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REVIEW ARTICLE

Advances in resistance breeding and integrated strategies for managing anthracnose in leguminous vegetables

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Abstract

Anthracnose, caused by hemibiotrophic fungi of the *Colletotrichum* genus, is a major fungal disease of leguminous vegetables, leading to substantial yield losses and economic damage worldwide. Currently, cultural practices and substantial use of synthetic fungicides are the primary approaches for managing anthracnose. However, there is a growing focus on developing advanced breeding lines and cultivars with improved resistance to anthracnose. Traditional breeding has led to the identification of a wide range of anthracnose resistance resources, particularly in common bean, soybean, lentil, cowpea and lupins. Recent advances in molecular approaches, including genomics, transcriptomics, proteomics and metabolomics, have enhanced our understanding of the pathogenesis and defense mechanisms involved in the *Colletotrichum*-legume interaction. Genetic manipulation through omics technologies improves the efficiency of breeding programmes thereby offers better scope to protect legumes from anthracnose. This review focuses on key pathogens causing anthracnose in legumes, including *C. truncatum*, *C. lentis*, *C. lupini, C. lindemuthianum* and their biology and epidemiology. We discuss disease management strategies, including progress with host resistance, genetic and breeding approaches and highlight critical knowledge gaps in conventional and molecular breeding programmes. The continuous advancement in developing breeding lines, cultivars and donor plants with enhanced resistance to anthracnose in legumes driven by omics-based approaches is providing new understanding of legume-pathogen interactions. This progress supports the development of more sustainable and efficient strategies for managing the diseases in the future.

Keywords: anthracnose; *Colletotrichum* sp.; cowpea; legumes; molecular markers

Introduction

Legumes are primarily grown either for their edible seeds, known as pulses or as fodder for livestock. Nonetheless, certain legume species are cultivated for their edible pods and immature seeds, which are consumed as vegetables. These vegetable legumes possess distinct sensory attributes and are widely valued for their vitamins, essential minerals, beneficial bioactive compounds and contains moderate content of carbohydrates compared to cereal grains. However, legumes also contain certain antinutritional components such as lectins, phytic acid, saponins and vicine (1). Additionally, legumes are recognized for their capability to form symbiotic associations with nitrogen fixing bacteria, making them valuable as green manure for enhancing soil fertility (2). Vegetable legumes are short season crops with limited shelf life, includes vegetable pigeon pea (*Cajanus cajan*), winged bean (*Psophocarpus tetragonolobus*), cluster bean (*Cyamopsis tetragonoloba*), dolichos bean (*Lablab purpureus)* and cowpea (*Vigna unguiculata*) (3).

Vegetable legumes have a higher water content than pulses, which results in a greater concentration of soluble carbohydrates and a lower starch level. This composition enhances their taste and texture compared to dry pulses (4). Moreover, vegetable legumes are richer in health promoting compounds such as carotenoids, vitamin A, chlorophyll, phenolics and vitamin C, making them a more nutritious dietary choice. Furthermore, the demand for processed vegetable legume products is steadily increasing, driven by growing awareness of their balanced nutritional profile and high content of bioactive health-promoting substances (5).

Pests and diseases represent significant biotic challenges to legume production globally, with anthracnose emerging as an increasingly widespread and serious threat in many of the leading legume-producing regions (6-9). Anthracnose is one of the most destructive fungal diseases caused by *Colletotrichum* spp. In India, the incidence of anthracnose disease was first reported from Maharashtra (10). Under conducive conditions, this disease can cause more than 60 % yield loss in production of legume vegetables like common beans (11, 12). Forecasted climate impacts facilitates more severe diseases. Recent studies indicates that in legumes this disease has a complex etiology,

with *C. truncatum* and *C. lindemuthianum,* the two most prevalent species affecting production of food crop legume (6, 13-15).

The genus, *Colletotrichum* belonging to the Class Sordariomycetes, represents a large and diverse group comprising over 200 recognized species. Based on the host range and molecular phylogenetics analyses, the genus is further categorized into fourteen species complexes and several standalone species (16). Ranked among the top 10 phytopathogenic fungi worldwide, *Colletotrichum* species infect over 3000 plant species, causing substantial yield losses of food crops (17, 18). Several species complexes of *Colletotrichum*, such as *C. acutatum* (lupin species), *C. truncatum* (lentils and soybeans), *C. destructivum* (clover, alfalfa, cowpea and lentil), *C. orchidearum, C. magnum* (soybean), *C. dematium* (cowpea), *C. spaethianum* (common bean), *C. gloeosporioides* (cowpea, beans), *C. chlorophyti* (soybean) and *C. coccodes* (soybean) infect legumes worldwide (19, 20). This genus exhibits a hemibiotrophic lifestyle and amenable to laboratory manipulation, making it a beneficial model pathogen for physiological, genetic and biochemical studies (21).

Multiple species of *Colletotrichum* can infect a wide range of food crops like apple, pear, mango, citrus, dragon fruit, gourd family, coffee berries, olive, onion, chilli, black pepper and strawberry (22-32). This wide host range marks its importance in the field of research.

At present, leguminous anthracnose disease is mainly managed by means of non-genetic strategies, including cultural practices, synthetic fungicides and natural control agents. However, non-genetic methods such as chemical treatments often face limitations due to resistance development, environmental concerns and cost, highlighting the need for genetic approaches. However, the identification and use of genetic resistance remain a major focus for legume breeders. Significant advancements have been achieved in developing anthracnose-resistant legume varieties and cultivars through both conventional breeding and omics-based techniques. Despite this progress, most resistance efforts have targeted specific *Colletotrichum* spp., which proves insufficient when anthracnose occurs as a complex involving multiple *Colletotrichum* spp. This underscores the pressing need for a thorough review and reassessment of the existing research on legume anthracnose.

This review focuses on major *Colletotrichum* pathogens causing anthracnose in leguminous vegetables. It covers their biology, epidemiology and the disease management strategies, with particular emphasis on advances in host resistance, genetic and breeding approaches. This review also reveals critical knowledge gaps in current breeding programmes highlighting the need for more research on molecular marker-based approaches to improve anthracnose resistance in legume cultivars.

Present scenario of anthracnose in leguminous vegetable crops

Colletotrichum, a genus with a sexual stage known as *Glomerella*, is a prominent member of the Kingdom Fungi, specifically within the Ascomycota division (Order: Glomerellales, Class: Sordariomycetes). Notably, despite its asexual morphology, molecular phylogenetic analyses confirm its classification within the Ascomycota (33).

The pathogenicity of *Colletotrichum* species in legumes remains poorly defined, with the number and type of species exhibiting pathogenicity still unknown. Filling this knowledge gap is crucial, as it can enable the development of targeted resistance breeding strategies and inform more effective disease management practices. Nevertheless, numerous countries have reported the presence of at least one *Colletotrichum* spp. associated with major legume crops, highlighting the global significance of this fungal pathogen. Countries like USA, China, India, Taiwan and Brazil exhibit the highest diversity of *Colletotrichum* species, followed by Mediterranean nations, Canada, Myanmar and various other South Asian countries (18).

Historically, *C. truncatum* and *C. lindemuthianum* have been recognized as the most widespread anthracnose-causing species in legumes globally, responsible for causing yield losses ranging from 30 % to complete crop failure (100 %) in cowpea and common bean (34, 35). The distribution of various *Colletotrichum* spp. (*C. truncatum, C. gloeosporioides, C. lindemuthianum, C. lupini* and *C. lentis*) is significantly correlated with relative humidity and atmospheric temperature, reflecting the influence of these factors on pathogen ecology (36).

Symptomatology

Colletotrichum inflicting diseases can manifest at any growth stage of leguminous vegetable crops, exhibiting a range of symptoms. These include seed symptoms such as yellow to brown lesions on infected seeds, resulting in poor germination. Pre- and post-emergence damping-off is marked by seed rot, seedling wilt and development of dark, sunken, irregular lesions on petioles, stems and pods, ultimately causing premature leaf drop (8, 37). Cotyledon symptoms include small, dark brown to black lesions on diseased cotyledons, leading to premature senescence and stunted growth. Moreover, hypocotyl symptoms such as rust-coloured specks that enlarge longitudinally, resulting in sunken lesions.

Numerous *Colletotrichum* spp. are responsible for these symptoms, including *C. gloeosporioides, C. lindemuthianum* and *C. truncatum*. Notably, *C. truncatum* causes hexagonal necrotic spots on stems, as observed in soybean and mungbean crops (38, 39). Circular, sunken and tan-colored spots on leaves, elongated, sunken lesions on stem, circular, sunken lesions on pods. Premature defoliation and plant death are some of the other symptoms of anthracnose in leguminous vegetables.

Disease cycle

The disease cycles of four *Colletotrichum* spp.- *C. lindemuthianum*, *C. lupine, C. lentis* and *C. truncatum*-have thoroughly been documented in the scientific publications (40, 41). In contrast, the epidemiology of other *Colletotrichum* spp. associated with legume anthracnose remains poorly understood. The well-studied species exhibit several shared characteristics such as surviving capability in both soil and seeds, allowing them to persist between growing seasons and initiate new infections. Additionally, they can overwinter in infected crop residues and wild host plants, which serve as reservoirs for the pathogens.

A key feature of these species is the production of virulent microsclerotia-specialized survival structures that enhance their ability to endure unfavorable environmental conditions. Microsclerotia are especially difficult to control due to their resilience, ability to survive in soil for extended periods and resistance to environmental stresses. Among the various inoculum sources, infected seeds are considered the primary

means of dissemination, contributing significantly to both local outbreaks and long-distance spread of these pathogens through seed trade and exchange. The global seed trade has facilitated to the dissemination of virulent pathogen strains into new production regions (41). Weeds or alternative hosts do not appear to play a significant role in the disease epidemiology. Throughout their lifecycle, *C. truncatum*, *C. lupine*, *C. lentis* and *C. lindemutianum* employ a common infection strategy to invade and colonize the leaf or stem surfaces of host plants (10, 17).

The infection process of *Colletotrichum* spp. follows a hemibiotrophic life cycle, characterized by an initial biotrophic phase followed by a necrotrophic phase. The cycle begins with the germination of conidia on the host plant surface, leading to the formation of appressoria, which facilitate mechanical penetration of the plant epidermis. Following penetration, a primary hypha emerges from the penetration peg and initiates colonization. During the biotrophic phase, specialized structures known as biotrophic vesicles form in the host cells, situated between the plasma membrane and the cell wall, allowing the fungus to extract nutrients without immediately killing the host. This is subsequently followed by the necrotrophic phase, during which the fungus transitions to an aggressive mode of infection. Secondary hyphae develop and spread both intra- and intercellularly, extensively colonizing plant tissues and inducing host cell death (42).

In some cases, *Colletotrichum* species can adopt an endophytic lifestyle, colonizing internal plant tissues without causing visible disease symptoms (14, 43). During the necrotrophic phase of anthracnose, acervuli form with conidia, which spread locally through splashing water that dissolves their mucilage coating. *C. lindemuthianum* disease cycle is presented in Fig. 1.

Host range

Several other species of *Colletotrichum* causes anthracnose disease in legumes. These include *C. lupini* on lupin, *C. lentis* on lentil, *C. lindemuthianum* on beans and blackgram and *C. sojae*, *C. chlorophyti*, *C. gloeosporioides*, *C. coccodes*, *C. cliviae*, *C. plurivorum*, *C. incanum*, *C. musicola*, *C. destructivum* and *C. brevisporum* on soybean (9, 20, 37, 38, 44-50). These *Colletotrichum* spp. infect other food crops also (Table 1). The disease thrives in conditions of high humidity, elevated temperatures and frequent rainfall and can affect legume crops at all growth stages including seedlings, mature plants, pods and seeds (37). Due to its necrotrophic nature, the pathogen can lead to complete defoliation of both young and mature plants. Under favorable conditions-particularly high humidity and temperatures around 30 °C yield losses can reach up to 100 %. Such environmental conditions are commonly observed in countries like India, China, Myanmar, Turkey and the USA (37).

Pre-disposing factors

Warm and humid conditions favour *Colletotrichum* infection in different plant hosts including gymnosperms, angiosperms, grasses, ornamentals, vegetables and fruit plants (69). In a study, scientists observed a reduction in pod yield (0.3 to 0.33 qha^{-1}) due to every 1 % increase in area under disease progress curve (AUDPC) (70).

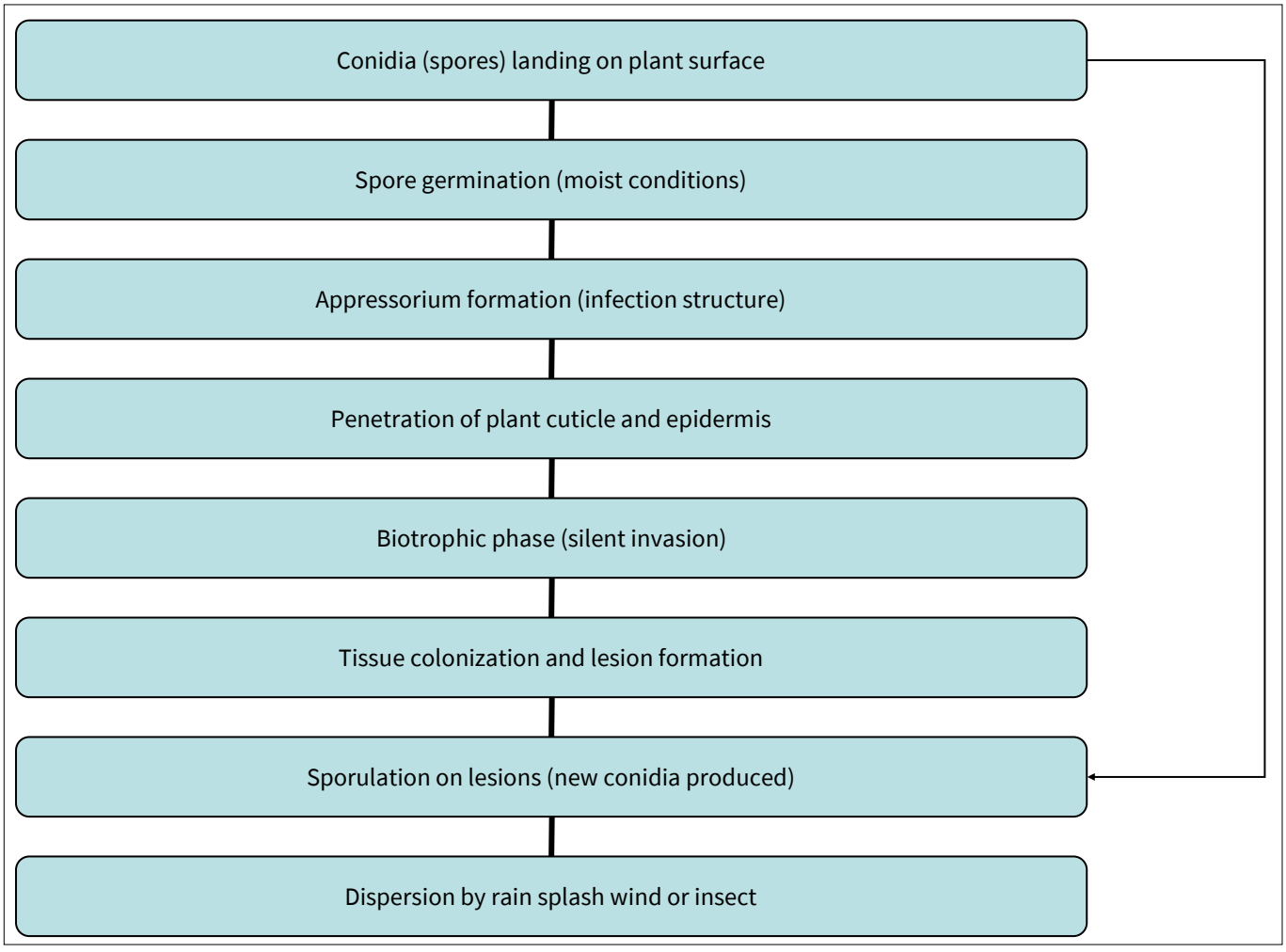

Fig. 1. Disease cycle of *C. lindemuthianum.*

Management strategies for anthracnose in leguminous vegetables

Cultural practices

Several cultural practices aim to reduce or eliminate pathogen inoculum, minimize infection rates and create unfavorable conditions for legume vegetable anthracnose disease spread and development (71). Since it is a seed-borne pathogen, treatment with hot water at 52-55 °C has been shown to effectively reduce seed-borne anthracnose in mung bean, black gram and white lupin (39, 72). However, this treatment has adverse effect in germination and viability of seed, hence restricting its adoption for anthracnose management.

Alternative methods have been explored, which includes the use of vinegar to reduce white lupin anthracnose incidence (73). Common bean anthracnose has been shown to get reduced with the use of soil solarization which indicates that the pathogen is soil borne (74). However, certain *Colletotrichum* spp. such as *C. dematium*, *C. truncatum*, *C. gloeosporioides* and *C. destructivum* are capable of surviving at a higher temperature than that achieved through soil solarization (39, 75).

Other cultural practices that are utilised to control leguminous anthracnose disease comprise of a non-host crop rotation, using disease free seeds and minimising sources of anthracnose from affected crop remaining (71). These practices can help minimize the risk of disease spread and development, especially during the winter months when the pathogen can survive and sporulate.

Chemical methods

The most common method for managing fungal diseases in legumes is the use of synthetic fungicides (39). Conventionally, broad-spectrum fungicides have been applied as seed treatments as well as foliar sprays to control diseases in legumes (76). Both protectant and systemic fungicides have been used, with systemic fungicides applied prior to or during disease development and protectant fungicides applied before or at the onset of disease. A combination of fungicides is commonly applied as foliar sprays to slow down the progression of anthracnose in legumes. Methyl benzimidazole carbamate is the most used fungicides which includes carbendazim and thiophanate-methyl, work by inhibiting fungal mitosis, thereby blocking their growth and reproduction (77). These fungicides are used to control anthracnose in various legume crops, including beans, mung bean, soybean, black gram and chickpea.

Despite their widespread use, synthetic fungicides have several limitations. Multiple fungicide resistance has been reported in populations of *C. truncatum*, *C. gloeosporioides* and *C. lindemuthianum* (50, 78-80). Additionally, synthetic fungicides are relatively expensive, toxic to human health and the environment and require timely application (81). Fortunately, the use of cultivar resistance or tolerance, combined with accurate disease forecasting, can significantly reduce the need for fungicide application (39). This integrated approach can help minimize the limitations of synthetic fungicides while effectively managing legume anthracnose.

Table 1. *Colletotrichum* species complexes involved in legume anthracnose.

Hosts	Species	Distribution (country)	GenBank accession number	References
Common vetch (*Vicia sativa* L.)	*C. lentis*	China	KY241666.1	Unpublished
Bean (*Phaseolus* sp.)	*C. lindemuthianum*	USA	AJ301958	(51)
Blackgram (*Vigna mungo* (L.) Hepper)		India	–	(52)
Common bean (*Phaseolus vulgaris* L.)		Mexico	–	(53)
Common bean		United Kingdom	GU227800	(45)
Cowpea (*Vigna unguiculata* (L.) Walp.)		Nigeria	–	(54)
Sunflower (*Helianthus annuus* L.)		Argentina	–	(55)
Soybean	*Colletotrichum sojae*	USA	KC110830	(38)
Peanut (*Arachis hypogaea* L.)	*Colletotrichum chlorophyti*	China	MN688797	(56)
Soybean		USA	GU227894	(57)
Almond (*Prunus amygdalus* Batsch.), Avocado (*Persea americana* Mill.) Apple (*Malus domestica* Borkh.)	*C. gloeosporioides*	Israel		(58)
Banana (*Musa* spp.)		Ecuador	MG564348	(59)
Banana		Malaysia	JX163228	(60)
Banana		C^ote d'Ivoire	MG515233	(61)
Cocoa (*Theobroma cacao* L.)		Indonesia	–	(62)
Mango (*Mangifera indica* L.)		Southwestern Nigeria	–	(63)
Papaya		Mexico	JF749805	(64)
Peanut		Korea	–	(65)
Soybean		Malaysia	JX669450	(46)
Strawberry (*Fragaria* x *ananassa* Duchesne)		China	FJ608625	(66)
Strawberry		China	–	(67)
Pea (*Pisum sativum* L.)	*C. coccodes*	Brazil	HM171679	(68)
Soybean		USA	–	(47)
Soybean (*Glycine max* (L.) Merr.)	*C. cliviae*	Brazil	KT696282–87	(48)
Soybean	*C. plurivorum*	Germany	NR_160828.1	(45)
Soybean	*C. incanum*	USA	KC110788	(38)
Soybean	*C. musicola*	Brazil	WIGM00000000	(49)
Soybean	*C. destructivum*	USA	–	(31)
Soybean	*C. brevisporum*	China	MT36107	(50)

Biological control

Biological seed treatment is a promising approach for improving legume productivity and managing anthracnose. A recent global meta-analysis revealed that biological seed treatment has a higher yield gain potential in legumes compared to other field crops (76). Combinations of various biological agents have shown considerable promise in managing anthracnose in legume vegetables (77). Several biological agents have been found effective in controlling anthracnose in legumes. For example, inoculation of seeds with *Trichoderma* species and *Pseudomonas fluorescens* was observed to reduce anthracnose incidence by up to 80 % in common bean and black gram (82-84). Likewise, biocontrol of three races of *C. lindemuthianum* has been achieved using a combination of *P. chlororaphis* and *P. fluorescens* (85). A combination of *Rhizobium leguminosarum* RPN5, *Pseudomonas* sp. PPR8 and *Bacillus* sp. BPR7 has also been observed to have potential against a *Colletotrichum* sp. related to anthracnose in common bean (86).

Foliar application of *Trichoderma* biocides has also been found effective in reducing anthracnose severity in soybean, common bean and cowpea by up to 75 % (54, 87, 88). Additionally, 75-80 % reduction of anthracnose disease severity has been observed by using aqueous extracts of certain plants, such as *Lawsonia inermis*, *Melia azedarach* and *Eucalyptus* sp. in soybean, black gram and common bean (84, 87, 89).

Even though biological agents and natural products have shown promise in controlling anthracnose, their adoption has been limited due to inconsistent efficacy and low field performance. However, next-gen fungicides formulated from plant derived active compounds show great promise as eco-friendly, effective and low dose alternatives for managing leguminous anthracnose diseases (12).

Resistant cultivars: Breeding and deploying resistant cultivars

Breeding programmes have utilized various techniques to develop anthracnose-resistant legume cultivars. These approaches involve identifying and introgressing desirable genetic traits from resistant donor parents into susceptible commercial varieties. By combining traditional breeding methods with modern genetic tools, researchers aim to develop legume cultivars with durable and broad-spectrum resistance to anthracnose, ultimately reducing the economic and environmental impacts of this disease. Reducing economic losses in legumes due to anthracnose can be achieved most effectively and efficiently through the development of resistant cultivars, offering a cost-effective and long-term mitigation strategy (49). To achieve this goal, several conventional and genetic methods have been employed to develop legume varieties with enhanced resistance to the disease.

Conventional method

Several methods are available for screening legume germplasm against anthracnose, including detached leaf assays, artificial inoculation techniques in glasshouses or greenhouses and evaluation under natural disease pressure in the field. Under field conditions these screening methods are particularly effective because of intense disease pressure or through artificial inoculation. To assess the severity of disease, researchers have employed both qualitative and quantitative disease rating scales (8).

Presence of TIR-NBSLRR type R protein encoded by *RCT1* gene in *Medicago truncatula,* offers broad spectrum anthracnose resistance and is analogous to *An 1*, an independent dominant gene which confers resistance to *C. trifoli* race 1 (57). Pusa Komal and Lola, the susceptible varieties along with Arimbra Local and VU 53, the resistant varieties were evaluated by SDS-PAGE for their response to *C. lindemuthianum* causing anthracnose disease in cowpea and a disease severity of 100 % and 68.8 % was observed in bush type Pusa Komal and vine type Lola, whereas, the bush type immune cultivar Kanakamony was symptomless and vine-type Arimbra Local recorded 8.80 % disease severity (90).

A study was conducted on the inheritance of resistance in 36 hybrids using nine commercial cultivars of common bean to six strains of *C. lindemuthianum* race 65 (91). Segregation in the F_2 generation indicated that resistance to each strain is governed by two independent but functionally identical genes, suggesting gene duplication, with the dominant allele conferring resistance. Allelism tests on F_2 populations from the crosses between the cultivar Paloma and the common bean cultivars MDRK, Cornell 49-242, Ouro Negro, TO, G 2333, PI 207262, TU and AB 136 revealed a consistent 15:1 segregation ratio, suggesting that anthracnose resistance is governed by two dominant genes (92). In the 127 F_2 plants from the AND 277 × Rudá cross, inoculated with *C. lindemuthianum* race 73 segregation analysis showed co-segregation of 95 resistant and 32 susceptible individuals. This indicates the monogenic resistance in the AND 277 cultivar to race 73 of *C. lindemuthianum*, which is most likely conferred by the *Co-1*^{4} gene (93).

Multi-year screening of mini-core accessions at two locations identified MC-24, MC-51, MC-75, MC-127, MC-208, MC-207 and MC-292 as resistant in both Hyderabad and Palampur and may serve as a resistance donors for developing anthracnose-resistant varieties in mung bean (8). The identified genetic resources for resistance to anthracnose in legume vegetables are presented in Table 2. Primarily, resistance has been identified in several key legume crops, including cowpea and common bean. These resistant sources provide valuable genetic material for breeding programmes aimed at developing anthracnose-resistant legume vegetable varieties. Cowpea varieties exhibit varying levels of resistance to anthracnose, with field/ bush types generally more resistant than vegetable/ trailing types, which are highly susceptible (116).

Screening of yard long bean (a trailing type of vegetable cowpea) genotypes for resistance to anthracnose resulted in the identification of resistant varieties through artificial inoculation followed by detached leaf assay (117). Notably, anthracnose-resistant sources in cowpea have been primarily identified in Nigeria and India and these sources also exhibit resistance to multiple foliar diseases, including rust, target spot, *Cercospora* leaf spot and bacterial pustule (118).

Molecular method

Extensive research has been conducted to determine common bean genotypes exhibiting resistance to specific anthracnose races worldwide, with several genotypes showing promising capability as resistance gene donors in marker-assisted selection programmes (Table 2). MAS enhances breeding efficiency by improving selection accuracy, reducing the breeding cycle and

Table 2. Resistant genotypes of common bean and cowpea against *C. lindemuthianum*.

Legumes	Country	Anthracnose resistant genotypes	Reference
Common bean	Spain	Cornell 49242, Mexico 222 (susceptible to race 102), PI207262, TO (susceptible to race 787), TU (susceptible to race 787), AB136, BAT 93, A252, A321, A493, A1220 and A1231	(94)
	Brazil	Ouro Negro (Honduras 35), a Meso-American common bean that contains a *Co-10* resistant gene	(95)
	Spain	TU (resistant to races, 3, 6, 7, 31, 38, 39, 102 and 449) and MichiganDark Red Kidney (MDRK) (resistant to races, 449 and 1545)	(96)
	Spain	Kaboon against above eight anthracnose races	(97)
	Brazil	Tlalnepantla 64 (PI 207262)	(98)
	Brazil	Ouro Negro (Honduras 35), PI 207262 and Widusa, *Co-1* (MDRK), *Co-12(*Kaboon), *Co-13* (Perry Marrow), *Co-2* (Cornell 49-242), *Co-3* (Mexico222), *Co-4* (TO), *Co-42*(SEL 1308), *Co-5*(SEL1360), *Co -6*(AB 136)	(98)
	Brazil	G2333 was demonstrated to possess resistance against 14 specific races	(95)
	USA, Brazil	SEL1360, SEL 1308 derived from G2333), K13, K10, BRS Esteio and Widusa	(102)
	Brazil	The Andean cultivar, Paloma was resistant to Mesoamerican and Andeanraces	(99)
	China	Andean cultivars Hongyundou	(51)
	Brazil	CDRK	(93)
	Brazil	Pitanga (*Co-14)*	(100)
	Brazil	Michelite *(Co-11)*	(101)
	Brazil	Jalo Listras Pretas landrace *(Co-11)*	(102)
	Tanzania	Twenty-eight lines from the Andean Diversity Panel showed resistance to six races, while *Uyole 98*, a yellow bean variety, exhibited resistance to all eight races	(103)
	Kyrgyzstan	Vaillant and Flagrano carrying the *Co-2* gene resistance to races 23 and102 of pathogen	(104)
	Canada	Bolt	(105)
	Brazil	Crioulo 159, Awauna UEM, Flor Diniz UEM, Pitanga and Corinthiano	(106)
	Brazil	Ten lines had moderate/resistant landraces	(107)
	Brazil	Beija Flor	(108)
	Brazil	18 Mesoamerican accessions were resistant	(109)
	India	WB-1634 and WB-967 were resistance to all the five races, whereas WB-716 was resistant to four races. WB-1637 was resistant to races 2047,3, 87 and 503.	(110)
	India	PL 1, EC-400397, Hur 137, IC-199277, IC-258273, S 2, EC-400442, KB 4, Utkarsh, Hur 15, IC-260299, PDR 14, VL 125, Amber, Arun, EC-398591, EC-121013, S 6, BR 31, IC328372, KB 12 and KB 6	(111)
Cowpea	Nigeria	28 lines	(112)
	Nigeria	5 MDR	(113)
	Nigeria	IAR7/180-4-5	(114)
	India	VBN3	(115)
	India	Arimbra local	(90)
	India	Kanakamony	(116)

facilitating the identification of resistant lines at early stages. These programmes aim to transfer anthracnose resistance genes into agronomically desirable susceptible genotypes. The genetic basis of anthracnose resistance in French beans has been found to be determined by single independently inherited genes commonly denoted by the Co symbol, confer specific resistance to anthracnose (119).

Inheritance studies and genetic mapping

Research on the inheritance of anthracnose resistance has primarily focused on cowpea and common bean, with limited studies on lentil, black gram, soybean and lupin. Notably, there is a significant knowledge gap regarding anthracnose resistance in other legume crops, including mung bean, chickpea, peanut and pigeon pea. In contrast to the gene-for-gene hypothesis of qualitative resistance, which suggests that host resistance specificity is controlled by specific host *R* genes and pathogen *avr* genes interactions, anthracnose resistance in legumes is considered a complex quantitative trait (120). This trait is influenced by multiple gene interactions and environmental factors, rather than a single gene or hypersensitive response (116). As a result, understanding the genetic basis of anthracnose resistance in legumes is a challenging task that requires further research.

In cowpea, a single study indicated that resistance to anthracnose is either dominant or polygenic. Co-segregation of one RAPD marker (OPAO2) and two ISSR markers (UBC810 and UBC811) were found with anthracnose disease resistance genes (116). In common bean, most anthracnose resistance genes are dominant, apart from the recessive *Co-8* gene (93, 119). More than 20 distinct anthracnose resistance genes, mapped to various loci from both the Mesoamerican and Andean gene pools, have been identified in common bean (121). The genes, QTLs and/or markers linked to anthracnose resistance in common bean are summarized in Table 3. Additionally, a few partially dominant genes (one to three) exhibiting additive effects in conferring resistance have also been reported (129). In the resistant cultivar Jalo EEP558, an additional gene, *KTR2/3*, located at the Co-x locus, confers resistance to anthracnose (130). This gene expresses a truncated and chimeric *CRINKLY4* kinase (CR4), situated including a *CRINKLY* kinase cluster and becomes activated in leaves in response to pathogen infection.

Multiple single nucleotide polymorphisms (SNPs) linked to anthracnose resistance in common bean have been identified across several chromosomes (110). On Pv04, SNPs associated with resistance to races 3, 87 and 503 are found in genes encoding NB-ARC domain-containing LRR proteins, including *Phvul.004G023900*, a methyltransferase linked to race 503

Table 3. Anthracnose related QTL/markers in common bean.

Gene/QTL	Markers	Linkage group	References
Co-1 (Co-12, Co-13, Co-14, Co-1HY)	OF10530, SEACT/M CCA, TF1/Clp-N1, PvSNP8p1922017/ PvSNP8p1574781, TGA1.1, ATA3, ATA03, PvM97, CV542014	B1	(51, 100, 108, 118)
Co-u	NDSU_IND_2_40.3966, NDSU_IND_2_40.4411, I gene, SW13	B2	(121, 123)
Co-2	PV-ag001, OQ4 1440, B3551000, SCH20, SCAreoli, OH13 480, SH13b	B11	(35, 94, 121)
Co-3/9	SW12, g1375, SB12, Pv-ctt001, ss715649427/ss715642306, SB10, BM161, OAH18 1100/600, SB12	B4	(109)
Co-42	OH 18, OBB14, SHI8, SBB14, SAS13, OPY20830 , SY20	B8	(123, 124)
Co-5	SAB3, OAB3 450, BM210, SCARAZ20, g1233, Phs	B7	(96, 123)
Co-6	OAH1 780, OAK20 890	B7	(125)
Co-v	–	B7	(126)
Co-8	OPAZ20	–	(95)
Co-3 and Co-3 2	-–	B4	(127)
Co-10	F10, g2303	B4	(101)
Co-13	OPV20680	B3	(101, 124)
Co-15	–	B4	(123)
Co-16	g2467900/800	B4	(106)
Co-y	–	B4	(128)
Co-z	–	B4	(128)
Co-17	–	B3	(124)
CoPv01	CDRK /PhgPv01CDRK ss715645251/ss715645248	B1	(93)
Co-Pa	SS82/SS83	B1	(99)
Co-14	–	B1	(100)
Co-w	–	B1	(121)
Co-x	–	B1	(121)
CoPv02	–	B2	(119, 121)
Co-AC	SS102/SS165	B1	(122)

resistance. Another SNP on Pv09, within *Phvul.009G169600*, encodes a zinc finger protein also linked to resistance against race 503. For race 73, QRLs were mapped to Pv08 near the *Co-4* gene and an LRR protein-encoding gene (*Phvul.011G202300*) on Pv11 also showed association. Resistance to race 2047 is linked to loci on Pv03, Pv09 and Pv11. Additionally, SNP *ss715645251* on Pv01 (in *Phvul.001G243800*) encodes an LRR receptor-like kinase, while Pv02 resistance is associated with a *MAPK* gene (*Phvul.002G328300*). On Pv04, SNPs *ss715642306* and *ss715649432*, within cytochrome P450 genes, are also linked to resistance.

The minor QTLs associated with moderate resistance to race 7 were identified on Pv10 and Pv11. On Pv10 resistance was linked to SNP ss715648754 within the gene *Phvul.010G025500*, while on Pv11, SNP ss715645476 within gene *Phvul.011G021500* was associated with resistance (103). More recently, using recombinant inbred lines derived from Ruda AND277 crossing, Co-1 4 allele was mapped in the cultivar AND 277 using markers ss715645251 and BARCPVSSR01356 and reported two resistant genes, namely *Phvul.001G243800* and *Phvul.001G243900* within Co-14 (9). Therefore, the linkage of the *Co-1^4* allele with markers ss715645351 and BARCPVSSR01356 is crucial for plant breeding programs, as it facilitates the transfer of resistance genes into elite cultivars through marker-assisted selection.

Identification and functional characterization of potential resistance genes in this region will enable the development of precise markers for anthracnose resistance, thereby enhancing the efficiency of marker-assisted selection (131). SNPs or SSRs (simple-sequence repeat) markers associated with anthracnose resistance were identified on 10 common bean chromosomes through genome wide association studies (GWAS) (13). Using NBS (nucleotide-binding site)-SSR markers, nine loci for anthracnose disease resistance were identified, NSSR73, NSSR24 and NSSR265 were located at new chromosome regions for anthracnose resistance (132). In addition, two markers NSSR271 and NSSR281 on chromosome 11 and NSSR24 on chromosome 2, have been linked to anthracnose resistance. Previous studies suggest that several associated markers, NSSR65, NSSR8, NSSR234, NSSR117, NSSR281 and NSSR271 may be located within the same genomic regions on their respective chromosomes (13, 103, 133). Meta-QTL (MQTL) analysis combines data from multiple studies to refine confidence intervals and enhance consistency. In common bean, 11 MQTLs were identified on chromosome 6 and 10 QTL hotspots on chromosome 7 associated with anthracnose resistance. The study also identified 1251 genes, including many resistance (*R*) genes such as protein kinases, NBS-LRR proteins and other defense-related genes (134). These MQTLs, hotspot QTLs and potential candidate genes hold significant value for marker-assisted breeding programs in common bean, as well as for gene mapping and the cloning of genomic regions associated with anthracnose resistance.

Omics approaches for anthracnose management

Recent advances in omics technologies offer unprecedented opportunities to elucidate the molecular mechanisms underlying responses of legume to *Colletotrichum* spp., thereby enhancing the detection and diagnosis of these pathogens. The genomes of *Colletotrichum* spp. contain unique sets of genes that contribute to their virulence and population genomic studies can help unravel the genetic basis of these traits (135). For instance, the virulence gene [*CgNPG1*] has been identified in *C. gloeosporioides* and linked to host-pathogen interactions (136).

Techniques such as GWAS, QTL mapping and genome scans for selective sweeps and selection signatures can be employed to identify fungal pathogen genes involved in host-specific interactions (137). The availability of genome sequences for *C. lindemuthianum*, which infects common bean, has enabled comparative genomic analyses that characterize effector repertoires and host-pathogen interactions (138). Several legume species have sequenced genomes available in the GenBank database, including cowpea, which provides valuable resources for understanding the plant defense system against *Colletotrichum* spp. (139). These genomic resources can be used to identify candidate genes responsible for the virulence of *Colletotrichum* spp. and to target potential genes in legumes that confer resistance.

Access to genome sequences of both legumes and *Colletotrichum* spp. will accelerate breeding for durable anthracnose resistance by enabling the targeting of pathogen virulence genes and selection of host defense genes. Though current breeding programs are limited, genomic resources will support future efforts. Additionally, *Colletotrichum* genomes will aid in developing diagnostic tools for early detection and offer molecular insights into pathogenesis, driving more effective control strategies (140).

Transcriptomic studies

Multi-omics approaches enable the discovery of resistance genes and provide insights into the molecular defense mechanisms against legume diseases, including anthracnose. RNA sequencing facilitates the study of plant-pathogen interactions by identifying genes and pathways involved in different phases of the plant defense response (141). In legumes, RNA-seq is most applied during the biotrophic phase to capture early host-pathogen interaction dynamics. The gene *RGA2* also confers partial resistance to common bean anthracnose (142).

WRKY transcription factors (TFs) play a key role in regulating plant responses to pathogens by controlling the expression of camalexin and resistance-related genes (143). In a susceptible genotype of bean, four WRKY TFs were upregulated with expression levels increasing over time during *C. lindemuthianum* infection (88). A few WRKY transcription factors have been linked to the negative regulation of defense signaling, thereby increasing the host's susceptibility to anthracnose (65). Tissue-specific expression of WRKY transcription factors has been reported in common bean. Although these TFs are distributed across all chromosomes, the majority are predominantly expressed in roots, with a few showings' expression in leaves at various time points (144). Taken together, the upregulation of WRKY TFs may account for the host's susceptibility.

The roles of signaling hormones like jasmonic acid (JA), salicylic acid (SA), ethylene and IAA in activating disease resistance are well known (145). In a susceptible common bean genotype, upregulation of AP2 and ethylene-responsive TFs suggests that mis-regulation of JA and SA mediated pathways may weaken resistance. Other TFs, such as bZIPs, along with kinase-related defense genes, also appear to contribute to anthracnose resistance (88).

The involvement of over 50 nucleotide-binding site (NBS) genes in disease resistance has been identified in legumes (146). In common bean, 171 NBS genes have been reported, of which 67 showed differential expression between anthracnose-resistant and -susceptible genotypes. Notably, in the susceptible genotype *Jingdou*, 48 genes were upregulated and 19 were downregulated compared to the resistant genotype *Hongyundou*, suggesting a possible mis-regulation of defense responses. Among these, *Phvul.010G054400* typically exhibits high expression in resistant cultivars, but its expression significantly declined following infection with *C. lindemuthianum* race 81. Conversely, no change in expression was observed in the susceptible genotype, implying that this gene may function as a negative regulator of anthracnose resistance during host-pathogen interaction, thereby contributing to increased susceptibility.

These findings have significantly enhanced our understanding of NBS gene functions in common bean, especially in disease response. Another study identified 3,250 DEGs in near-isogenic lines, with more upregulated in resistant lines during the necrotrophic than the biotrophic phase (88). Key resistance-related genes encode peroxidases, lipoxygenases and PR proteins. Further, genes such as *PvPR1*, *NPR1*, *FLS2* and *β-GLUC* were significantly overexpressed in a resistant genotype following inoculation with race 65 of *C. lindemuthianum*, highlighting their crucial roles in the defense response (18). Additionally, the *pacCl* gene, encoding the PacC transcription factor of *C. lindemuthianum*, displayed distinct expression patterns between the biotrophic and necrotrophic phases, indicating its regulatory role during the pathogen's lifestyle transition (147).

Metabolomic and proteomic studies

While several studies have characterized specific metabolites in response to anthracnose, comprehensive metabolomic analyses related to disease and pest resistance in legumes remain limited. So far, only a single study has provided proteomic data on the legume-*Colletotrichum* interaction in common bean. Through two-dimensional electrophoresis and mass spectrometry, it identified the accumulation of 17 proteins in infected common bean plants. These proteins were associated with a range of cellular functions, including photosynthesis, antioxidant activity, carbon metabolism, defense responses, genetic regulation, protein folding, stress response and the biosynthesis of phenylpropanoid and flavonoid compounds (148). The accumulation of PR1 protein and antioxidant proteins in infected plants supports transcriptomic findings, while early over accumulation of chalcone isomerase highlights its role during the necrotrophic phase. Integrating transcriptomics and proteomics will improve understanding of protein regulation under biotic stress, aiding protein resistance identification. Metabolomics will also become key in legume breeding, enhancing trait selection and accelerating variety development.

Conclusion

Anthracnose represents a major constraint to leguminous vegetable production on a global scale. Effective management depends on understanding the pathogen, its symptoms and control strategies, with resistance breeding being the most cost-effective and sustainable approach. To develop sustainable and effective management practices, future research must prioritize areas such as pathogen genetics, host resistance mechanisms, MAS, biological control and disease epidemiology. Resistance sources have been identified in several legumes, enabling QTL mapping and cultivar development, but further validation is needed for MAS. Advanced omics tools (genomics,

transcriptomics, metabolomics, proteomics) and high throughput technologies are deepening insights into host-pathogen interactions, aiding the discovery. Despite relatively slow progress in developing genomic resources specific to legume-anthracnose interactions, MAS has already demonstrated broad utility in crops such as common bean (*Phaseolus vulgaris*), lentil (*Lens culinaris*) and soybean (*Glycine max*). Recent advancements in phenotyping platforms, high-throughput sequencing technologies and functional characterization of metabolites and proteins are expected to further enhance our understanding of the molecular basis of resistance and facilitate the discovery of novel resistance genes. Genome editing technologies, particularly the CRISPR/Cas system, have been successfully employed in various crops to confer resistance by targeting both host and pathogen genomes. However, this approach remains underexplored in legumes with respect to anthracnose resistance. The implementation of CRISPR/Cas technology holds considerable promise for generating novel genetic variation, thereby enabling the development of advanced, disease-resistant cultivars. In the context of climate change and a growing global population, it is imperative to deploy an integrated breeding and biotechnological approach to develop climate-resilient, high-yielding legume cultivars. This review underscores existing knowledge gaps and highlights critical research priorities in the study of anthracnose resistance in legumes. Emphasis is placed on the development of robust marker-assisted selection tools, the discovery and application of novel biological control strategies and comprehensive epidemiological studies aimed at improving long-term anthracnose management.

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