PG 06102, a DRR resistance genotype. The population was comprised of 129 lines. These were phenotyped for DRR resistance by the blotter paper technique. The authors concluded that the resistance to DRR is monogenic. Among the F2:3 mapping lines, 27, 38, and 64 mapping lines show a homozygous resistance, susceptible, and heterozygous disease reaction to DRR, respectively. Thus, the segregating population showed a 1:2:1 Mendelian ratio. Two markers, ICCM0299 and ICCM0120b, were identified in the population for DRR resistance. They reported that the DRR resistance region was between the two markers, and the distance of the DRR resistance gene (named *DRR1*) from ICCM0299 was 7.75 cM and 22.48 cM from the ICCM0120b marker (Talekar et al. 2017).

Karadi et al. (2021) developed a population of 182 recombinant inbred lines (RILs) obtained from the cross between ICCV 08305 (moderately resistant) and BG

212 (susceptible line). The RIL population was developed by the single seed decent technique between the generation advancement from F2 to F9. They phenotyped these lines for DRR resistance by blotter paper technique and used Affymetrix Axiom CicerSNP Array for genotyping the RIL population. A total of 13,110 SNPs were used to construct a linkage genetic map across eight linkage groups with a total length of 1224.11 cM. They identified a minor QTL (qDRR8) on the linkage group CaLG8 for DRR resistance with a phenotypic variance of 6.70% and a LOD score of 3.34. Furthermore, they reported that the QTL is flanked by the markers Ca8_3970986 and Ca8_3904895.

Therefore, the development of these two mapping populations represents only a small region of the chickpea genome or a minor QTL. However, it cannot provide more information about the genetic basis of DRR resistance. Hence, research is required to identify genomic regions conferring DRR disease resistance. Further, these regions will be the pillar of the next-generation resistance breeding strategy for DRR.

4.6 Prospective of Next Generation Breeding in DRR Resistance of Chickpea

4.6.1 Disease Phenotyping

DRR phenotyping includes field sick plot assay, sick pot-based assay, and paper blotter techniques. The rapid way of DRR phenotyping is the blotter paper technique, which requires seedling preparation, fungal culture, and assessment of disease. After incubation, the necrotic lesions and root rot will be observed for disease assessment. Based on the visual observations of infected roots, a score between 1 and 9 will be assigned based on disease reaction from resistant to highly susceptible (Irulappan and Senthil-Kumar 2021). The blotter paper technique is advantageous over sick plot and sick pot assay due to its low time requirement. In addition, the DRR phenotyping for a large number of chickpea germplasm is easy and fast by blotter paper approach relative to other techniques.

HTP is an emerging technology for rapidly analyzing the physical characteristics of many plant individuals to identify genetic variations that may be associated with a specific trait of interest (Song et al. 2021). It is a recent and accurate phenotyping technique that can also be possible with DRR screening techniques. Nondestructive imaging and sensing, including RGB (red, green, and blue), thermal infrared, spectral and hyperspectral, fluorescence, 3D, and computed tomographic imaging by X-ray and MRI (magnetic resonance imaging) techniques, and the use of whole root scanning, will advance the measurement and acquisition of HTP in chickpea phenotyping for DRR. Here we discuss the prospect of using RGB images for HTP in DRR of chickpeas in the greenhouse experiment for the aerial part. Images could be captured between 15 and 30 days of sowing in the greenhouse. The three bands in RGB images are used to compute vegetation indices for further analysis. The images

can be processed using a MATLAB-based algorithm to develop a highly accurate disease score of DRR phenotyping (Bari et al. 2023).

Phenotyping for the disease incidence on root trait can be possible by scanning the whole root using a root scanner, and the scanned image is further processed using software like WinRHIZO™ (Regent Instruments Inc.) and RhizoVision Explorer (Seethepalli et al. 2021). These HTP data of disease resistance traits will be further used for linking the genomic information (Song et al. 2021).

4.6.2 Next-Generation Sequencing in Chickpea and Genotyping

NGS and third-generation sequencing technologies have facilitated the development of a high-quality chickpea reference genome (CDC Frontier and ICC4958) and pan-genome. The estimated genome size of chickpea is 738 Mb. The CDC Frontier genome sequence spans 532.29 Mb, which contains 28,269 genes, while the chickpea pan-genome spans 592.58 Mb and contains 29,870 genes (Varshney et al. 2013, 2021). Combining multi-omic assays, large diversity panels, and HTP can bridge the gap between genome-phenome maps (Varshney et al. 2021b).

NGS and third-generation technologies will facilitate efficient allele mining in chickpea. Allele mining is an approach to identifying the new alleles in the genome of cultivars, landraces, and wild relatives. The whole genome survey of the available diversity panel of chickpea (Table 4.2), and high-throughput phenotyping of DRR resistance traits can be associated with the genome marker through GWAS in multi-parental populations (Varshney et al. 2021a) (Fig. 4.3). GWAS have been extensively employed to pinpoint the genetic basis for several crop agronomic features. The recent example of GWAS in chickpeas is 429 genotypes from chickpea-growing countries for drought and heat-related stress (Varshney et al. 2019), and 3366 chickpea accessions for yield-related traits were already available (Varshney et al. 2021). GWAS has been conducted in a few legumes under *M. phaseolina* stress.

Table 4.2 Details of sequenced chickpea genotypes for facilitating disease-resistant breeding

S. No.	Number of accessions	Average sequencing depth/ resequencing/genotype by sequencing (GBS)	Genetic variants	References
1.	429 cultivated chickpea	6.8X/resequencing	4.97 million SNPs	Varshney et al. (2019)
2.	3171 cultivated chickpea	10X/ resequencing	3.94 million SNPs	Varshney et al. (2021)
3.	195 wild accessions	10X/resequencing	19.57 million SNPs	Varshney et al. (2021)
4.	100 desi chickpea accession	GBS	44,844 high-quality SNPs	Kujur et al. (2015)

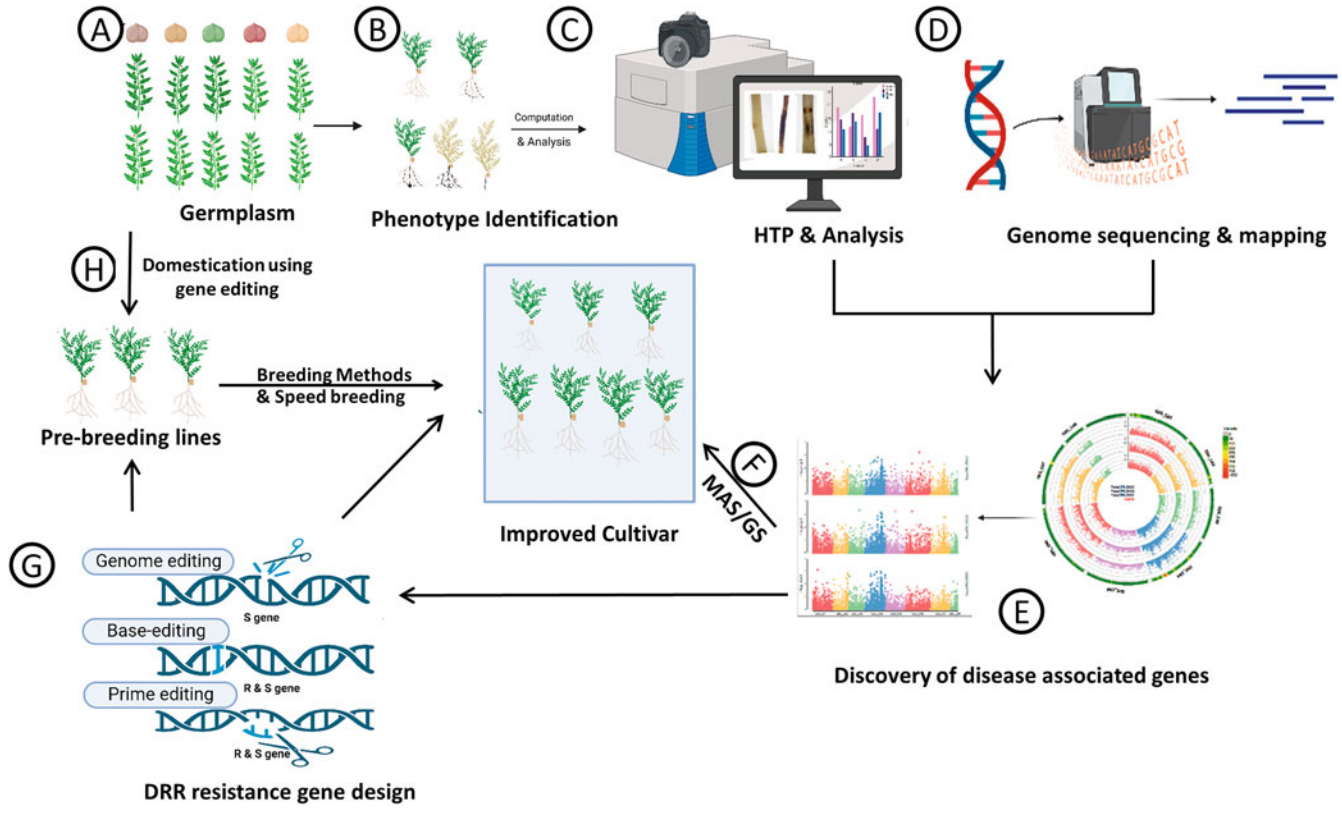

Fig. 4.3 Resistance breeding model for DRR of chickpea. This diagrammatic model depicts the steps involved in DRR resistance breeding in chickpeas. The collection of a large set of chickpea germplasm which represents high genomic diversity (**a**) will be used for DRR phenotyping (**b**), and HTP could be possible

Cosar et al. (Coser et al. 2017) identified 19 linked SNPs by GWAS of soybean against charcoal rot (caused by *M. phaseolina*). Similarly, Muchero et al. (2011) reported eight QTLs in the cowpea RIL population associated with charcoal rot caused by the same fungus. Another powerful method to identify new R genes is resistance gene enrichment sequencing (RanSeq). An understanding of the disease resistance mechanism of the host, the pathogenicity of the fungus, and identification and characterization of the genomic region or disease-contributing alleles can act as a potential pre-breeding material for resistance breeding.

4.6.3 Role of Speed Breeding

Once the GWAS approach has identified the resistance-associated alleles or R genes, speed breeding technology can be utilized. Speed breeding or rapid generation advancement (RGA) involves modulating the photoperiod, humidity, temperature, and the harvesting/germination of immature seeds. Chickpea is a quantitative long-day plant. The chickpea growth period varies from 90 to 160 days, depending on the cultivar and growing conditions. Up to seven generations of chickpea can be completed in a year using this technology (Samineni et al. 2020) by optimizing the life cycle duration. The alteration of photoperiod and temperature is responsible for early flowering and maturation in chickpea. It activates development activities such as germination, leaf expansion, and shoot growth. Samineni et al. (2020) reported that one chickpea generation could be completed in 50–60 days through speed breeding. It can be efficiently employed to accelerate the development of nearly isogeneic lines (NILs) and recombinant inbred line (RIL) populations after crossing two contrasting genotypes. Thus, the speed breeding approach can be utilized for the rapid development of DRR-resistant varieties of chickpea.

Fig. 4.3 (continued) by using cameras and root scanners and their computational analysis to get the traits information (**c**). High efficient genome sequencing and mapping information can be possible by the use of NGS technology (**d**). This can be done parallelly with the phenotyping of germplasm. The DRR phenotype information and chickpea germplasm sequencing information can be further utilized for GWAS analysis to identify associated genomic regions for the identification of genes involved in DRR disease resistance (**e**). Such genomic regions can be utilized in three ways for DRR resistant improvement in chickpea: directly utilized in resistance breeding by marker-assisted selection and genome selection for the development of DRR resistance population (**f**), the use of genome editing tool (CRISPR) for modification of S or R-genes for broad-spectrum resistance that can be used as pre-breeding lines or improved cultivar (**g**), and germplasm can be used for stepwise *de novo* domestication using genome editing for development of pre-breeding material (**h**), and further breeding methods and speed breeding can be used for development of improved cultivar. *Illustration created with* Biorender.com

4.6.4 Role of Genome Editing

A drawback of using specific R gene-mediated resistance to develop cultivars is that resistance could be broken down over time due to the arms race between the host and the pathogen. However, genetic engineering of particular R genes may aid in overcoming this drawback. The receptor regions could be engineered to decrease their specificity and enable them to recognize a broad spectrum of effectors (Segretin et al. 2014). Given that the coding areas of resistance alleles only differ by a small number of nucleotides, CRISPR-mediated homology-directed repair and prime genome editing technology can be utilized to generate new alleles with a broader resistance spectrum (Fig. 4.3) (Deng et al. 2020). An alternate way of improving chickpea resistance against DRR is engineering susceptibility (S) genes. Mutating S-genes typically results in broad-spectrum resistance. However, it has inevitable trade-offs as most S-genes are involved in the host's growth, development, or metabolic functions (Li et al. 2020). Hence, CRISPR-mediated base genome editing can engineer S-genes to produce novel elite alleles that confer broad-spectrum resistance to DRR while potentially alleviating growth and reproductive trade-offs. This has been recently achieved in rice by editing specific SWEET genes (Oliva et al. 2019). Similarly, CRISPR could be used to develop pre-breeding material or cultivars, which can be used in chickpea DRR resistance breeding programs.

4.7 Model for DRR Resistance Breeding

A breeding model for DRR resistance breeding based on the next-generation breeding approach is depicted in Fig. 4.3. An extensive chickpea germplasm can be exploited to explore the available diversity of DRR disease resistance. Phenotyping of this germplasm is required to discover the resistant genotypes. HTP can significantly and efficiently accelerate the analysis of disease resistance traits. The high-throughput advanced genome sequencing platforms or NGS technologies can be used for sequencing and mapping with the reference genome of the chickpea. The phenotypic data and identified single nucleotide polymorphism (SNP) markers can be utilized to conduct a GWAS to identify associated genomic regions or SNPs associated with the studied DRR trait. Once the resistance marker is elucidated, it could act as a source of information for resistance breeding. Alternatively, the associated SNPs or genomic regions can be directly utilized for MAS or genomic selection (GS) to develop new resistant cultivars. The GS approach can predict the genomic estimated breeding values (GEBVs). GEBVs help a breeder to know about the offspring of the crossing program, which serves as parents for the next generation in the breeding cycle. Genomic selection has an advantage over MAS and traditional breeding methods in terms of per annum genetic gain. In contrast, CRISPR-based genome editing can be utilized for broad-spectrum resistance of DRR by engineering the linked genes to recognize a broad range of pathogen effectors. In addition, speed breeding can be employed for RGA. These cutting-edge technologies can help develop DRR-resistant cultivars or improve the chickpea germplasm.

4.8 Conclusion

The number of reported DRR-resistant chickpea cultivars or breeding populations so far is low, only two chickpea breeding populations are known, and a few genotypes reported resistance to DRR. Thus, exploring available chickpea germplasm is required to identify DRR resistance sources. The phenotyping techniques should be robust for the identification of resistance. We highlight that HTP is more feasible and cost-effective and can be utilized for the phenotyping of the germplasm. The DRR disease phenotyping done up to date is insufficient to capture the available germplasm diversity. Currently, more than 3500 chickpea accessions have been sequenced. This information can be exploited for genome-wide analysis if phenome information is available. In the context of DRR, HTP and NGS information could be used to identify genetic variations that confer resistance to the disease in chickpea. The marker-trait association will provide information on the putatively associated locus in the genome for resistance to DRR. Further, the discovered genomic region (s) can be utilized to improve the chickpea germplasms against DRR (Fig. 4.3). Speed breeding and genome editing are cutting-edge technologies that can lead to broad-spectrum resistance and accelerate breeding efforts. Efficient and robust use of the abovementioned tools will be essential in driving the efforts towards breeding for DRR resistance.

Acknowledgment This work was supported by the National Institute of Plant Genome Research Core Funding and the Council of Scientific and Industrial Research (CSIR) junior research fellowship [CSIR File no. – 09/0803(13718)/2022-EMR-I] to S.R. and [CSIR File no. – 09/803 (0177)/2020-EMR-I] to R.M. The authors also thank Mr. Aswin Reddy Chilakala for providing the field image. The authors acknowledge Dr. Prachi Pandey for suggestions on this manuscript.

Conflict of Interest The authors declare that there are no conflicts of interest.

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