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REVIEW ARTICLE

Navigating towards dry root rot resistance in mungbean: impacts, mechanisms, and management strategies

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Abstract

Vigna radiata L., commonly referred to as mungbean or green gram, holds significant importance as a pulse crop in India. However, its productivity is severely impacted by the combined incidence of dry root rot disease and drought stress. Dry root rot, caused by *Macrophomina phaseolina*, manifests as reduced yield and compromised produce quality. *M. phaseolina* is a necrotrophic fungus with a broad host range. Screening studies in several crops' germplasms have shown a skewness towards susceptibility. Further, the fungus has augmented virulence and survivability in soil under low moisture and high heat. Thus, concurrent drought and dry root rot leads to significantly higher yield losses. This review highlights the status of the disease in mungbean and its future implications owing to the changing climate scenario. We also highlight the molecular and genomic studies conducted in mungbean and several other crops to elucidate the mechanisms involved in *M. phaseolina* resistance. The review also suggests management practices which can alleviate yield losses in dry root rot affected fields. Understanding the physiological and molecular mechanisms of dry root rot, drought, and their interaction on disease proliferation can help mitigate the challenges associated with dry root rot management and aid future research.

Keywords Mungbean · *Macrophomina phaseolina* · Dry root rot · Charcoal rot · Drought · Combined stress

Introduction

Vigna radiata L., commonly referred to as mungbean or green gram, is widely grown in East Asia, Southeast Asia, and the Indian subcontinent. Global mungbean cultivation spans approximately 7.3 million ha, with an average yield of 721 kg/ha (source: https://iipr.icar.gov.in/mungbean/). Myanmar, India, China, Indonesia, Thailand, and Kenya are the key global producers of mungbean (Nair et al., 2020).

In India, mungbean is the third most significant leguminous crop, contributing approximately 16% to the overall pulse production. According to estimates from the Government of India (averaged for 2017–18 to 2021–22), mungbean is grown on 48.5 lakh ha, with a total production of 26.5 lakh tonnes and a productivity of 546 kg/ha. Rajasthan is the major mungbean-growing state, with an acreage of 23.3 lakh ha (46% of the total area), production of 11.2 lakh tonnes (45% of the total production), and productivity of 480 kg/ha.

Other significant mungbean-growing states include Madhya Pradesh (5.1 lakh ha), Maharashtra (4.3 lakh ha), Karnataka (4.1 lakh ha), Odisha (2.4 lakh ha), Tamil Nadu (1.7 lakh ha), Bihar (1.6 lakh ha), Gujarat (1.4 lakh ha), and Andhra Pradesh (1.1 lakh ha). The productivity of mungbean in many Indian states is much lower than the national average (~24%). The low productivity of mungbean is mainly due to production constraints, including biotic and abiotic stresses that affect the crop throughout its life cycle. Fungal and viral pathogens pose significant threats to mungbean cultivation, with more than half of the crop losses attributed to soil-borne pathogens. The situation is exacerbated by climate change, leading to frequent occurrences of abiotic

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stresses such as drought and heat, which further promote the proliferation of soil-borne pathogens. Breeding for climate-resilient cultivars possessing adaptive traits that confer resistance/tolerance to the combined biotic and abiotic stresses is a viable strategy to realize higher productivity in mungbean.

Dry root rot—a globally emerging disease in mungbean

Dry root rot (DRR) is caused by the pathogen *Macrophomina phaseolina* and is known to affect over 500 plant species, including agricultural crops. The pathogen is also known to occasionally affect humans (Arora et al., 2012). The phytopathogenic fungus affects all stages of plant growth, from germination to maturity (Anupriya et al., 2023). In vulnerable plant species, the infection can manifest as damping-off, stem blight, stalk rot, leaf blight, or pod rot (Khan et al., 2023). The emergence of DRR has become a significant concern for mungbean cultivation worldwide (Kaur et al., 2012; Mallaiah & Rao, 2016; Pandey et al., 2021). The disease has caused 25–48% yield loss in South Asia (Bashir & Malik, 1988; Iqbal & Mukhtar, 2014). In India, the yield loss in mungbean due to *M. phaseolina* infection ranged from 30 to 44% (Kaur et al., 2023), up to 30% in Rajasthan (Tyagi et al., 1988; Sharma & Singh, 2000; Basandrai et al., 2021), up to 25% in Andhra Pradesh (Mallaiah & Rao, 2016), and up to 10.8% in Haryana (Tyagi et al., 1988). The disease is widely occurring in other states as well.

In addition to direct yield losses at the field level, the pathogen causes seed contamination during storage, leading to significant deterioration of seeds and consequent losses (Pandey et al., 2021), reduction in seed germination, and protein content. DRR has been reported to cause up to 36% deterioration in stored mungbean (Ashwini & Giri, 2014; Basandrai et al., 2021) and a 12.3% loss in protein content (Kaushik and Chand, 1987; Ahmad et al., 2015).

Dry root rot incidence in mungbean

DRR in mungbean is a widely prevalent disease in Asia, Africa, and Australia (Batzer et al., 2022). In Asia, the disease is a menace in Myanmar and is rapidly spreading in South Asia, particularly in India, Pakistan, and China (Iqbal & Mukhtar, 2014; Pandey et al., 2021; Zhang et al., 2011). The first report on DRR incidence in India was from Jabalpur in Madhya Pradesh (Singh et al., 2022a, 2022b). The disease has been devastating in several districts of Rajasthan (Kumar et al., 2017a) and Maharashtra (Khaire et al., 2023). A systematic survey has been conducted to assess the level of disease incidence and spread of DRR in a few mungbean-growing states of India (Fig. 1).

DRR incidence ranging from 0.5 to 38% was observed in seed samples collected from 11 districts of Rajasthan (Sharma & Singh, 2000). The incidence of DRR was found in all the seed samples collected from mungbean grown in the farmers' fields of Chamarajanagar, Mysore, and Gundlupet taluks of Karnataka (Murthy et al., 2003). Based on farmer's field surveys, DRR incidence of 5.7–12% was reported in Chittoor district of Andhra Pradesh (Mallaiah & Rao, 2016). Similarly, about 30% disease incidence was reported in Namakkal district of Tamil Nadu, based on roving surveys conducted in Mohanur, Namakkal, Senthamangalam, and Rasipuram areas (Chandraprakash et al., 2022). In Telangana, DRR incidence was observed to the tune of 5.3 to 31.7% based on roving surveys conducted in villages of Adilabad, Warangal, Khammana, and Mahububabad districts (Avanija et al., 2023).

The emergence of DRR has also become a significant concern for the cultivation of other *Vigna* species. DRR incidence ranging from 16 to 33% was reported as early as 1999 in urd bean grown in rice-fallow regions of Karaikal (Rettinassababady and Ramadoss, 1999), where both mungbean and urd bean are preferred after the rice crop. The disease incidence was reported in cowpea grown in Cuddalore, Thiruvannamalai, and Vellore districts of Tamil Nadu (Mohanapriya et al., 2017), signifying the prevalence and threat of DRR in mungbean-growing areas in the state. Variations in the level of disease incidence depended on prevailing weather conditions, physiochemical attributes of the soil, inoculum load, and pathogen virulence.

The dry root rot pathogen

M. phaseolina (Tassi) Goid. is a necrotrophic, soil-borne Ascomycete phytopathogenic fungus belonging to the family *Botryosphaeriaceae*. The fungus exists in a sporulating and a non-sporulating stage. The sporulating stage is generally not associated with DRR and can be observed in the above ground symptom stage (generally referred to as charcoal rot). Further, in some plants such as chickpea, the sporulating stage is not reported (Irulappan et al., 2021) Morphologically, the pathogen produces hyphae that appear as thin-walled, transparent strands ranging from light to dark brown with multiple septa. Their branches typically emerge right-angled to the parent hyphae, constricting at the starting point. Initially, sclerotia are light brown and darken over time, shifting from irregular, spherical, oval, to oblong shapes. However, morphological and genetic variations exist among the isolates that determine their virulence to infect host species.

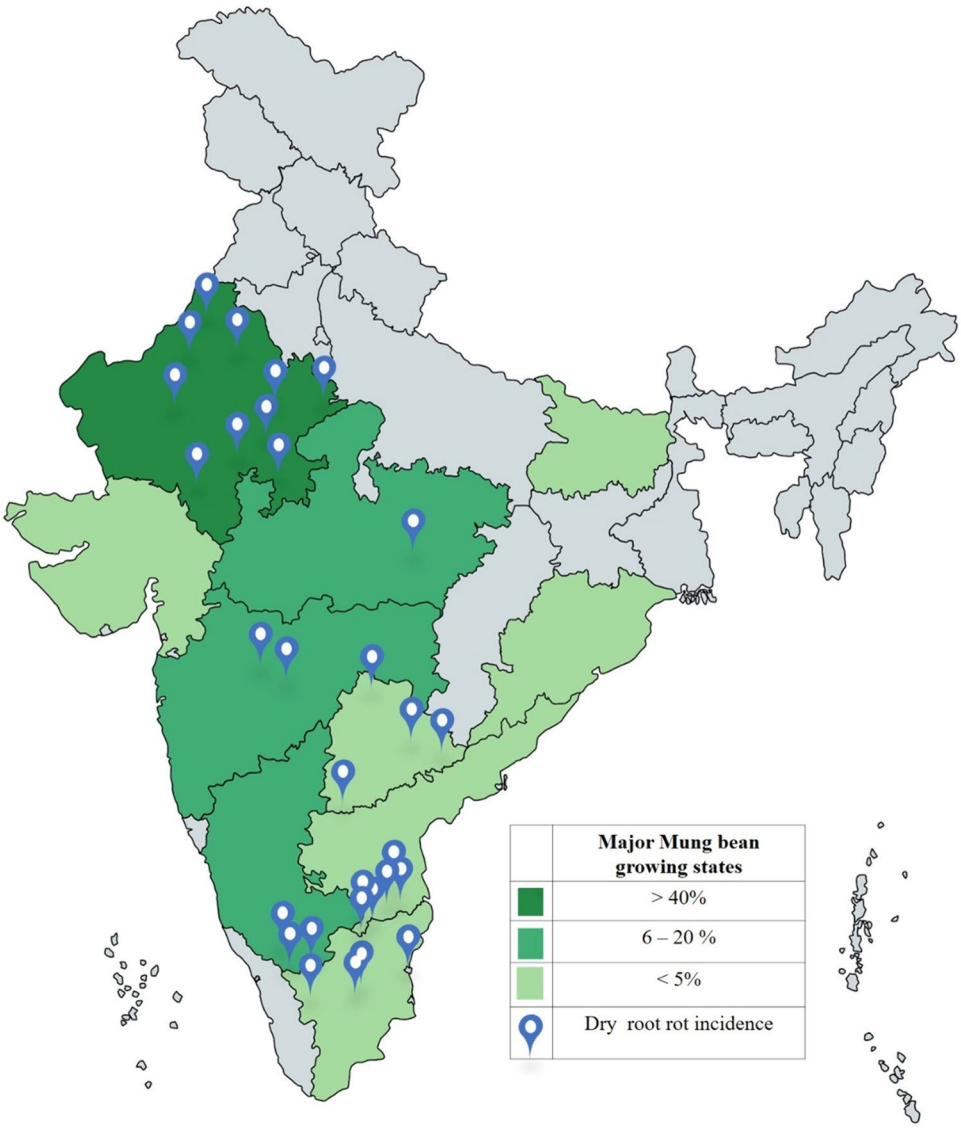

Fig. 1 Spread of dry root rot incidence in major mungbean growing states of India. Extensive literature survey was conducted to mine studies/surveys conducted on mungbean DRR incidence in various locations across India. Pins represent the districts/locations where mungbean DRR incidence surveys were conducted. Colour grades of the states is based on the average DRR disease incidence in mungbean

Cultural and morphological variability of *M. phaseolina* isolates collected from mungbean

M. phaseolina isolates from disease-affected mungbean plants from various geographical regions exhibit variations in morphology and virulence levels. As a polyphagous plant pathogen, isolates from distinct hosts also display morphological differences (Pandey et al., 2020). Climatic factors, such as temperature, seasonality, and rainfall, significantly influence the genetic variation in *M. phaseolina* (Ortiz et al., 2023). Common morphological variations among isolates include colony color, sclerotial color, shape, size, weight, count, diameter, and growth pattern (Iqbal & Mukhtar, 2014; Pandey et al., 2021).

A total of 56 isolates from mungbean and urd bean collected from 11 different locations representing North, South, Northeast, and Central India were grouped into six distinct categories based on morphological characterization (Prameela Devi & Singh, 1998). Furthermore, these isolates were classified as highly virulent, moderately virulent, and weakly virulent strains based on their intensity on the host and disease incidence. Iqbal and Mukhtar (2014) characterized 65 isolates from Pakistan based on sclerotial size, weight, radial growth, and observed no relationship between these morphological parameters and pathogenicity of isolates.

In an investigation of *M. phaseolina* isolates from 11 distinct locations (10 from India and one from Myanmar) in mungbean, Pandey et al. (2021) noted variations in the shape of sclerotia from round to oblong, with sclerotial counts ranging between 141.7 and 208.4/9 mm disc, and diameters spanning from 76.0 to 113.2 µM/9 mm disc. The sclerotial count correlated with pathogenicity, suggesting that isolates with higher sclerotial counts tend to

be more pathogenic compared to those with lower counts. Additionally, sclerotia exhibited varying shades of greyish white, greyish black, blackish grey, black, dark brown greyish (Khaire et al., 2023; Mallaiah & Rao, 2016; Pandey et al., 2020, 2021). The growth pattern also fluctuates, transitioning from less feathery to moderately feathery and eventually to more feathery structures. Despite widespread cultural variation among the isolates, their morphology remains quite similar and has been used as the primary method for identification of the pathogen.

Molecular characterization of *M. phaseolina* isolated from mungbean

While morphological features are useful for the initial identification of the fungus, molecular tools are employed for further confirmation and strain typing. DNA marker systems, such as restriction fragment length polymorphism (RFLP), randomly amplified polymorphic DNA (RAPD), simple sequence repeats (SSR), and amplified fragment length polymorphism (AFLP), have been utilized for molecular characterization and assessing genetic variability among isolates of *M. phaseolina* from various host species. The RAPD technique has been instrumental in identifying and differentiating isolates of *M. phaseolina* infecting mungbean (Babu et al., 2010; Fuhlbohm et al., 2013). The internal transcribed sequences (ITS) of 18S rRNA have been pivotal in molecular characterization of *M. phaseolina* isolated from various hosts, for species-level identification. Sequence analysis has revealed a high degree of similarity among the isolates (Mahdizadeh et al., 2011; Pandey et al., 2021; Zhang et al., 2011). In addition to ITS sequences, *Macrophomina*-specific primers (MpKF1 and MaKR1) have also been utilized in mungbean for confirming the pathogen's identity (Zhang et al., 2011). Next-generation sequencing (NGS) technologies have also been employed for characterizing isolates of *M. phaseolina*, shedding light on genetic divergence and distinct genetic clumping at the continental level (Oritz et al., 2023). Isothermal amplification techniques, such as loop-mediated isothermal amplification (LAMP), capable of fungal detection at a constant temperature within a short time with a high degree of specificity and sensitivity, are also being utilized (Notomi et al., 2015). Although the use of LAMP assay to detect *M. phaseolina* isolates in mungbean has not been reported to date, the technique has been employed to detect the pathogen in other hosts such as common bean (Rocha et al., 2017), soybean (Lu et al., 2015), chickpea (Ghosh et al., 2018), and strawberry (Burkhardt et al., 2018).

Mungbean-*M. phaseolina* interaction and disease cycle

M. phaseolina can infect mungbean at almost all growth stages, with propagules penetrating the seedcoat, endosperm, and embryo, leading to a significant reduction in seed germination and viability (Buts et al., 2014). The disease cycle consists of four stages: germination, penetration, parasitic, and saprophytic phases, with microsclerotia serving as the primary inoculum. The pathogen further spreads via airborne pycnidiospores and sclerotia, facilitating secondary dissemination (Singh et al., 2022a, 2022b). Root exudates stimulate microsclerotia germination. Upon germination, microsclerotia develop germ tubes and generate appressoria that aid in penetration into host cells. During the parasitic phase, germinated microsclerotia give rise to hyphal branches, while in the saprophytic phase, infectious hyphae penetrate plant tissues through wounds or cells on the root surface (Gupta et al., 2023), producing enzymes and toxins that aid in breaking down plant cell walls, facilitating entry into root tissues (Irulappan et al., 2021). As the fungus's hyphae grow inside plant cells, they disrupt water and nutrient transport, resulting in visible symptoms as the fungus progresses within the plant. Subsequently, neighbouring cells collapse, potentially leading to the death of heavily infected plants. The extent of invasion depends on both the plant's defense response and the pathogen's ability to counteract it (Marquez et al., 2021). Since disease outbreaks are severe under optimal environmental conditions, they often result in the premature death of host plants. Following the decay of dead roots and other plant parts, microsclerotia are discharged into the soil in clusters, serving as inoculum, and the disease cycle continues (Ghosh et al., 2018) (Fig. 2). Microsclerotia capable of enduring in soil and root debris for three years or longer enable the fungus to survive in unfavourable environmental conditions in the field (Marquez et al., 2021).

M. phaseolina harbours several potentially virulent elements that actively interfere with the host plant's defense mechanism. Initially, the pathogen establishes communication with the host via a class II hydrophobic protein and adheres to the root through the action of CEBL (cellulose-binding elicitor lectins) and transglutaminase-like proteins. Phytotoxins such as botrydiploidin, phaseolinon, and patulin secreted by the pathogen play a crucial role during the initial stages of pathogenesis. On perceiving the pathogen associated molecular patterns (PAMPS), the host immune system begins the first line of defense response by producing signaling molecules like salicylic acid. The pathogen counteracts this initial host defense by secreting compounds like salicylate-1-monoxygenase and penetrates the host tissues. The invasion process is regulated by cAMP dependent and mitogen activated protein (MAP) kinase pathway (Islam et al., 2012). Upon invading the host

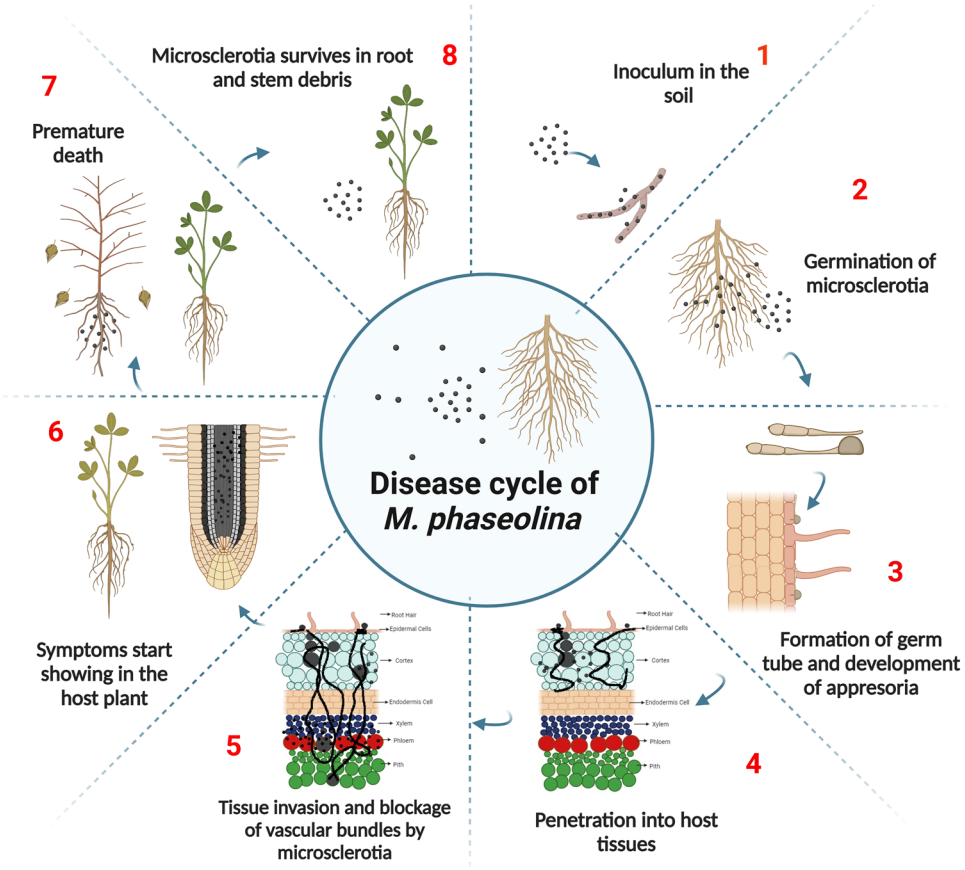

Fig. 2 Disease cycle of *Macrophomina phaseolina.* Microsclerotia in close vicinity host roots germinate upon recognition of host root exudates. Upon contact with the root, germ tube and appressoria are formed leading to tissue penetration. Necrotic lesions begin to appear on the host roots. Vascular bundle plugging leads to premature plant death. Microsclerotia survive in host debris and in soil which serves as inoculum in the next cycle

tissues, a wide repertoire of hydrolytic enzymes, cell wall-breaking enzymes, and effector proteins released by *M. phaseolina* are involved in the infection process, facilitating disease development, and eventually causing host cell death (Islam et al., 2012; Marquez et al., 2021) (Fig. 3). Sinha et al. (2022) identified 117 proteins, including xylanase, endoglucanase, and amylase, in the secretome of *M. phaseolina*. It has been observed that *M. phaseolina* can produce indole acetic acid (IAA), a hormone known to stimulate plant growth through several synthesis pathways (Amairani et al., 2023). This hormone plays a dual role in plant-pathogen interaction, acting both as a plant hormone that modifies host physiology to enhance susceptibility and as a microbial signal that impacts the pathogen to increase virulence (Kunkel et al., 2021). The elicitor molecules produced by the pathogen during the infection process trigger a series of signaling molecules involved in defense reactions that accumulate inhibitors, enzymes and pathogeneis related (PR) proteins in the host cells to prevent infection and disease progression (Fig. 3). One such elicitor molecule isolated from *M. phaseolina* was used to treat cell cultures of mungbean cultivars. The treated host cells responded to the elicitor treatment by producing increased levels of phenolics and enzymes like phenylalanine ammonia lyase and peroxidases, known to impart resistance in host plants against pathogen infection (Vidyasekaran et al., 2002).

The pathogen infests every part of the mungbean plant, from roots and stems to branches, petioles, leaves, pods, and seeds. It severely affects the overall health of the plant, weakening it by reducing its ability to uptake water and nutrients. This leads to stunted growth, reduced yield, and in severe cases, complete crop loss. The pathogen can affect plants in both pre-emergence and post-emergence stages. Initially, it causes seed rot and kills germinating seedlings. After emergence, cotyledons may be affected due to soil or seed-borne infections (Fuhlbohm et al., 2013). Usually, the onset of symptoms coincides with the crop's flowering period.

The fungus primarily targets the stem near ground level in one-month-old crops, forming localized, raised white cankers that expand and develop into upward-spreading brown streaks (Seethapathy et al., 2017). Infected plant leaves exhibit silvery-grey coloration of stems and lateral branching, with senesced leaves still attached to the plant (Zhang et al., 2011). Leaves may show dark green, mottled patterns and reduced size, followed by sudden wilting and drying, leading to a drastic decline in flowering and pod production (Singh et al., 2022a, 2022b). Necrotic lesions can appear on pod surfaces without specific placement.

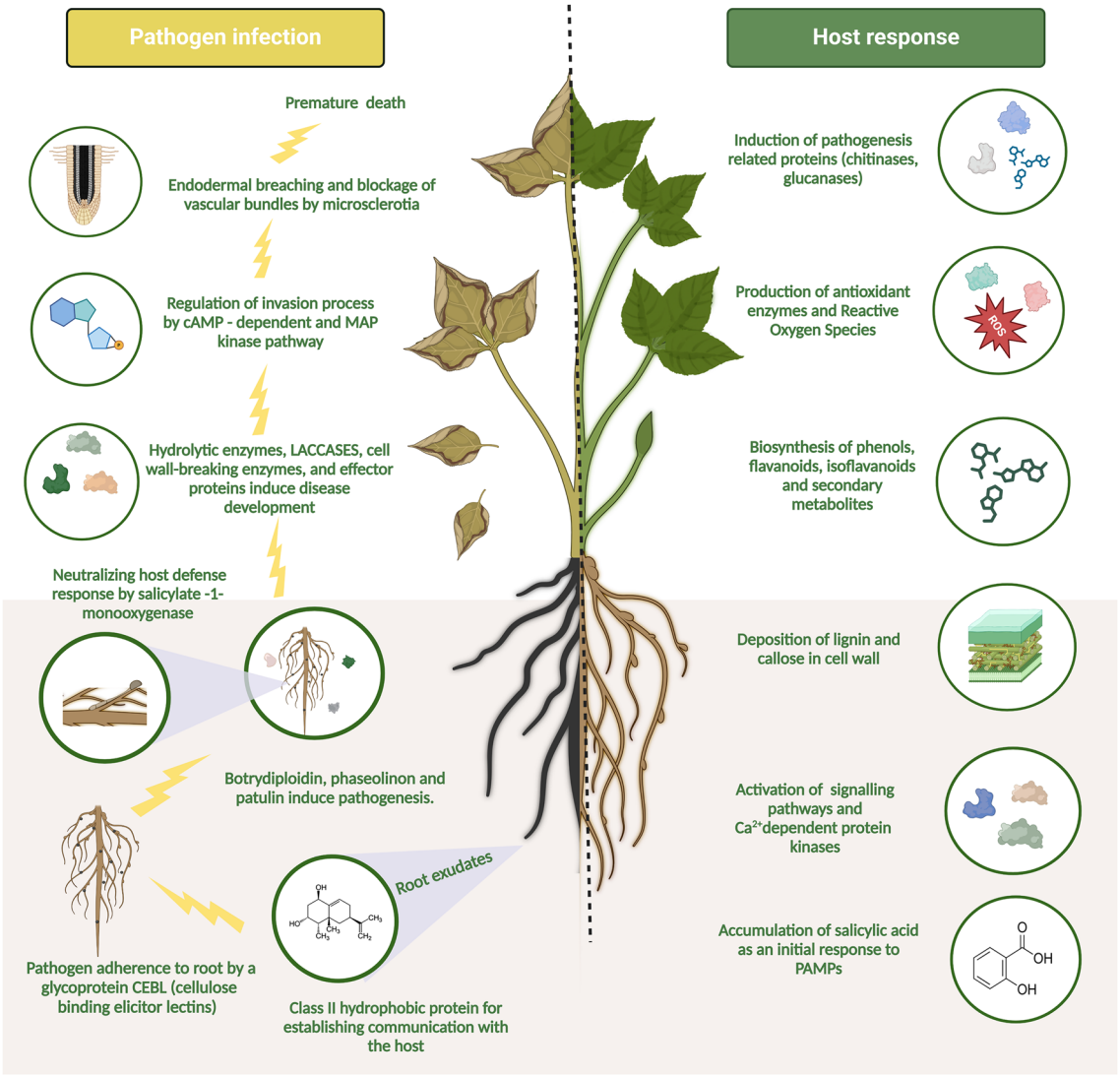

Fig. 3 Molecular mechanisms underlying pathogen virulence and plant defense in the *Macrophomina*-host interface. During successful infection, root exudates are identified by *M. phaseolina* which in turn activates pathways to induce necrosis and dampen host defences. As the fungus traverses the cortex, it eventually breaches the endodermis subsequently plugging the vascular bundles with developing microsclerotia, leading to premature plant death. In an attempt to defend against *M. phaseolina*, the host employs several strategies such as activation of SA mediated signal cascade, Ca^{2+} mediated responses, cell-wall depositions, secondary metabolite synthesis, ROS signalling, and PR proteins

Initially, infected green pods exhibit a blue-green color, transitioning to brown or reddish color. Mature dry pods infected by this fungus appear white to grey and bear scattered or widespread black structures. The fungus penetrates both pods and grains, and affected grains either abort earlier or desiccate, resulting in emptiness (Ghosh et al., 2018). Seeds obtained from infected plants appear shrunken, brown, and sometimes have scattered black *M. phaseolina* sclerotia (Akhtar et al., 2011). Vertical splitting of the drying and wilt-affected plants reveals discoloration in internal tissues (Basandrai et al., 2021). The affected plants can be easily uprooted, leaving behind dried, decayed root sections in the soil. The rotten, decaying stem and root tissues show dark discoloration due to the presence of numerous small black sclerotia, hence the symptom is popularly described as charcoal rot (Singh et al., 2022a, 2022b). Additionally, deterioration of secondary roots, shredding of the cortex area in the taproot, dark brown necrotic lesions on the exterior surface of the taproot, underneath the epidermis, and pith of lower stems in wilt-affected plants are also prominent signs of infection caused by the pathogen (Fig. 4A to D). Furthermore, at 7 days post-inoculation (dpi), the *in planta* fungal DNA significantly increases in mungbean seedlings, implying

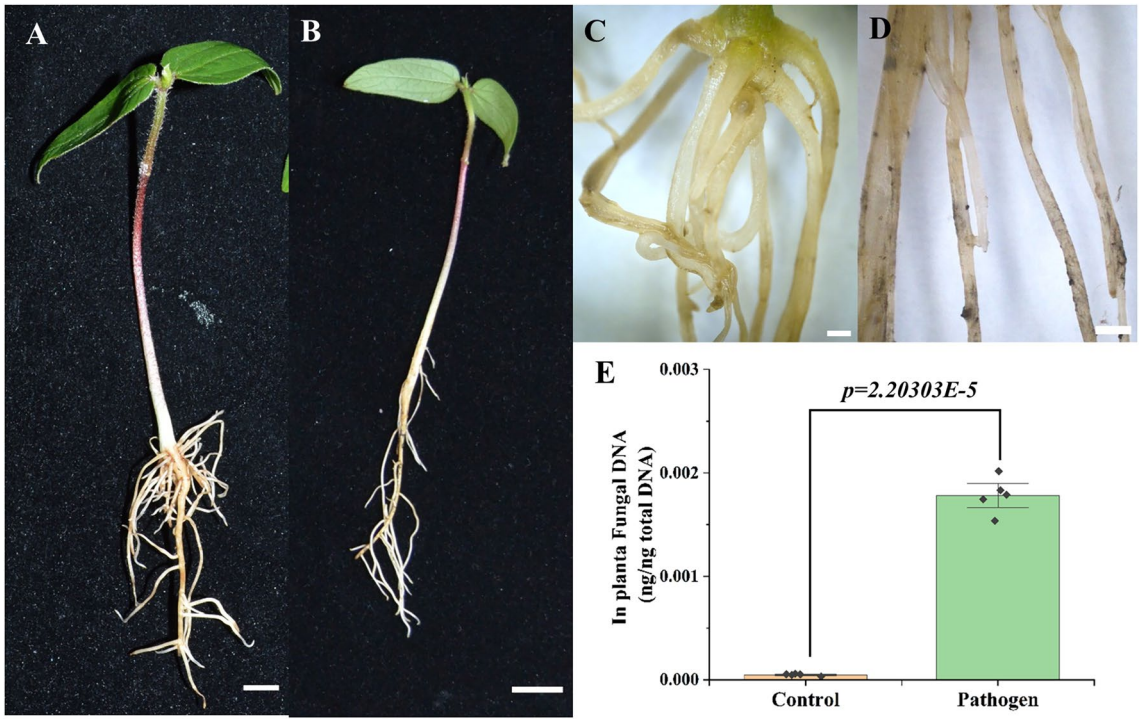

Fig. 4 Symptoms of dry root rot on mung bean caused by *Macrophomina phaseolina* (Tassi) Goid. The mung bean (*Vigna radiata* L.) variety TM 2000–2 was tested for its response to *M. phaseolina* using the blotter paper assay. Typical root necrotic lesions were observed at 7 days after inoculation (DAI). Images of the whole plant at 7 DAI: **A** Control, **B** Pathogen. Scale bars—1 cm. Stereomicroscopic observations of the roots of mung bean at 7 DAI: **C** Control, **D** Pathogen. Scale bars—250 µm. **E** In planta fungal DNA quantification using ITS primers specific to *M. phaseolina*. N = 5, significance was tested using one-way ANOVA followed by Tukey's post-hoc test. Error bars represent the standard error of mean

extensive cortical colonization by *M. phaseolina* (Fig. 4E, Supplementary File 1).

Drought and heat favor dry root rot incidence

An optimal disease cycle entails a susceptible host, virulent pathogen, and conducive environmental conditions. DRR disease incidence caused by *M. phaseolina* across various host crops is favored by maximum ambient temperatures exceeding 30 °C and dry conditions inducing moisture stress during the plant's reproductive stages (Seethapathy et al., 2017; Rai et al., 2022). This is attributed to *M. phaseolina's* capacity to thrive and endure well in high-temperature and water-stressed environments (Chamorro et al., 2015). Although a wide temperature range of 15 to 40 °C supports the growth of *M. phaseolina*, optimal conditions for infection occur between 28 and 35 °C. At 20 °C and 25 °C, a reduction in the size of microsclerotia is observed compared to temperatures of 30 °C and 35 °C (Akhtar et al., 2011; Basandrai et al., 2021). Higher root rot disease incidence is observed under low moisture conditions, with maximum disease incidence recorded at 40% soil moisture content (Kumar et al., 2019; Soni et al., 2022). The low level of disease incidence at high soil moisture content is attributed to the fungal sclerotia's inability to survive under wet soil conditions (Kumar et al., 2019). Additionally, apart from drought and heat, other abiotic factors such as soil properties also determine the incidence of DRR (Irulappan et al., 2022).

The combined effect of drought stress and *M. phaseolina* infection has been studied in various crops such as sorghum (Goudzrzi et al., 2011), common bean (Mayek-PÉrez et al., 2002), chickpea (Chilakala et al., 2023; Irulappan et al., 2022), cotton (Ghaffar & Erwin, 1969), and strawberry (Sanchez et al., 2019). In all these studies, observations consistently indicated that drought stress exacerbated DRR infection by altering key physiological mechanisms due to disrupted plant-water relationships. Particularly in chickpea, it was found that drought stress weakened the plant's defense mechanisms and compromised the integrity of the endodermal barrier, accelerating the spread of the pathogen within the roots. Furthermore, in response to drought stress, the expression of genes linked to hormone regulation was differentially regulated, exacerbating DRR by affecting the plant's innate resistance to infection (Irulappan et al., 2022).

Conversely, similar studies in mungbean (Fulbohm et al., 2013; Kaur et al., 2023, 2024) and soybean (Mengistu et al., 2018) have found no or limited association, highlighting the need to consider several factors when analysing the impact of these combined stresses. Fulbohm et al. (2013) observed increased seed infection by the pathogen in the Australian mungbean cultivar Beken during the rainy period, likely due to localized pod infection rather than systemic plant infection. In a study by Kaur et al. (2023), drought stress impeded the systemic progression of the pathogen from the root to the leaf and enhanced a better defense response in tolerant cultivars by accumulating antioxidants and lignin deposition.

Continuing this line of research, Kaur et al. (2024) screened ten-day-old seedlings of six mungbean cultivars by subjecting them to combined drought stress and *Macrophomina* infection in three combinations: (i) drought followed by pathogen infection and normal watering, (ii) drought followed by pathogen infection and drought again, (iii) pathogen infection followed by drought stress. The results showed that cultivars exposed to drought stress prior to *Macrophomina* infection performed exceptionally well in terms of yield and nutritional quality. The resistance response under drought followed by fungal infection was primarily due to callose deposition, while under fungal infection followed by drought stress, it was due to increased accumulation of proline and soluble sugars, indicating different defense strategies adapted by the genotypes in response to the order of combined stresses encountered. These findings, arising from limited research, require further elucidation and suggest that the eventual impact of drought on DRR incidence in mungbean cannot be predicted and is subject to genotypic responses as well as the sequential order, duration, and severity of stresses encountered by the host species. The morphological, physiological and biochemical changes induced in mungbean on exposure to *Macrophomina* infection and combined stress are presented in Table 1.

Host plant resistance to dry root rot in mungbean germplasm

Resistance or tolerance to the combined stresses of DRR and drought is crucial for improving mungbean production under climate change scenarios. Managing DRR is exceptionally challenging due to the soil-borne nature

Table 1 Morphological, physiological and biochemical changes induced in mungbean exposed to dry root rot and combined drought stress conditions

Stress	Morphological/biochemical changes in mungbean	References
Macrophomina infection	Decrease in shoot length, shoot fresh weight, shoot dry weight, root length, root fresh weight, root dry weight	Khan et al. (2016); Shahid and Khan (2016a, 2016b); Khan et al. (2019); Kaur et al. (2023); Kaur et al. (2024)
	Decrease in pods/plant, seed yield/plant, seed weight, functional nodules, nodular dry weight, and leghaemoglobin Increase in non-functional nodules	Shahid and Khan (2016a, 2016b); Khan et al. (2019)
	Decrease in total chlorophyll content	Shahid and Khan (2016a, 2016b); Hasheem et al. (2017)
	Increase in callose deposition	Kaur et al. (2024)
	Increase in lignin, phenols, hydrogen peroxide, starch content, soluble sugars	Hasheem et al. (2017); Kaur et al. (2023); Kaur et al. (2024)
	Increase in total antioxidant capacity, catalase, superoxide dismutase, guiacol peroxidase	Kaur et al. (2023); Kaur et al. (2024)
	Increase in proline, free aminoacids, Absicisic acid	Hasheem et al. (2017)
	Increase in salicylic acid	Kaur et al. (2023)
Macrophomina infection and drought concurrently	Increase in shoot length, dry weight Increase in lignin content Increase in protein and soluble sugars Increase in phenols, hydrogen peroxide and antioxidant capacity Decrease in root length and fresh weight Decrease in starch content	Kaur et al. (2023)
Macrophomina infection + Drought sequentially	Increase in soluble sugars and proline	Kaur et al. (2024)
Drought + *Macrophomina* infection sequentially	Increase in callose	Kaur et al. (2024)

of the pathogen, its asexual reproduction, the prolonged longevity of microsclerotia, and its complex relationship with drought conditions. Additionally, the virulence of *M. phaseolina* isolates appears to vary significantly across locations (Bimla et al., 2016; Kumar et al., 2017a). Varieties possessing an innate ability to resist or withstand the disease under drought conditions are essential for a long-term, eco-friendly, and economically viable strategy to combat DRR.

Large-scale screening of mungbean germplasm is essential to identify resistant sources to DRR. Various phenotypic screening methods, such as the paper blot assay, sick pot technique, sick plot technique, and field evaluation, are utilized for this purpose. The paper blot assay, for instance, involves placing eight to ten-day-old seedlings with roots dipped in fungal inoculum inside paper towels, allowing disease development under controlled conditions, with scoring based on symptom severity (Nene et al., 1981; Pandey et al., 2021). Other techniques, like the sick pot and sick plot methods, involve inoculating susceptible genotypes with *M. phaseolina* to assess symptom development under controlled conditions (Choudhary et al., 2011; Irulappan et al., 2021).

Although germplasm screening for DRR began decades ago, vigorous screening has gained momentum only recently due to the dramatic rise in disease incidence (Table 2). Several studies have reported mungbean genotypes exhibiting resistance or tolerance to DRR using different screening techniques (Avanija et al., 2023; Choudhary et al., 2011; Khan & Muhammad, 2007; Pandey et al., 2020, 2021). However, identifying donor sources with consistently high levels of resistance has been challenging due to the skewed distribution curve towards susceptibility (Talekar et al., 2021). Therefore, continued disease phenotyping of unexplored germplasm accessions is necessary to identify consistent and durable resistant sources for use in breeding programmes.

Given the simultaneous occurrence of drought and DRR, evaluating genotypes under combined stress conditions would be beneficial. While investigations on the effects of combined stress on morphological, biochemical, and physiological traits have been conducted in some legume crops, such as chickpea and soybean, screening for genotypes with combined tolerance to both stresses remains in its early stages in mungbean (Kaur et al., 2023, 2024; Mengistu et al., 2018). Identifying genotypes with combined tolerance to

Table 2 List of resistant genotypes identified through various screening techniques in mungbean germplasm

Screening technique	No. of genotypes screened	Resistant genotypes identified	Reference
Field	–	LM 220, MS 9385	Vidhyasekaran et al. (1977)
Paper towel	29	NCM 252-10, 40536	Khan and Muhammad (2007)
		40504, NCM 257-5, 40457, NCM 251-4, 6368-64-72	
Sick plot	25	MSJ-118, KM 4-44 and KM 4-59	Choudhary et al. (2011)
Sick plot technique	27	Azri 2006, NM 2006 and AUM 9	Haseeb et al. (2013)
Field	50	13,989, 14,047, 14,095, 14,100, 14,112	Atiq et al. (2014)
		13,961, 13,962, 13,984, 14,069, 14,090, 14,102, 14,103, 14,114 14,118 14,125	
Sick pot	26	MNUYT-317, NM-2011	Akhtar et al. (2018)
Field trial	40	BPMR-145	Thombre and Kohire (2018)
Sick plot technique	19	GP-1, G-4, MUM-2, ISGP-3, IPMO-2-3	Sangeeta et al. (2018)
Paper towel	43	EC693364, EC693368, EC693369, IPM-02-17, IPM-02-3, IPM205-7, IPM99-125, V04718, VC6173 B-10	Pandey et al. (2020)
Sick pot technique	3	IPM99-125, EC693368, EC693369	
Paper towel	296	VI001509AG	Pandey et al. (2021)
		VI000203BBR, VI000319AG, VI000732AG, VI000764AG, VI000766BG, VI000818BG, VI001244AG, VI001268BG, VI001282AG, VI001284AG, VI001400AG, VI001419BG, VI001490AG, VI001535BG, VI001548AG, VI002529BBL, VI003699BBG	
Sick pot	18	VI000766BG, VI001244AG, VI001268BG, VI001282AG, VI001400AG, VI001490AG, VI001509AG, VI001535BG, VI003699B-BG	
Field screening	18	VI000203B-BR,	
		VI000815BG, VI001244AG, VI001400AG, VI001482BG, VI001509AG, VI002529B-BL, VI002587AG, VI002859BG, VI004024AG, VI004811AG	
Sick pot	47	MGG-529, MG-549, WGG-42, MG-505, Pusa 9072, WGG-25	Avanija et al. (2023)

both drought and *Macrophomina* infection under field conditions would facilitate their effective deployment in resistance breeding programmes.

Currently, no studies to determine the genetic loci in mungbean associated with DRR resistance have been conducted. However, research conducted in legumes and other crops can provide insights into extending similar approaches for DRR resistance breeding programmes in mungbean. Inheritance studies have indicated the role of dominant genes with epistatic interactions for dry root resistance in common bean (Hernández-Delgado et al., 2009; Vitaeri and Linnaes, 2022), while QTL mapping studies in several other crops have established the polygenic nature of the trait (Table 3). Based on their mapping study, Olaya et al. (1996) identified two RAPD markers, B386900 and B4591600, associated with DRR resistance. Using AFLP analysis, Hernández-Delgado et al. (2009) discovered a potential QTL on linkage group 1 of the common bean conferring resistance to charcoal rot using an F2 population derived from a cross between BATT477 (resistant to both charcoal rot and drought) and cvPintoUI-114 BATT477. Using the RIL population of the same cross, nine QTLs for charcoal rot and three QTLs for drought were mapped; however, no overlapping QTLs for resistance to both stresses were detected. Surprisingly, the QTL identified on LG1 by Hernández-Delgado et al. (2009) was not detected in this study. The markers BPC40M12 and BPC54M150 associated with DRR resistant QTLs located on chromosome 8 and 10 were prominent candidates for marker-assisted selection (Méndez-Aguilar et al., 2017).

Karadi et al. (2021) reported a single minor QTL ('qDRR-8') associated with *M. phaseolina* in chickpea. In soybean, da Silva et al. (2019) mapped three QTLs associated with dry root resistance, one on chromosome 15 and two on chromosome 16 using an $F_{2:3}$ population derived from the cross PI567562A x PI567437 genotyped using a 6 K SNP array. The QTL on chromosome 15, which explained 29.4% of the phenotypic variance, overlapped with a patented marker Satt512 used for selection of genotypes tolerant to DRR-drought complex. However, QTLseq analysis based on genotyping by sequencing (GBS) of resistant and susceptible bulks from the same population detected QTLs on three other chromosomes, namely 5, 8, and 14. The differences in the sequencing platforms were speculated as a reason for the contradictory results (da Silva et al., 2020). Muchero et al. (2011) reported nine QTLs associated with resistance to *M. phaseolina* in cowpea; of which, only three QTLs co-located with drought tolerance QTLs, suggesting that responses to *M. phaseolina* infection and drought stress could possibly be mediated by different genetic mechanisms. Tomar et al. (2017) reported three QTLs, including a major QTL, associated with resistance to *M. phaseolina* in castor.

The limitations in QTL mapping strategies involving the development of mapping populations and construction of genetic linkage maps have been overcome by genome-wide association studies (GWAS). Coser et al. (2017) reported SNPs associated with *M. phaseolina* through GWAS in a collection of 459 accessions from the USDA Soybean germplasm core collection based on field and greenhouse screening. The SNPs detected for their association with *M. phaseolina* under field and greenhouse conditions were different, suggesting that the genetic mechanisms underlying resistance to *M. phaseolina* in soybean could be complex and influenced by the environment. GWAS and SNP-based haplotyping in soybean identified TAC and CGA haplotypes associated with markers Gm08_18909193_A_G, Gm08_44422211_T_C, and Gm19_34320762_A_C to confer resistance against charcoal rot in a panel of varieties cultivated by Brazilian farmers (Vinholes et al., 2019). Recently, Zatybekov et al. (2023) detected 11 QTLs associated with resistance to *M. phaseolina* in a panel of 252 accessions using the 6 K SNP array and whole-genome resequencing (WGRS) technology. GWAS based on WGRS data set in a biparental mapping population derived from the cross BAT 477/NY6020-4 in common bean identified a novel QTL governing resistance to *M. phaseolina* on chromosome 3. Two SNP markers strongly associated with this QTL were part of the drought-sensitive gene Phvul.003G175900 (Viteri et al., 2022). Nelson et al. (2021) reported three loci (FaRMp1, FaRMp2, FaRMp3) conferring resistance to *M. phaseolina* in strawberry through genome-wide SNP genotyping and pedigree-based analysis (Table 4).

Functional annotation of the resistance loci mapped using QTL and GWAS analysis has identified disease resistance gene analogues (Viteri et al., 2022) and candidate genes involved in plant defense and stress signaling pathways related to pectin metabolism (Muchero et al., 2011), calmodulin, cell wall degradation, ethylene response factor, protection from oxidative stress (Coser et al., 2017), late embryogenesis (LEA) protein synthesis (Zatybekov et al., 2023), flavonoid, and isoflavonoid biosynthesis (Adeyanju et al., 2015).

The draft genome sequences of mungbean, urdbean, and cowpea have been published (Kang et al., 2014; Ha et al., 2021; Pootakham et al., 2021; Lonardi et al., 2019). A high level of conservation at the genome level is observed among these three *Vigna* species, facilitating the discovery of genes and QTLs associated with valuable agronomic traits through association genetics. Although no QTLs have been mapped for DRR resistance in mungbean, the high level of synteny among the three *Vigna* species has been utilized to identify conserved resistance loci with similar functions in mungbean. An EST-derived SNP marker (1_10853) linked to QTL Mac-2 on chromosome 3 governing resistance to charcoal rot in cowpea was functionally annotated to code for pectin esterase inhibitor. Based on comparative genomic analysis, the SNP marker (1_10853) was mapped to genes

Table 3 QTLs associated with resistance to *Macrophomina phaseolina* mapped in legumes and other agriculturally important crops

Host	Mapping population	QTL identified	Chromosome	Position (cM)	Flanking marker	R^2 (%)	Reference
Common bean	100 F2 plants derived from BAT 477 X *cv*Pinto UI-114	–	1	–	ATA/AGT-19	–	Hernandez-Delgado et al. (2009)
Common bean	94 RILs derived from BAT 477 X *cv*Pinto UI-114	–	3	7.5	C3.LOC7.5	–	Mendez-Aguilar et al. (2017)
		–	3	24.0	BPC1M6	–	
		–	5	76.0	BPC4M74	–	
		–	6	17.7	BPC74M243	–	
		–	8	0.0	BPC40M127*	–	
		–	9	45.0	C9.LOC45	–	
			10	107.0	BPC54M150*	–	
Cowpea	RIL population derived from IT93K-503–1 X CB46	Mac-1	2	77.4	1–070	14.5	Muchero et al. (2011)
		Mac-2	3	1.3	1–1533	26.5	
		Mac-3	3	42.3	1–0853	10.6	
		Mac-4	3	64.2	1–0604	13.3	
		Mac-5	11	70.8	1–0464	10.3	
		Mac-6	5	59.3	1–0079	16.2	
		Mac-7	5	41.0	1–0804	19.4	
		Mac-8	6	29.7	1–0678	8.6	
		Mac-9	6	40.9	1–0030	8.3	
Soybean	140 $F_{2:3}$ derived from PI 567562 × PI 567437	–	15		Satt575-Sat_136	29.4	da Silva et al. (2019)
		–	16		BARC-041267-BARC-07957	25.4	
		–	16		Satt244-Satt547	8.4	
Chickpea	182 RILs derived from BG 212 9 × ICCV 08305	qDRR-8	8	67	Ca8_3970986-Ca8_3904895	6.7	Karadi et al. (2021)
Castor	$F_{2:3}$ population derived from JI 357 × SKI 338	–	2	65.6	CST261-CST 159	71.2	Tomar et al. (2017)
		–	6	106.8	CST162-M165	12.5	
		–	9	51.0	CST112-CST236	11.3	

Table 3 (continued)

Host	Mapping population	QTL identified	Chromosome	Position (cM)	Flanking marker	R^2 (%)	Reference
Sesame	548 RILs derived from ZZM2748 x Zhongzhi No. 13	qCRR3.1	3	24.50	ZMM2997-ZMM1033	3	Wang et al. (2019)
		qCRR3.2	3	39.30	ZMM5636-ZMM5775	12	
		qCRR3.3	3	52.30	ZMM2218-ZMM4682	10	
		qCRR3.4	3	58.40	ZMM4682-ZMM5444	9	
		qCRR5.1	5	116.80	ZMM1155-ZMM0314	4	
		qCRR8.1	8	10.50	ZMM5060-ZMM5061	4	
		qCRR8.2	8	115.70	ID0041-ZM638	5	
		qCRR8.3	8	123.70	ZM638-ZMM1682	5	
		qCRR9.1	9	104.70	ZMM2323-ZMM0205	8	
		qCRR12.1	12	53.80	ID0046-ID0013	6	
		qCRR12.2	12	89.80	ZMM0913-ZMM3752	14	
		qCRR12.3	12	106.10	ZMM3683-ZMM2365	3	
		qCRR13.1	13	43.90	ZMM1307-ID0030	4	
		qCRR13.2	13	73.50	ZMM2344-ZMM2343	8	
Maize	190 $F_{2:3}$ lines derived from CML495 x CML474	qMSR3	3	101	PZA03391_1–ZA00316_10	5.72	Rashid et al. (2021)
		qMSR4	4	15	PHM3963_33–PHM259_7	6.49	
		qMSR6	6	17	PHM12904_7–S6_103513378	5.65	
		qMSR8	8	59	PZA01964_29–PHM4757_14	13.86	
	257 F_3 lines derived from CML578 x CML474	qFMSR6	6	26	PZA01029_1–S6_103513510	6.56	
		qFMSR7	7	37	PZA02643_1–PZA03166_1	6.51	
Sorghum	93 RILs derived from IS22380 x E36-1		A	51.27	Ac13	10.76	Reddy et al. (2008)
			B	163.3	xtxp297	19.29	
			D	47.01	xtxp213	12.54	
			D	0.01	xtxp343	11.01	
			D	23.64	M9	11.24	
			I	28.85	xtxp176	7.89	

Table 3 (continued)

Host	Mapping population	QTL identified	Chromosome	Position (cM)	Flanking marker	R^2 (%)	Reference
Sorghum	93 RILs derived from SPV 86 × E36-1	–	A	96.1–110.1	AC13-xiabt224	8.9–17.8	Ayyana gouda et al. (2012)
		–	B	460.3–473.8	xiabt275-xiabt241	8.0–16.1	
		–	B	59.8–63.3	xtxp201-xiabt378	9.8–17.7	
		–	B	324.0–340.0	xtxp297-xiabt73	5.9–19.29	
		–	B	367.9–393.4	xiabt 92-xiabt62	8.8–18.9	
		–	D	1.8–3.9	xtxp343-xtxp12	9.2–13.7	
		–	I	32.8–37.1	xtxp176-xtxp312	7.89–11.9	
		–	I	45.2–62.8	xtxp274-xiabt29	6.9–19.9	
		–	J	22.0–40.9	xtxp338-xiabt420	8.7–17.8	
		–	H	15.41–16.61	Ac19-xtxp254	11–12	
		–	I	49.2–50.1	xtxp274-xiabt29	25–29	
		–	B	51.05–51.5	xtxp303-xtxp301	10–12	
		–	D	26.4–28.46	xiabt374-xtxp9	22–23	
		–	H	12.14–13.17	xtxp329-Ac19	14–15	
		–	I	42.11–43.2	xtxp274-xiabt29	17–19	
		–	A	372.4–372.11	xiabt 92-xiabt 67	19–23	

Table 4 List of association panels developed and SSR/SNP markers identified associated to dry root rot/charcoal rot resistance identified in various crops

Crop	Association mapping panel	Genotyping platform	Phenotyping method	Assayed SNP/SSR	Associated SNP/SSR	QTLs	Chromosomes	Reference
Soybean	459 PI lines from USDA germplasm	SNP50K chip	Cut-stem inoculation	35,683	19	8	6, 8, 9, 12, 18, 20	Coser et al. (2017)
			Field screening			5	4,14,18	
	169 core farmers' varieties	SNP6K	Field screening	3780	6	4	8,18,19	Vinholes et al. (2019)
	252 accessions of Kazakhasthan	SNP6K	Field screening	4495	5	5		Zatybekov et al. (2023)
		WGRS	Field screening	44,385	63	11	2,3,7,8,9,15, 16,19	
Common bean	126 RILs of BAT 477/ NY6020-4	WGRS	Stem inoculation	72,017	2	1	3	Viteri et al. (2022)
Maize	396 lines of CIMMYT Asia association mapping panel	GBS	Tooth pick technique	296,497	19		1,3,4,5,6,8,9,10	Rashid et al. (2021)
Sorghum	242 accessions of ICRISAT mini core collection	EST—SSR	Sick plot	31	6	-	A,B, D, E	Kumar et al. (2017b)
	107 landraces	SSR	Sick pot	181	13	9	1,2,3,4,5,7,9	Mahmoud et al. (2018)
	300 diverse lines	GBS	Tooth pick	79,134	14	10	2,3,4 7,8,9	Adeyanju et al. (2015)

encoding for pectin esterase inhibitor on chromosome 7 (Vradi07g27890) in mungbean and chromosome 1 in urd bean (Pootakham et al., 2021).

Host-*M. phaseolina*-omics and gene expression studies

Similar to the annotated genes and pathways underlying QTLs, gene expression and transcript profiling of resistant and susceptible genotypes to *M. phaseolina* in a few legumes like soybean, groundnut, alfalfa, and other crops such as sorghum and jute have also revealed the role of a wide array of genes encoding for pathogenesis-related compounds like chitinase, stilbene synthase, nucleotide-binding leucine-rich repeat regions, jasmonic acid, salicylic acid, flavonoid and isoflavonoid biosynthesis, secondary metabolites, auxin homeostasis and transport, and stress signaling pathways involved in plant defense against the pathogen (Biswas et al., 2014; Irulappan et al., 2022; Iwuala et al., 2020; Mah et al., 2012; Marquez et al., 2018; Sharma et al., 2014). Additionally, a study in sesame has demonstrated the existence of a biotrophy-necrotrophy switch in *M. phaseolina* (Chowdhury et al., 2017). Significantly higher transcript levels of BAS3 (biotrophy-associated protein 3) and NIP (necrotrophy-inducing protein) marked the onset of the necrotrophy phase. SiPCHY levels were the highest at the necrotrophy phase, indicating active lignin biosynthesis. Moreover, higher levels of SA (salicylic acid) were observed in the host during the biotrophic phase, while higher levels of JA (jasmonic acid) were accumulated during the necrotrophic phase, which correlated with the transcript levels as well. A similar trend was observed in the Arabidopsis thaliana root transcriptome post-*M. phaseolina* infection. The upregulation of JA, SA, and ET (ethylene) responsive genes and their mutants displayed greater susceptibility to the pathogen (Schroeder et al., 2019). Gaige et al. (2010) developed a novel model pathosystem to study the molecular interactions between host-*M. phaseolina*. Although they observed only a weak upregulation of the JA/ET pathway genes in *Medicago truncatula* roots inoculated with *M. phaseolina*, they showed that priming the plants with JA/ET prior to inoculation enhanced resistance (Table 5).

Transcriptomics of arbuscular mycorrhizal fungi (AMF) colonized roots of soybean revealed an upregulation of defense, pathogenesis-related, and secondary metabolism genes (Marquez et al., 2018). They also showed that AMF relieved the defense-growth trade-off stress in soybean. Although no clues have been gained on cross talking among a network of pathways activated under pathogen infection and/or combined stress situations, the expression of certain compounds like auxins and LEA proteins under DRR infection as well as under drought stress indicates that common pathways may be involved in plant defense against both these stresses.

Several studies have been conducted on *M. phaseolina* as well. The first genome sequence of *M. phaseolina* was published by Islam et al. (2012), and since then, genome sequences of several strains from varying hosts have been published (Shirai et al., 2023). A transcriptomic study revealed that reactive oxygen species (ROS) pathways are involved in microsclerotia formation (Liu et al., 2022). In addition to cell wall-degrading enzymes (CWDEs), several studies of gene expression of secondary metabolomic pathways have shown the role of toxins in virulence (Shirai et al., 2023). Independent *M. phaseolina* secretome analyses

Table 5 Differentially regulated miRNAs and their role in modulating defense pathways in diverse host species in response to *Macrophomina* infection

S.No	Host	Key miRNA	Role in stress response pathways	Reference
1	Chickpea	miR397	MiR397 target LAC transcripts, which regulate lignin deposition	Sharma et al. (2023)
2	Lentil	miR156	Modulates developmental processes and stress tolerance by targeting SPL (SQUAMOSA PROMOTER BINDING PROTEIN-LIKE) transcription factors	Mishra et al. (2021)
		miR159	Regulates MYB transcription factors	
		miR167	Controls auxin response factors, affecting root development and response to biotic stress	
		miR169	Targets NF-YA (Nuclear Factor Y, subunit A) transcription factors	
		miR482	Targets nucleotide-binding site-leucine-rich repeat (NBS-LRR) resistance genes,	
3	Jute	miR-845b miR-166	Targets mRNA coding for disease resistance proteins with NBS-LRR motifs, providing NBS-LRR and ROS-mediated defense	Dey et al. (2016)
		miR154 miR210 miR211	Initiates "phasiRNA" which targets salicylic acid/ Jasmonic acid/ Abscisic acid pathway precursor genes	Biswas et al. (2014)
		miR219	Targets WIN1 motif of the HopW1-1-Interacting protein 1 domain	
		miR218a miR218b miR218c	Targets the sequences encoding well-conserved TIR1motif and P-loop	

conducted by Sinha et al. (2022) and Pineda-Fretez et al. (2023) revealed 117 and 250 secreted proteins, respectively, among which several effectors, CWDEs, and peptidases were identified. These -omics studies in model pathosystems can lay a foundation for future studies on *M. phaseolina*-host interaction in non-model crops/plants such as mungbean.

A common defense mechanism observed in plants subjected to drought and pathogen infection is the deposition of lignin in the secondary cell walls facilitated by the cell wall catalyzed multicopper oxidase family enzymes (LACCASES) encoded by LAC genes. Short non-coding RNA molecules known as microRNAs have emerged as potential players in modulating the defense response by regulating transcriptional and post-transcriptional gene expression. In chickpea, microRNA397 was found to play a key role in regulating tolerance to DRR and drought through the root lignification process (Sharma et al., 2023). In jute, the miR-845b and miR166 superfamily regulate the Nucleotide-binding site—leucine-rich repeat (NBS-LRR) and ROS mediated defense (Dey et al., 2016). The pathways involved in all these 'omics' studies reveal that the host plant deploys a two-tier defense strategy against *Macrophomina*, with the first level primarily aimed to prevent/delay the entry of the pathogen into the host cell and the second level aimed at initiating a destructive war against the invaded pathogen.

While the role of microRNAs in regulating DRR resistance in mungbean is not yet fully understood, their role in regulating drought tolerance has been established. The microRNA Vra-miR165 contributes to drought tolerance by targeting the mungbean NAC transcription factors, which also participate in biotic stress (Tariq et al., 2022). Kumar et al. (2022), identified five potential microRNAs (Vra-miR160, Vra-miR164, Vra-miR167, Vra-miR394 and Vra-miR398) that regulate drought response in the mungbean genotype K851 by targeting auxin response factor, NAC transcription factor, serine acetyl transferase 1, and multicopper oxidase LPR 2 like genes. Two of these drought-responsive microRNAs, namely miR160 and miR398, also participate in defense against *Mungbean Yellow Mosaic India Virus* (MYMIV) by regulating auxin perception and NAC transcription factors (Kundu et al., 2017). Interestingly, since all these genes are also reported to be involved in biotic stress response, they may be possible targets of microRNAs regulating DRR resistance in mungbean. Elucidating the role of genetic factors regulating key signalling pathways can help understand the evolutionary dynamics during host–pathogen interaction, thereby imparting resistance in plants and virulence in pathogens.

A wide array of secretory fungal proteins produced by *M. phaseolina* are essential for disease pathogenesis and serve as potential virulence factors to break the host defense mechanisms. In silico prediction based on whole genome sequence analysis reveals an abundant secretion of peroxidases, oxidases, cellulolytic and hydrolytic enzymes by the pathogen to decompose plant cell walls that are barriers for its entry into the host. Among the 362 carbohydrate active enzymes (CAZymes) encoded by *Macrophomina* genome, about 219 belong to glycoside hydrolases (GH) which is comparatively higher than the average GH possessed by other known phytopathogenic fungi (Islam et al., 2012). Proteomic analysis revealed an arsenal of secretory proteins (ranging from 117 to 250) predominated by cell wall degrading enzymes such as glucananses, xylanase and amylases and peptidases that are involved in infection process (Sinha et al., 2022; Pinedo-Fretez et al., 2023). In addition, secretome analysis identified putative effector proteins secreted by the pathogen that help in colonising the host by manipulating and suppressing the host immune system (Pinedo-Fretez et al., 2023). Understanding the role of these secretory fungal proteins and effector molecules can help in gaining insights on the fungal proteins associated with pathogenesis and their role in host–pathogen interaction, eventually helping in devising management strategies to mitigate dry root rot.

A few omics studies such as transcriptomics and metabolomics have been conducted to study the *M. phaseolina*-host interactions in several crops such as soybean, sorghum and in the model pant *Arabidopsis thaliana* (Arafat et al., 2024; Bandara et al., 2018; Bosmaia et al., 2023; Radadiya et al., 2021; Schroeder et al., 2019; Silva et al., 2021; Singh et al., 2022a, 2022b; Yan et al., 2021). However, such omics-based approaches have not yet been utilized for gaining insights into mungbean-*M. phaseolina* interactions. Further, CRISPR/Cas based genome editing to confer resistance to a wide range of phytopathogens has been extensively utilized (Langner et al., 2018). However, genome editing based approaches towards engineering *M. phaseolina* resistance are yet to be utilized in crops, including mungbean. Moreover, certain genome edited lines can be utilized as pre-breeding material to aid conventional breeding towards resistance. Integration of various omics techniques with genome editing techniques are fundamental tools in research towards *M. phaseolina* resistance in mungbean.

Integrated management strategies to mitigate dry root rot

Integrated management techniques, including the use of fungicides, biocontrol agents, botanical extracts, and organic amendments, have shown promising effects in controlling and reducing DRR incidence in mungbean (Deshmukh et al., 2016; Kumari et al., 2012). Seed treatment with systemic fungicides such as carbendazim has proven effective in minimizing DRR incidence in mungbean (Kumari et al., 2015; Murthy et al., 2003).

Fungal and plant growth-promoting rhizobacteria (PGPR) such as *Trichoderma viride, T. harzianum, Glomus claroideum, Bacillus subtilis, Pseudomonas fluorescens, P. putida, P. aeruginosa*, and *Burkholderia* species exhibit antagonistic effects on *M. phaseolina* growth. Seed and soil treatment with these biocontrol agents, either alone or in combination, have demonstrated effectiveness in reducing mungbean disease incidence in various greenhouse and field experiments (Raguchander et al., 1993; Thilagavathi et al., 2007; Mansoor et al., 2007; Chandra et al., 2007; Satya et al., 2011; Shahid and Khan, 2016a, 2016b; Hashem et al., 2017; Choudhary & Ashraf, 2019; Ahmed & Shete, 2022; Khaire et al., 2023). These antagonists induce resistance against the pathogen by synthesizing enzymes that can lyse fungal cells, mimicking host plant defense mechanisms, and competitively colonizing host plant roots, thereby eliminating the harmful pathogen from the ecological niche. Notable increases in defense-related enzyme activities such as phenylalanine ammonia-lyase, polyphenol oxidase, superoxide dismutase, and peroxidase have been observed in mungbean genotypes treated with *P. putida* (Khan et al., 2023).

Noreen et al. (2019) examined the function of fluorescent *Pseudomonas* linked to mungbean root nodules in rhizobia-induced nodulation, highlighting the potential of beneficial microbes in disease management. Additionally, botanical extracts from mustard, neem, sesame, onion, garlic vine, *Eucalyptus*, *Datura*, *Sisymbrium*, *Launaea* and palmarosa (*Cymbopogon martini*) have also been used to treat mungbean for mitigating DRR incidence (Mansoor et al., 2007; Javaid and Siddique, 2011; Haseeb et al., 2013; Kalaivani et al., 2023).

Agronomic practices such as crop rotation with non-host crops, fallowing fields, and soil amendments to improve soil fertility are also recommended practices to reduce *M. phaseolina* inoculum levels in the soil (Choudhary et al., 2010). Exposure of mungbean seeds to ultraviolet radiation for 5–20 min significantly reduces root-infecting fungi (Siddiqui et al., 2011). Given the crucial role of temperature in *M. phaseolina* survival, soil solarization can stimulate the temperature conditions necessary to reduce the viable population of the pathogen (Polakala et al., 2023). While these strategies help combat DRR incidence in mungbean, their cost-effectiveness and eco-friendliness on a large scale remain major limiting factors for field recommendations. Considering these factors, exploring host plant resistance is a viable strategy for developing mungbean cultivars tolerant to DRR and combined stresses.

Conclusions and future perspectives

Host plant resistance remains the most viable eco-friendly strategy to realize the potential yield and counteract virulent pathogenic strains. However, exploiting and utilizing genetic and genomic resources to combat DRR in mungbean requires significant progress. Despite the identification of limited resistant sources to date, large-scale screening of mungbean germplasm is essential to identify potential donors with durable resistance against DRR. The development of a rapid, sensitive, and reliable screening technique for high-throughput phenotyping is crucial to handle large sets of germplasm. Incorporating artificial intelligence tools and sensor-based imaging technologies that precisely capture DRR symptoms can aid in scoring disease severity accurately.

While dry and hot conditions predispose mungbean to DRR, there is no strong association to presume that selection for drought tolerance will favor DRR resistance. Therefore, selection for both traits needs to be done individually in environments displaying the combined stresses. Although mapping strategies in a few crops have indicated the polygenic nature of DRR resistance, the genetics of this trait still needs elucidation in mungbean.

The recent emergence of DRR as a globally devastating disease and challenges in identifying suitable donor sources with high levels of resistance have delayed the development of bi-parental mapping populations for QTL studies. Identification of major genomic regions associated with DRR needs to be expedited to develop marker-assisted selection programs and fast-track introgression into cultivated varieties. Co-localization of drought and DRR QTLs, as observed in legumes like soybean, can facilitate selection for tolerance against the dual complex.

With gold-standard NGS technologies and high-density SNP genotyping becoming more affordable, mungbean core and mini-core collections representing holistic diversity can be effectively utilized as association mapping panels for GWAS to identify target genomic regions governing DRR resistance. Once identified, functional annotation of these QTLs using bioinformatic tools can provide insights into genes, signaling pathways, and their interactions involved in host defense mechanisms.

The RNAseq approach to analyze transcriptomes in resistant and susceptible mungbean varieties can identify differentially regulated genes that explain genotypic responses triggered by the Mungbean-*M. phaseolina* interaction. Investigating the role of microRNAs in regulating tolerance towards the drought-dry root complex can help modulate the defense response in mungbean.

With the draft genome sequence available for *Vigna* species, synteny analysis can pave the way for identifying conserved resistance loci for DRR and drought among mungbean, urd bean, and cowpea. A pangenomics approach can capture haplotypic diversity contributing to individual and combined stress tolerance.

Despite significant research on management aspects of DRR in mungbean, there is an urgent need to prioritize and

revive the DRR resistance breeding programme. Complementing conventional breeding strategies with the 'omics' toolbox can lead to the development of climate-resilient mungbean cultivars, ensuring food and nutritional security.

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Declarations

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

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