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REVIEW

Understanding the genetics of *Cercospora* leaf spot (CLS) resistance in mung bean (*Vigna radiata* L. Wilczek)

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Abstract

Cercospora leaf spot (CLS) is a deadly biotic stress caused by the fungus *Cercospora canescens*, making mung bean cultivation difficult worldwide. The progress made in creating CLS-resistant mung bean varieties is encouraging. However, as the pathogen rapidly evolves, it is critical to understand the pathogen dynamics and develop effective screening procedures. Plant breeders need to know about the genetic diversity of mung beans and their wild relatives, gene function and accessible molecular markers. Molecular mapping of pathogen resistance genes in mung bean varieties is now possible due to advancements in next-generation sequencing methods and the availability of genetic sources. Breeding programmes will be accelerated by developing the potential markers linked with resistance to the fungal pathogen. This method saves time by preventing time-consuming breeding to change genetic backgrounds. This review focuses on the current status of knowledge on the disease, genetic resources available for this and advances made in traditional and marker-assisted breeding for CLS resistance in mung bean worldwide.

Keywords Genetics · *Cercospora* leaf spot · Mung bean · Molecular breeding

Introduction

Mung bean (*Vigna radiata* L. Wilczek) is a popular commercial species of the genus *Vigna*, and its production is steadily increasing in South and Southeast Asia. It is a popular legume because of its short-lived life cycle and fast-growing activity during cultivation (Chen et al. 2021). In addition, fixing atmospheric nitrogen through a symbiotic relationship with *Rhizobium* can supplement its nitrogen demand. This improves soil health and increases crop yield (Jat et al. 2012). Mung bean has valuable nutritional and health benefits due to its high digestibility, vitamin B and protein content with no health risks compared to other cereals and other legumes. Mung bean has a small genome size (494–579 mb) (Wang et al. 2015; Chen et al. 2015; Chand et al. 2015; Srivastava et al. 2018). It is a self-pollinated crop with genomic homology with other important legume crops. However, mung bean productivity is sensitive to biotic stresses like CLS and powdery mildew. Mung bean often succumbs to *Cercospora canescens* or *Cercospora cruenta*, the causal organism of CLS disease, but requires special attention as it can affect plant growth and reduce seed yield (Mew 1975). Fresenius first described *Cercospora canescens* in 1863 (Fuckel 1863; Crous 2003; Crous et al. 2011). An overview of *Cercospora canescens* is indexed in Table 1 (PaDIL Database 2022).

The incidence of mung bean CLS is widespread in India during the *kharif* season in warm and humid climatic conditions, causing considerable losses to mung bean growers (Agarwal et al. 2006, 2007; Chand et al. 2013). In the warm and wet seasons, yield losses of up to 47% under the northeast

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Table 1 Overview of *Cercospora canescens*

Particulars	Description
Disease	Leaf spots are circular to angular, 1 cm in diameter and often pale brown or grey with a reddish-brown margin
Morphology	Pale brown conidiophores in fascicles, mainly on the lower leaf surface
Synonymy	*Cercospora apii* sensu lato
Commodity type	Pigeon pea, hyacinth bean, lime bean, butter bean, kidney bean, mung bean, yard long bean, cowpea and other Fabaceous produce
Distribution	In the tropics and subtropics
Host family	*Cajanus cajan* (L.) Huth. *Calopogonium mucunoides* Desv, *Crotalaria juncea* L., *Desmodium tortuosum* (Sw.) DC, *Lablab purpureus* (L.) Sweet, *Macroptilium atropurpureum* (DC.) Urb., *Phaseolus lunatus* L., *Phaseolus vulgaris* L., *Psophocarpus tetragonolobus* (L.) DC., *Vigna marina* (Burm. f.) Merrill, *Vigna radiata* (L.) Wilczek, *Vigna unguiculata* ssp. *sesquipedalis* (L.) Verdi, *Vigna unguiculata* ssp. *unguiculata* (L.) Walp

plain zone in India (Singh 1981; Kumari et al. 2018), 61% in Australia and Okara, Pakistan (Sompong et al. 2012; Rasool et al. 2021), 23–75% in Thailand (Somta et al. 2015) and 37.4% in South Korea (Pan and Zhao 1994; Bushra et al. 2013) have been documented across the world. The disease arises between early blooming (30–40 days) and pod maturity, and the selected cultivar including the surrounding environment determine its severity (Bushra et al. 2013). Under favourable temperature (25–30 °C) (Rossi and Battilani 1991; Windels et al. 1998; Vereijssen et al. 2007; Skaracis et al. 2010) and humidity (90–100%) (Weiland and Koch 2004; Chen et al. 2007), it spreads rapidly in susceptible varieties causing premature defoliation and reduced size of pods and seeds.

In this aspect, *Cercospora canescens* genomic research provides insights into the pathogenic process and a better understanding of its virulence inside the mung bean host (Dahiya et al. 2013, 2015; Abbas et al. 2020). However, recent advances in genetic transformation and marker-assisted selection have been widely helpful and accepted as potentially valuable tools for improving legume yields to achieve biotic stress tolerance like CLS in mung bean (Singh et al. 2014a, 2014b). Molecular markers, primarily DNA-based markers, are widely used for gene mapping and tagging. This strategy has dramatically helped the accurate selection of elite varieties for accelerated breeding programmes to improve disease resistance in plants. Therefore, understanding the genetics of CLS resistance is essential for exploring molecular markers closely related to the candidate genes or quantitative trait loci (QTLs) that underlie the traits for use in CLS resistance breeding.

Genome organization and life cycle of *Cercospora canescens*

Cercospora canescens is a hemibiotrophic pathogen that causes mung bean leaf spot disease. Its whole genome (approx. 33.97 Mb) (Chand et al. 2015) is put together from 8239 contigs that cover 10,627 protein-coding genes (Table 2). Most of these proteins are involved in the infection mechanism of compromising nutrition or damaging host tissues; signal transmission; wall disintegration; transporters; host stomata sensing; adhesion; polyketide synthase; and coding for cercosporin, glycosidases, transposases and cytochrome P450 genes (Chand et al. 2015). In addition, a well-known 528 simple sequence repeat markers were discovered from the genome collection assembly, which aids in identifying similarities and variations in parts of the varied genomes of *Cercospora* sp., which provides insights into the pathogenic mechanism and a better understanding of its virulence differentiation (Chand et al. 2015; Das et al. 2020; Wilken et al. 2020; Liu et al. 2021).

It will also help to identify similarities and differences in regions among the genomes of different species of *Cercospora*, which will eventually explain the gene regulation and control of gene expression for CLS disease in mung bean and other crop species. One of the most effective strategies for genetically apprehending *Cercospora* species is phylogenetic analysis based on partial sequences from the intervening 5.8S rRNA, actin, calmodulin and histone H_3 genes. However, without extensive pathogenicity studies, this technique is ineffective in determining the host type of

Table 2 Features of *Cercospora canescens* whole-genome assembly

Cercospora canescens genome organization	Values
Genome size	33,967,224 bp (~33.97 Mb)
Contigs available	8239 numbers
Contigs available greater than 10 kb	1119 numbers
Contig length	79,323 bp
Number of B_{N50} available	13,944 numbers
Availability of PCD genes	10,627 numbers
Percentage of G + C content	51%

B_{N50}, N50 bases; *PCD genes*, protein-coding genes; *bp*, base pairs

Cercospora sp., even if it offers crucial information on a specific strain's identity (Gomes et al. 2013; Bakhshi and Zare 2020). Genetic variation exists among the isolates, although there is no known sexual state. The fungus *C. canescens* is reproduced asexually by exogenic needle-shaped spores or conidia, and borne externally on fungal hypha or conidiophores (Fig. 1). The conidia are the infectious agents for CLS in mung bean. In a CLS-infected plant, leaf spots (2–4 mm and maximum 10 mm in diameter) appear with reddish-brown edges and yellow halos (Fig. 2) (Bhat et al. 2014). This typical disease symptom starts on leaves within 30 to 40 days after planting (Das et al. 2020). Besides these symptoms, spots also appear on pods, and the fungus spreads inside them, affecting seed development (Nair et al. 2019). At a later stage of infection, the leaf spots get dried, and the resulting infected plant debris is mixed with the soil, where the fungus thrives mainly as desiccation-resistant pseudostromata. These subsequently produce conidiophores and conidia, which follow either anemochory or ombrohydrochory dispersal (Chand et al. 2015) and infect healthy plants as primary inoculum (Chand et al. 2012; Laosatit et al. 2018). Besides, the fungal spores also spread directly from the infected plant to other healthy plants as secondary inoculum, causing a drastic effect on growth and productivity in mung bean.

Cercospora isolation, culture and preparation of inoculum

Cercospora canescens is isolated from mung bean leaves with characteristic CLS symptoms (Fig. 2). The spores of the pathogen are collected at the tip of the inoculation needle from the ash grey centre of the lesion(s) and dispersed over a 2% water-agar plate, and then incubated at 25 °C. Germinated spores are indicated under the microscope (100×) after 6 hour of incubation (Chupp 1954; Braun 1995; Goodwin et al. 2001; Bensch et al. 2012; Sautua 2021). Individual germinated spores are extracted using a sterilized cork borer and put in culture tubes over potato dextrose agar medium. *C. canescens* is then recognized by its anticipated growth, cercosporin production (Kumar et al. 2021), development of conidia and conidiophores (El Housni et al. 2021). Multiple small, angular, necrotic water-soaked grey sporulating lesions with chlorotic margins occur when the normal *C. canescens* isolates are inoculated (Edet et al. 2021; Prasad et al. 2021) on potato dextrose agar medium.

Fig. 2 CLS disease symptoms in mung bean

Sorghum grain-based inoculums are created for inoculum multiplication. Sorghum grains are cooked until soft without shattering the seed coat and then distributed in the shade to eliminate excess moisture. Sorghum grains (200 g) are placed in a polypropylene bag (30 × 20 cm^2) and sterilized

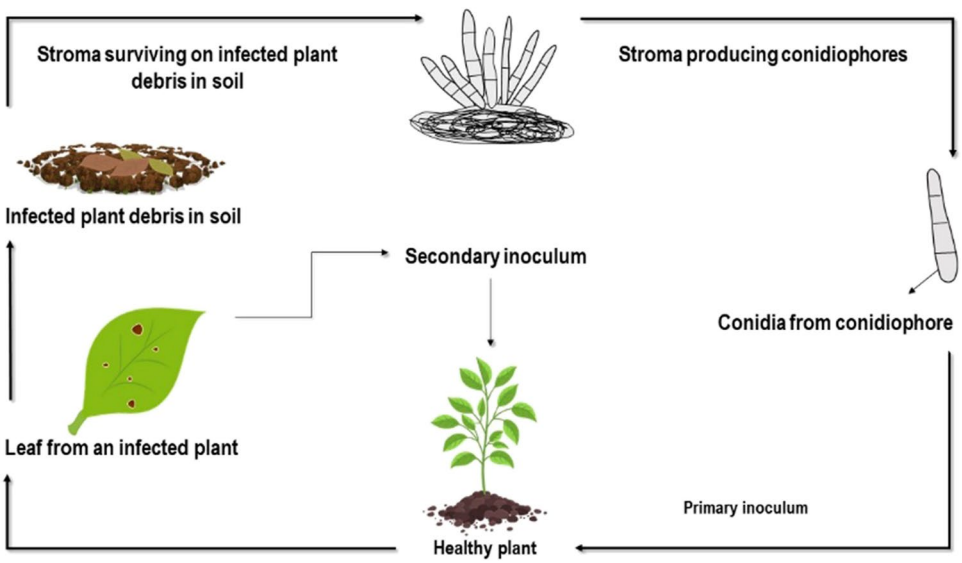

Fig. 1 Life cycle of *Cercospora canescens*

twice in an autoclave at 121.6 °C for 45 min at 15 p.s.i. pressure. These bags are injected with ten pieces of fungal mycelia with a diameter of 7 mm, collected from a 15-day-old culture. These bags are incubated for 20 days at 25 °C for *Cercospora* mycelia colonization. Following complete colonization, the bags are aggressively shaken to disrupt the mycelia network and incubated for additional 5 days at 25 °C. Spore production is detected after 25 days of incubation at 25 °C (Bublitz et al. 2021; Sucianto and Abbas 2021).

This type of inoculum applies to the soil at planting time, but spraying inoculum containing spores onto leaf surface is usually done using conidia suspensions from colonies produced on agar media (Sucianto and Abbas 2021). However, scientists in some previous studies also described that sporulation in the culture is best on carrot leaf decoction agar and residual carrot leaves (Rathaiah and Pavgi 1971). In some previous studies, secondary conidiophores and conidia are also observed in the stale bread sporulating cultures (Rathaiah and Pavgi 1973; Maiti et al. 1985; Dange and Pandey 1992; Kolte 2018).

Screening and agro-morphological assessment for CLS resistance

CLS is an important phyto-pathological problem of mung bean, which is a multiuse legume crop. Field screenings for resistant plants, although accurate and effective, demand significant time and a sizable workforce to accomplish. Also, weather conditions in the field may not always be favourable for uniform disease spread, which eventually may lead to failure of the overall experiment. Therefore, it is essential to know the symptoms of the CLS disease in mung bean and to identify a suitable screening method to distinguish the CLS resistance cultivars from the susceptible cultivars. After multiplication and spraying of *Cercospora* culture to mung bean germplasms, common symptoms of CLS are observed (Fig. 2), which is screened by using a suitable rating scale. CLS disease screening procedures are generally based on any rating scale from 0 to 5 (Andrade et al. 2021; Singh et al. 2021), 1 to 9 (Mishra et al. 2021; Kashiwa et al. 2021) and 1 to 5 (Sahoo et al. 2022a). Numerous lines or genotypes were somewhat resistant, tolerant or vulnerable after being screened by several workers (Table 3). In Eastern India, two-third of the area under mung bean is cultivated using local cultivars during the winter season, mainly in rice fallow under the rainfed situation in less fertile marginal and sub-marginal lands. In such continuous minimal cultivation, the local landraces sustain low productivity, and the plant types have adapted to survive following natural selection against biotic and abiotic stresses. This results in many landraces to get adapted to a wide range of agro-climatic conditions.

Genetic variability in the available germplasm of mung bean is limited. Besides, repeated use of selected genotypes in various breeding programmes has resulted in genetic erosion in the gene pool. However, to develop truly revolutionary new cultivars for tomorrow, plant breeders will need access to the wealth of genes that exist only in exotic and/or local gene pool, including related wild species (Tripathy et al. 2016). In this context, morphological characterization of genetic resources is vital in generating new desirable plant types that help in increasing crop production and producing quality. Therefore, scientists have explored local landraces, wild varieties and improved mung bean varieties for grouping them into different genetic clusters (Tripathy et al. 2016). The above genotypes were found morphologically unique, had desirable agro-economic traits, formed small divergent clusters, and may serve as a valuable material for genetic improvement in mung bean through hybridization for different biotic and abiotic stress tolerances (Tripathy et al. 2016). Morphological features include both quantitative and qualitative features based on plant morphology (Pratap et al. 2021). Scientists have highlighted morphological characteristics to assess variability (Sabatina et al. 2021).

However, some researchers also reported that anthocyanin pigmentation in hypocotyl is essential in mating-based breeding programmes to recognize pure mating (Sabatina et al. 2021) during CLS infection as hypocotyl pigmentation could be used as a critical morphological character for ascertaining varietal distinctiveness among genotypes (Dhaliwal et al. 2020). Subsequently, scientists also highlighted genotypes with green or purple hypocotyls for sprout production during CLS infection (Soehendi et al. 2021; Mwangi et al. 2021), and reported that yellow seeded mung bean genotypes are low in phytic acid and can be used as donors to improve mung bean seed quality and for biotic stress resistance as genotypes with low phytic acid in the seed may show increased assimilation of nutrients (Dhole and Reddy 2015).

Besides this, a positive relationship also exists between seed index and seed yield per plant (Sineka et al. 2021), as some previous reports indicated that high yielding mung bean varieties should possess larger leaf area, higher total dry mass production ability, superior crop growth rate at all growth stages and high relative growth rate and net assimilation rate at the vegetative stage which would result in superior yield components (Mondal et al. 2012). Scientists found that the juvenile phase, i.e. a period of vegetative growth after emergence, during which the plant is unresponsive to photoperiod, is some excellent criteria for developing disease resistance mung bean plants (Basandrai et al. 2021). Some scientists also considered morphological characterization is an essential step in describing and classifying plant germplasm (Tantasawat et al. 2021). However, some scientists also suggested that selecting suitable parents play a vital role in successful plant breeding programme (Agbeleye et al.

Table 3 Screening of resistance to *Cercospora* leaf spot in mung bean

No. of varieties screened	No. of resistance varieties found	Name of the HR varieties	References
200 accessions	3 (HR)	ML-5, ML-15 and ML-3	Mew (1975)
72 accessions	3 (HR)	11/99, 11/395 and 1b-303–20-3-g	Singh and Gurha (2007)
130 accessions	1 (HR); 2 (MR)	MB-53	Hossain et al. (1981)
27 accessions	10 (MR)	-	Jadhav and Sharma (1983)
183 accessions	3 HR; 6 (MR)	1815, PLU-2A and 14/8	Gurha and Mishra (1985)
238 accessions	7 (HR); 80 (MR)	-	AVRDC (1987)
2028 accessions	2 (HR)	V3 417 and V4 483	Sandhu et al. (1988)
-	12 (HR)	-	Mathur et al. (1989)
18 accessions	3 (HR)	Shantung, VC 1560D, CNT 8507	Pichitporn et al. (1990)
108 accessions	5 (HR); 41 (MR)	ML-3, ML-5, ML-15, PLM 448 and CES 1D-21	Raguchander et al. (1990)
2287 accessions	31 (HR)	-	Bisht et al. (1991)
-	5 (HR)	ML-371, ML-353, UPM-85–3, UPM-83–6 and UPM-6–2	Sahoo and Hota (1991)
87 accessions	4 (HR); 12 (MR)	-	Iqbal et al. (2009)
8 accessions	2 HR	P-27 and P-32	Kaushal and Sharma (1993)
150 accessions	2 HR	PMB-49, ML-820	Sandhu et al. (1996)
260 accessions	9 (HR); 28 (MR)	-	Sindhan et al. (1990)
58 accessions	12 (HR)	NM-98, 98-cmg-003, C2/94–4-42, NM-1, NM-2, 98cmg-018, BRM-188, CO-3, Basanti, PDM-11, BARI Mung-2 and VC3960-88	Iqbal et al. (2004)
116 accessions	5 (HR); 8 (MR)	BM 4, CO 4, CO 5, ML 515 and TM 98–50	Singh et al. (1998)
12 accessions	1 (HR)	SKUA-M-358	Bhat et al. (2008)
100 accessions	11 (HR)	013,987, 013,929, 014,219, 014,240, 014,241, 014,243, 014,245, 014,258, 014,259, 014,293 and 014,309	Iqbal et al. (2009)
31 accessions	8 (HR); 22 (MR)	-	Kumar et al. (2011)

HR, highly resistance; *MR*, moderately resistance

2021; Jain and Sharma 2021) for biotic and abiotic (Sahoo et al. 2020b) stress resistance.

Morphological characterization of mung bean germplasm helps to build groups with specified features and attributes to distinguish genotypes. Some morphological study findings are also published, such as for assessing viability (Sabatina et al. 2021), hypocotyl anthocyanin pigmentation (Win et al. 2021), green hypocotyls (Yimram et al. 2009), seed index and seed yield per plants (Tantasawat et al. 2021), pubescence (Pratap et al. 2021) and number of pods per plant (Patil et al. 2021), for mung bean development against various biotic stresses such as CLS and powdery mildew disease. Some studies have also observed a positive correlation between disease resistance and epidermal layer thickness in different pathogen-host systems (Rao and Panwar 2000; Samal et al. 2019). However, some scientists found that leaf thickness and the thickness of the epidermal layer with cuticles are not significantly affecting the severity of mung bean disease (Ahemad and Khan 2011).

The number of pods per plant is the essential trait for yield and yield attributing characters (Tripathy et al. 2013) and can be improved through breeding (Kumar et al. 2020). To date, few mung bean varieties are resistant or moderately resistant to *C. canescens*, but the selection, mating, mutation and advanced breeding methods have developed several improved varieties (Vrabl et al. 2022) mapped with major resistant genes (R genes) and quantitative trait loci (QTL) for powdery mildew, and CLS, which may be potentially used in marker-assisted selection (MAS) (Pandey et al. 2018) to develop resistance varieties.

Host plant resistance mechanism against CLS

Mung bean resistance to *C. canescens* is a single-gene dominant trait (Chauhan and Gupta 2004; Pratap et al. 2020). The pre-infection morphological defence structure limits the intensity of the initial attack of the pathogen, slows the progress of the infection and allows the host plant to develop a more efficient dynamic defence mechanism (Singh and Sharma 1981; Mittal 1991). The level of protection of mung bean may be due to the height of the trichomes and the infrequent frequency of stomata (Dutta et al. 2008). A positive correlation has also been reported between the stomatal frequency of mung bean and the susceptibility of CLS (Pramanick et al. 2013). In another study, 260 mung bean genotypes were screened for *C. canescens*, which revealed

higher total phenol and ortho-dihydroxy phenol but low carbohydrate content in the resistant genotypes (Abd El-Fatah et al. 2020). However, previously, it was found that the leaf spots are inversely proportional to the host plant's phenolic substances and soluble protein content (Dordas 2008), and the increased leaf phenolic levels are also reported to confer CLS resistance (Ishihara et al. 2021; Yaldiz and Camlica 2021; Bhat et al. 2022) in mung bean.

Resistance genetic sources against CLS

Several researchers have studied mung bean genotypes for foliar diseases such as CLS in different countries under controlled field conditions to identify the cause of resistance (Marappa 2008; Akhtar et al. 2014; Bhaskar 2020). However, only two cultivars resistant to CLS (ML131 and OUM115) have been reported in India (Singh and Ahlawat 2005; Shukla et al. 2022). It has shown an urgent need to identify mung bean lines to CLS disease (Kaur et al. 2011; Parihar et al. 2017) in India. However, while screening 20 mung bean genotypes against *C. canescens*, only 10 genotypes were resistant under field conditions (Hartman et al. 1993) in India. Another study indicates variable response of 58 mung bean genotypes to *C. canescens*, with 27 genotypes showing resistance and 17 others showing tolerant reaction (Iqbal et al. 2004) in Pakistan. Besides this, in another study, five elite mung bean genotypes were shown to have CLS resistance in 116 germplasm stocks (Singh and Gurha 2007) in India. Subsequently, 12 mung bean genotypes were tested for CLS resistance in a similar study in India, in which only one (SKUM358) was resistant, and the others were sensitive or very sensitive (Bhat et al. 2014). Table 4 comprehensively shows the resistant genotypes reported by several researchers for CLS fungal infections, which can be considered while designing the breeding programmes against CLS in mung bean.

The inheritance pattern of CLS in mung bean

It is essential to understand the inheritance pattern of CLS in mung bean for transferring resistance genes from donor to recipient parent through breeding programmes. However, genetic studies on the inheritance of CLS resistance using different sources of resistance have shown monogenic inheritance either by a single dominant gene (Leabwon and Oupadissakoon 1984; Chauhan and Gupta 2004; Kimber and Paull 2011; Singh et al.

Table 4 Resistant genotypes of mung bean against *Cercospora* leaf spot

Disease reaction	Genotypes	References
HR	1224–52 and 12,404, LGG-460, KMP-13	Zhimo et al. (2013); Yadav et al. (2014); Bhaskar (2000)
R	AC 5, AKM 9911, ATTIAMPALYAM, BL 849, CC 192, CO 4, CO 6, DHOLI, DM 2, DPI 701, G 122(D), GA 8810, GM 8413, KANGAYAM, KG 52, KKM 3, KLM 4, KM 1883, KM 2194, KU 44, LM 182, LM 1900, LM 2023, LM 565, LM 567, M 986, MAVT 807, MAVT 817, MAVT 849, MDU 2010, MDU 2196, MDU 2268, MDU 3156, MDU 3312, MDU 3385, MDU 3404, MDU3404/1, MGG 221, MGG 341, MGG 355, MH -1, MH 90–1, MIVT 843, MIVT 845, MIVT 847, MIVT 850, MIVT 852, MIVT 856, MIVT 862, MIVT 867, ML 173, ML 347, ML 520, ML 561	Kumar et al. (2020)
	V1471, V2757, V2773, V4718, V5036	Hartman et al. (1993)
	M5-22 and M5-25	Wongpiyasatid et al. (1991)
	NCM 255–2, NCM 257–6, ML-267, NCM 251–1, NCM 259–2, NCM 251–13, NCM 257–2, NM-92, NCM 251–12, VC-3960-A88 NCM 257–10, NCM 209, Mung-6 C1/94–4-19, VC 3960-A89 HR: BRM-188, NM-98, C2/94–4-42, 98-cmg-003, NM-2, NM-1, 98cmg-018, Basanti, CO-3, PDM-11, VC3960-88, BARIMung-2	Kumar et al. (2020)
	ML5, 443, 453, 515, 610, 611, 613, 682, 688, 713, 728, 735,746, 759 and 769	Singh et al. (2021)
	90 genotypes including PANT M103, PANT M3, PUSA 105, ML 613, PANT M2, ML 173, ML 347, ML 561, PANT M4, PDM 11	Marappa (2008)
	GM-02–08, GM-02–13, GM-03–03	Yadav et al. (2014)
	AKM 9910, IPM 02–5, ML 1299 and SML 668	Akhtar et al. (2014)
MR	ADT1, AGASTHIALINGAPUR, AKM 880, BBS-1–1 CHINAMUNG, GANGA 5, GM 8426, HG 1 9A, HM 912, HUM 6, K 851, K PUDUR 1, KALIKALA, KAVILPATTI, LAM 2, LGG 410, LGG 461, LGG460, MDU 1948, MIVT 854, MIVT 863, MIVT 866, ML 1670, MS 9384, PS16, RMG 62, SOBOURCUTE, SM29, ONAMUNG,VBNGG2,VELLAMPATTI, VELLATIKULAM, VS 191, WBM 4–31-1–1	Ishihara et al. (2021)

HR, highly resistance; *R*, resistance; *MR*, moderately resistance

2017) or a single recessive gene although few studies also indicated polygenic nature of gene action (Chankaew et al. 2011; Laosatit et al. 2020). Inheritance of CLS resistance in mung bean was investigated in 20 lines, including resistance × susceptibility, resistance × resistance and susceptibility × susceptibility line matings. A 3:1 (resistant/susceptible ratio) was observed for 14 F_2 lines with resistant × susceptible parents (Yundaeng et al. 2021). Therefore, the inheritance of CLS resistance seems to be regulated by a single recessive gene (Papan et al. 2021a, 2021b). Table 5 displays the inheritance pattern for CLS resistance in mung bean based on the available literature. Few researchers also reported the role of modifying genes for CLS resistance in the mung bean (Nair et al. 2013). However, the success of breeding programmes mainly depends on the choice of superior parents for hybridization and clear-cut understanding of genetic system involved in the inheritance of the yield trait during CLS infection (Singh et al. 2017). Therefore, more studies need to be carried out to understand the inheritance pattern of CLS in mung bean in future.

Availability of molecular markers against CLS

The introduction of DNA-based markers has also opened up new possibilities and opportunities for biological science in the areas of evolutionary studies (Arcade et al. 2000; Reddy et al. 2002; De la Rosa et al. 2003; Doucleff et al. 2004; Lanteri et al. 2006; Labdelli et al. 2020; Zargar et al. 2021), plant systematics (Michelmore et al. 1991; Sinha et al. 2021) and more recently, the tagging of genes coding for agronomic traits and biotic-abiotic stress-related traits (Reamon-Büttner et al. 1998; Negi et al. 2000). DNA markers are the known sequences of short oligonucleotides that frequently reflect sequence variations within a species and are passed down through the generations via mendelian inheritance (Witsarut 2019; Reddy et al. 2020). Owing to their high selection efficiency, molecular marker technology has considerably contributed to the speed breeding towards improving a number of agro-economic traits, including disease and insect resistance in mung bean.

In several crops, including cereal and legumes, molecular markers have been effectively generated using random amplified polymorphic DNA (RAPD) and inter simple sequence repeat (ISSR) markers (Pandey et al. 2018; Arsakit 2019). Various molecular markers which are linked to fungal disease resistance in mung bean (Lakhanpaul et al. 2000), black gram (Souframanien and Gopalakrishna 2004) and cowpea (Gwag et al. 2006; Dikshit et al. 2007; Lavanya et al. 2008; Ghalmi et al. 2010; Bangar et al. 2018, 2021) were also identified. In a previous study, Random amplification of polymorphic DNA (RAPD) analysis confirmed that wild accession of mung bean (*Vigna radiata* var. Sublobata) is closer to mung bean local landraces, than urdbean, and the identified genotypes could serve as valuable genetic materials in recombination breeding for CLS resistance (Tripathy et al. 2015).

Table 5 The inheritance pattern of *Cercospora* leaf spot

Population combinations	Crop	Population generation of population type	Inheritance pattern (resistance to CLS)	References
Kopergaon × HUM12 and Kopergaon × ML1720	Mung bean	ISC	DEI	Choudhary et al. (2021)
All the crosses except HUM-1 × Shekhar-2	Mung and urdbean	F_2	SDG	Singh et al. (2017)
UAM09-1055–6 × IT99K-573–1-1	Cowpea	F_1	SDG	Omoigui et al. (2019)
UAM09-1055–6 × IT99K-216–24	Cowpea	F_1	SDG	Omoigui et al. (2019)
KPS1 × V4718	Mung bean	F_2	SDG (segregation analysis)	Chankaew et al. (2011)
KPS1 × V4718	Mung bean	F_2	Major QTL (qCLS) (composite interval mapping)	Chankaew et al. (2011)
KPS1 × V4718) × KPS1	Mung bean	BC_1F_1	SDG (segregation analysis)	Chankaew et al. (2011)
KPS1 × V4718) × KPS1	Mung bean	BC_1F_1	Major QTL (qCLS) (composite interval mapping)	Chankaew et al. (2011)
CN72 (susceptible) × V4718 (resistant)	Mung bean	$F_{2:9}$ and $F_{2:10}$ RIL	QTL *qCLSC72V18-1* between the marker VR393 and I16274	Tantasawat et al. (2020)
CSR12906 (susceptible) × IT90K-59–120 (resistant)	Cowpea	$F_{3:4}$ population	Major QTL qCLS9.1	Heng et al. (2020)
populations developed from V4718″ (resistant) × KPS 1 (susceptible)	Mung bean	F_2 and BC_1F_1	Major QTL controlling CLS resistance (*qCLS*)	Yundaeng et al. (2021)

RIL, recombinant inbred line; *ISC*, inter-specific crosses; *DEI*, duplicate epistatic interaction; *SDG*, single dominant gene; *QTL*, quantitative trait locus

Mung bean markers, including microsatellite markers, are also developed (Koche and Chaudhary 2019; Asghar et al. 2021) for CLS disease resistance. Microsatellite markers are highly polymorphic and have the co-dominant inheritance. These markers can be employed to create genetic linkage maps to identify and map the resistance genes or QTLs for CLS resistance in mung bean (Yundaeng et al. 2021). SSR loci are predicted to be one in every 67 kb in the plant genome (Cardle et al. 2000), demonstrating genomic regions for CLS resistance on the mung bean SSR marker-based linkage map. Chankaew et al. (2011) also reported QTL mapping for CLS resistance in mung beans (Basamma 2011) by using SSR markers to identify the marker-trait association with powdery mildew and CLS in the F_2 segregating population. Besides, Restriction fragment length polymorphism (RFLP) technology was also used to explore the genetics of CLS resistance in mung bean (Rosenzweig et al. 2015). Some other markers are also employed in mung bean, such as sequence characterized amplified regions (SCAR) (Nietsche et al. 2000; Singh et al. 2014a, 2014b; Bhat 2019), ISSR (Souframanien and Gopalakrishna 2004), amplified fragment length polymorphism (AFLP) (Souframanien and Dhanasekar 2014; Mehandi et al. 2019; Sahoo et al. 2020a, 2020b; Mogali and Hegde 2020) and cleaved amplified polymorphic sequences (CAPS) (Mehandi et al. 2019) against CLS and other biotic stress resistances.

Molecular mapping and QTL identification for CLS resistance

The advent of molecular marker technology has provided a means to help in screening resistant types efficiently, even in the absence of disease. The construction of a genetic linkage map uses commercially available diverse mung bean cultivars and wild mung bean accessions. It provides valuable information on essential traits such as seed quality and disease resistance (Lambrides and Imrie 2000). The World Vegetable Center, or AVRDC, claims to have created 1481 core collections and 296 mini-core collections (Schafleitner et al. 2015) of resistance sources of mung bean for molecular breeding purposes. Genetic resources are also explored for diversity and phylogeny analysis, high-density linkage mapping and association mapping to map the CLS resistance genes in the mung bean genome using molecular markers (Kole et al. 2015; Khamari et al. 2022). However, many genomic resources for mung bean are now accessible at National Center for Biotechnology Information (NCBI), including expressed sequence tag (EST) (Shanthala et al. 2020). Mung bean crop improvement programmes through marker-assisted selection and gene mapping requires molecular markers. In this regard, simple sequence repeats (SSR) have great utility, because of high polymorphism, co-dominance in nature, random distribution and ample availability (Chavan and Gacche 2014; Sahoo et al. 2019) in the plant genome.

Moreover, EST-SSR markers are also useful for understanding population structure and evaluating genetic diversity, which is the requisite for utilizing available genetic resources in *Vigna* species (Chavan and Gacche 2014). However, some other investigations employed RFLP probes (Pandey et al. 2018), because these markers are co-dominant, and their application produces repeatable findings. Some researchers has also identified QTL regions (Chankaew et al. 2011) and SSR markers linked to powdery mildew resistance and CLS resistance in mung bean genotypes (Kasettranan et al. 2010) based on partial linkage maps with few linkage groups. In another study, it was also reported that CLS resistance in mung bean is controlled by QTL (*qCLS*) comprising a TATA-binding protein-related factor 5 (TAF5) at *LOC106765332*, which is a potential gene for resistance to CLS (Yundaeng et al. 2021). Some identified QTLs associated with CLS in mung beans are indexed in Table 5.

Association mapping for CLS resistance can effectively identify the appropriate haplotype on a panel of matched elite breeding lines (Shanthala et al. 2020; Sahoo et al. 2022c). As such, these haplotypes could have far-reaching breeding implications. Various approaches for breeding CLS disease resistance in mung bean are indexed in Fig. 3. Recent advances in omics approaches unravelled the genetic basis of biotic stress resistance against bruchids, yellow mosaic virus, powdery mildew and CLS in mung bean and other pulses. These resources have great potential to accelerate gene discovery, mapping and molecular breeding in the crop (Kanavi et al. 2019). The conventional breeding approach (Fig. 3) aims at transferring the gene for host resistance from a donor parent to the popular high yielding variety following backcross breeding. Some researchers have recently reported genomic resources and tools such as draft genome sequence, resequencing data, large-scale genome-wide markers, dense genetic maps, QTLs and diagnostic markers for further use in multiple genetic and breeding applications in mung bean (Omoigui et al. 2019). But this has its limitations, e.g. non-availability of acute disease pressure, suitable threshold conditions for disease occurrence and suitable donors with an intense level of resistance which hinder the pace of progress for CLS resistance breeding.

But, once developed, the tightly linked DNA markers may be suitably used to make the selection process much easier and more reliable. Recently, marker-assisted selection (MAS) seems to be an innovative tool for CLS resistance in pulses (Pandey et al. 2018). A genome-wide association study (GWAS) is useful for exploring marker-trait association for CLS resistance in mung bean (Breria et al. 2020). Recently, the MAS-supported haplotype-based breeding approach seems reliable for increasing breeding efficiency (Pandey et al. 2018; Witsarut 2019; Breria et al. 2020). In a recent

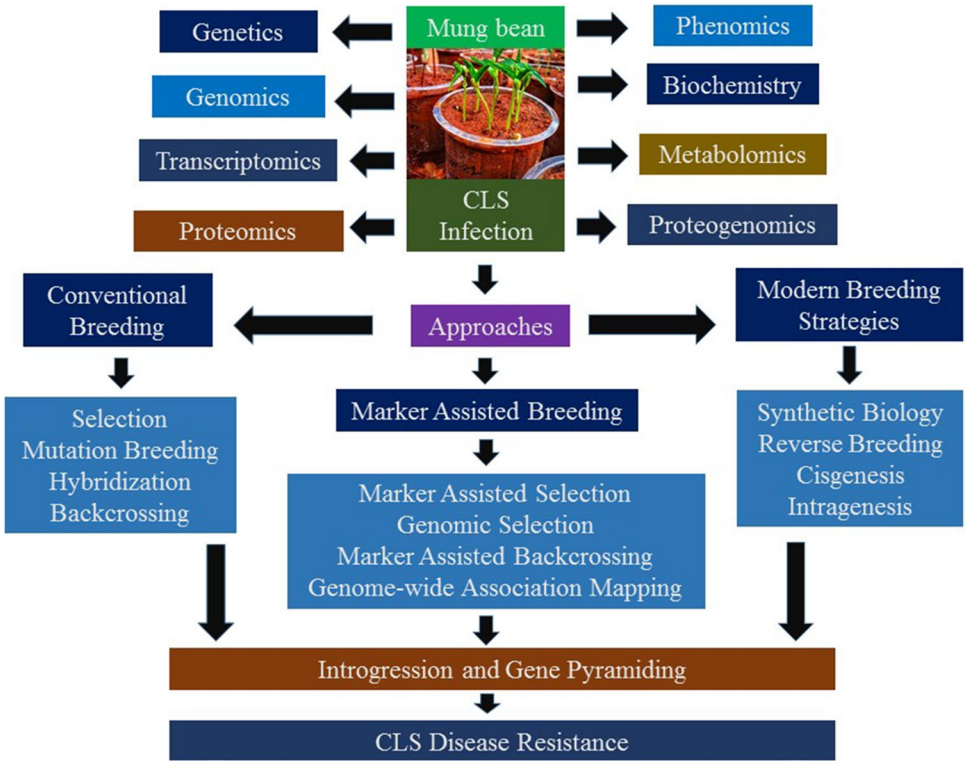

Fig. 3 Various approaches for breeding of CLS disease resistance in Mung bean

study, a CLS resistance gene and two powdery mildew resistance genes were pyramided from the donor parent D2 into a susceptible variety KING through marker-assisted backcrossing (MABC) and evaluated their agronomic traits and disease resistance under field conditions (Papan et al. 2021a, 2021b, 2022). These results could substantiate the usefulness of marker-assisted backcross breeding for transferring multiple resistance genes into an elite variety.

Furthermore, next-generation sequencing (NGS) can aid in detecting alleles and genotype–phenotype correlations (Shanthala et al. 2020; Sahoo et al. 2020a, 2020b). However, the cutting edge breeding strategies supported by genome engineering (cisgenesis, transgenesis, nano-particle-mediated gene delivery, genome editing, RNAi, micro-RNAs etc.), somatic hybridization (protoplast fusion), protoplast transfection, transcriptomic and epigenetic studies can lead to the transfer of target gene(s) in the recipient plants with a higher level of expression for CLS resistance (Groenewald et al. 2013; Shanthala et al. 2020; Sahoo et al. 2021, 2022b). Plant breeders can re-design their breeding strategies using these biotech tools to develop durable CLS resistance in mung bean.

Conclusion

CLS is one of the most serious mung bean diseases, resulting in a significant reduction in productivity. Because of the large strain variability of *Cercospora canescens*, strategic planning may be designed to explore long-term resistance sources across multiple *Cercospora* isolates for use in mung bean breeding. Although the mung bean is an important crop, so far, little information about its genetics and genomics is available in the public domain. The availability of its complete genome in the public domain and marker databases, including molecular markers for various stress resistance, would speed up the molecular knowledge of resistance and enable quick marker design for the application in future breeding programmes for CLS as well as other biotic and abiotic stress resistance. The publicly accessible markers may be confirmed and used in marker-assisted backcross breeding programmes to introduce CLS resistance genes or QTLs into various mung bean genetic backgrounds.

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Data availability All data generated or analysed during this study are included in this published article.

Declarations

Conflict of interest The authors declare no competing interests.

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