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CRITICAL REVIEWS IN PLANT SCIENCES
https://doi.org/10.1080/07352689.2023.2228122

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ABSTRACT

Anthracnose, caused by hemibiotrophic *Colletotrichum* spp., is a destructive disease of legumes and many other crops worldwide. *Colletotrichum* spp. constitute one of the top 10 phytopathogenic fungi, infecting ~3,000 plant species, attacking food and forage legume crops at all growth stages; including seed, seedlings, young, and mature plants; with consequent significant yield reductions. Presently, cultural practices and substantial use of synthetic fungicides are the most prevalent approaches for anthracnose management. In addition, there has been a strong focus toward developing advanced breeding lines and cultivars with improved anthracnose resistance. This has involved traditional breeding resulting in a wide range of anthracnose resistance resources being identified, particularly using advanced techniques within the common bean, soybean, lentil, mungbean, blackgram, and lupins. For instance, quantitative trait loci (QTLs) for resistance have been identified, enabling marker-assisted resistance breeding. More recently, molecular approaches; including genomics, transcriptomics, proteomics, and metabolomics; have been utilized to understand the pathogenesis and defense mechanisms involved in the *Colletotrichum*-legume interaction. Genetic manipulation through omics offers scope to better protect legumes from anthracnose by improving the efficiency of breeding programs. This review focuses on key pathogens (*viz.*, *C. truncatum*, *C. lentis*, *C. lupini*, and *C. lindemuthianum*) causing anthracnose in legumes, their biology, and epidemiology, the disease management levers embracing progress with host resistance, genetic and breeding approaches, and highlights critical knowledge gaps in conventional and molecular breeding programs. We conclude that the ongoing progress toward developing breeding lines/cultivars/donors with improved resistance in legume plant responses against anthracnose using omics approaches offers novel insights into legume-anthracnose pathogen interactions and ensures more sustainable and effective disease management strategies for the future.

KEYWORDS

Colletotrichum spp.; genetics; genomics; marker-assisted selection; metabolomics; proteomics; resistant gene; transcriptomics; virulent gene

I. Introduction

Legumes belong to the family *Fabaceae (or Leguminosae)* whose ripe and unripe seeds as well as pods play an important role in human nutrition due to their nutritional and health benefits since ancient times (Giugliano *et al.*, 2006; Reckling *et al.*, 2016; Clemente and Olias, 2017). Legumes are safe for consumption, being present in the diet of millions of individuals worldwide, also grown for livestock forage and fodder, and as a green manure to improve soil health (Tivoli *et al.*, 2006). They play a key role in crop rotation, offering cropping system diversification, while also providing many ecosystem services including atmospheric nitrogen fixation, enhancing colonization by arbuscular mycorrhizal fungi, and boosting water supply and nutrient uptake in host plants (Murphy-Bokern *et al.*, 2017). In addition, soil structure improvement and mobilization of phosphorus are

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key ecosystem benefits (Kamh *et al.*, 1999). Worldwide, beans (*Phaseolus vulgaris* L.), blackgram or urdbean (*Vigna mungo* (L.) Hepper), broad bean or faba bean (*Vicia faba* L.), chickpea (*Cicer arietinum* L.), cowpea (*Vigna unguiculata* (L.) Walp.), lentil (*Lens culinaris* Medik), white lupin (*Lupinus albus* L.), narrow-leafed lupin or blue lupin (*Lupinus angustifolius* L.), yellow lupin (*Lupinus luteus* L.), mungbean (*Vigna radiata* (L.) R. Wilczek), pea (*Pisum sativum* L.), peanut (*Arachis hypogaea* L.), pigeon pea (*Cajanus cajan* L.), and soybean (*Glycine max* (L.) Merr.) are grown as major food legumes depending upon the requirements and suitable conditions for their cultivation (Pagano and Miransari, 2016; Pandey *et al.*, 2018; Alkemade *et al.*, 2023). India is the major legume producer (6.3 MT ha, 4.5 MT), followed by Myanmar, Russia, China, Canada, Turkey, and the United States (Pandey *et al.*, 2018). Forage legumes, such as clovers (*Trifolium* spp.), and annual medic and perennial alfalfa (*Medicago* spp.), are of critical importance for animal production globally, particularly in temperate and Mediterranean-type climates (Jacob *et al.*, 2016), whereas *Stylosanthes* spp. are important in tropical-type environments (Chakraborty, 2004). Together with other forage legume genera/species, these contribute a major proportion of feed for ruminants in agriculture, frequently underpinning many and varied animal grazing enterprises. For example, some 29 m ha of annual *Trifolium* spp. has been planted in Australia alone (Hill and Donald, 1998). Likewise, the annual *Medicago* spp. play an important agronomic role in dryland farming regions worldwide (Walsh *et al.*, 2001) where they are often an integral component of cropping systems (Piano and Francis, 1992). Finally, *Stylosanthes* species are among the most versatile, widely adopted, and productive tropical pasture legumes commercially used in a range of agricultural systems in many countries with a tropical or sub-tropical climate (Chakraborty, 2004).

Pests and diseases are the major biotic stresses limiting the production of legumes worldwide, and among them, anthracnose is becoming a prevalent threat in major crop legume growing countries (Dias *et al.*, 2016; Nataraj *et al.*, 2020; Pandey *et al.*, 2021a; Lima *et al.*, 2023). For example, under favorable conditions, this disease can cause from 60 to 100% yield loss in-field crop legume production (Hartman *et al.*, 1999; da Silva *et al.*, 2020; Chakraborty *et al.*, 2022; Kaur *et al.*, 2023). Anticipated climate changes are likely to foster more severe diseases. For example, in Germany and Switzerland, *C. lupini* threatens lupin production with a current yield loss of >70% (Alkemade *et al.*, 2021a), which is predicted to reach up to 100% from future anticipated climate change. Despite efforts to reduce the risks of anthracnose epidemic development, there have been frequent failures, such as in mid 1990s in Europe where very high yield losses were observed and resulted in a rapid decline of the lupin cultivation area (Talhinhas *et al.*, 2016).

Important forage legume species, for example, clovers (Shivas, 1989; Jacob *et al.*, 2016), annual and perennial *Medicago* spp. (Lamprecht and Knox-Davies, 1984; Tivoli *et al.*, 2006; Jacob *et al.*, 2016), and *Stylosanthes* spp. (Irwin and Cameron, 1978; Chakraborty, 2004), can be severely attacked by one or more *Colletotrichum* spp. Examples of the latter include *C. trifolii* on clovers and annual and perennial *Medicago* spp. (Mackie *et al.*, 2003; Tivoli *et al.*, 2006), and species, such as *C. gloeosporioides* on *Stylosanthes* spp. (Irwin and Cameron, 1978; Lenné, 1994; Chakraborty, 2004). Losses from anthracnose are well-defined for crop legumes but the impact of the disease on the productivity and sustainability of forage legumes and animal grazing enterprises remain largely undefined due to a lack of established quantitative links between disease severity and sustainable animal production (Chakraborty *et al.*, 1996). The latter is perhaps a consequence of the insidious impact of anthracnose on forage legumes, resulting in a gradual decline of forage productivity leading to poor ground cover (Chakraborty, 2004). An exception among forage legumes is *Stylosanthes* spp., whereby foliar infection results from 40 to 100% yield losses in tropical forage legumes (Lenné, 1986; Kelemu *et al.*, 1999).

Current research indicates that anthracnose in legumes has complex etiology (Perseguini *et al.*, 2016; Dias *et al.*, 2018; Luo and Jiang, 2022), with *C. truncatum* and *C. lindemuthianum* the most prevalent species affecting food crop legume production (Sharma *et al.*, 2011). The genus, *C.* comprises a large clade of class Sordariomycetes with more than 200 accepted species. Based on the broad host range and molecular phylogenetics, the genus can be further classified into 14 species complexes and single species (Marin-Felix *et al.*, 2017). *Colletotrichum* species are one of the top 10 phytopathogenic fungi infecting ~3,000 plant species, resulting in significant yield reductions of food crops (Cannon *et al.*, 2012; da Silva *et al.*, 2020). Worldwide, several *Colletotrichum* species complexes, such as *C. acutatum*, *C. orbiculare*, *C. truncatum*, *C. destructivum*, *C. orchidearum*, *C. dematium*, *C. spaethianum*, *C. magnum*, *C. gloeosporioides*, *C. chlorophyti*, and *C. coccodes* infect legumes (Weir *et al.*, 2012; Damm *et al.*, 2014, 2019). This genus has a

hemibiotrophic lifestyle and can be manipulated in the laboratory, making it a valuable model pathogen for physiological, biochemical, and genetic studies (Perfect *et al.*, 1999).

In addition to *C. truncatum,* several other species of *Colletotrichum* cause anthracnose in food crop legumes. These include the following: *C. lupini* on lupin (Nirenberg *et al.*, 2002; Rychel-Bielska *et al.*, 2020), *C. lentis* on lentil (Damm *et al.*, 2014; Buchwaldt *et al.*, 2018), *C. lindemuthianum* on beans and blackgram (Lima Castro *et al.*, 2017) and *C. sojae* (Damm *et al.*, 2019), *C. chlorophyti* (Yang *et al.*, 2012), *C. gloeosporioides* (Mahmodi *et al.*, 2013), *C. coccodes* (Riccioni *et al.*, 1998), *C. cliviae* Yang (Barbieri *et al.*, 2017), *C. plurivorum* (Damm *et al.*, 2019), *C. incanum* (Yang *et al.*, 2014), *C. musicola* (Boufleur *et al.*, 2020), *C. destructivum* (Manandhar, 1986; Damm *et al.*, 2014) and *C. brevisporum* (Shi *et al.*, 2021b) on soybean. These species also infect other food crops (Table 1). The disease is common under high humidity and temperature with frequent rainfall (Yang and Hartman, 2015), and affects crops at all the physiological stages including pods and seed, seedlings, young and mature plants. The necrotrophic lifestyle of the pathogen can cause complete defoliation of seedlings and mature plants (Yang *et al.*, 2015), and results in yield reductions up to 100% under high humid conditions and temperature ~30 °C that commonly occur in countries, such as India, China, Myanmar, Turkey, and USA.

Mycologists now benefit in the era of molecular biology and no longer need to solely rely only on morphological features-based identification of *Colletotrichum* species characteristics that are highly influenced by environmental conditions (Jayawardena *et al.*, 2016). A polyphasic approach is currently used to identify species in this genus using morpho-cultural features and multiple locus phylogenetic analyses of DNA sequences (Liu *et al.*, 2016). Several species within *Colletotrichum* exhibit high genetic variability but the mechanisms behind such variability remain unclear (da Silva *et al.*, 2020). Further, genetic studies of *Colletotrichum* spp. have offered unique insights toward improvements in plant disease prevention and management strategies in various legumes (Ureña-Padilla *et al.*, 2002; Ciampi-Guillardi *et al.*, 2014; Pandey *et al.*, 2021a).

At present, most studies of anthracnose on food legumes concentrate on *C. truncatum*, *C. lentis*, *C. lupini*, and *C. lindemuthianum*, with little information regarding other opportunistic *Colletotrichum* spp. infecting them, which likely poses challenges for its management under field conditions (Ureña-Padilla *et al.*, 2002; Pandey *et al.*, 2018). It also raises questions as to which other complex species of *Colletotrichum* interact with these major four species thereby increasing disease severity. To prevent and manage the disease, it is crucial to accurately identify the causal agents. In legume anthracnose, multiple *Colletotrichum* species may differentially affect disease management where they respond differently to different management methods. This is perhaps one of the reasons why studies on the use of synthetic fungicides in managing anthracnose in legumes have shown contradictory efficacy (Dias *et al.*, 2016; Poti *et al.*, 2020).

Currently, anthracnose in legumes is primarily mitigated through non-genetic approaches, such as cultural practices along with the use of synthetic fungicides and natural agents. Nevertheless, locating and deploying genetic resistance has been keenly sought by legume breeders. Considerable progress has been made in developing anthracnose resistant varieties/cultivars in legumes using traditional and omics approaches. While, to date, genetic resistance has been searched for and utilized against a specific *Colletotrichum* species, such resistance is not effective when anthracnose is a disease complex caused by multiple *Colletotrichum* species. This highlights an urgent need for critical analysis and reappraisal of legume anthracnose literature. In this review, we provide a comprehensive overview of anthracnose in legumes caused by *C. truncatum*, *C. lentis*, *C. lupini*, and *C. lindemuthianum*, focusing on the pathogen's epidemiology, pathogenicity, host resistance mechanisms, and genetics and breeding progress using genetic and omics approaches toward developing breeding lines/cultivars with improved resistance to better manage legume anthracnose diseases.

II. Current status of anthracnose in legumes

The pathogen, *Colletotrichum* (sexual stage: *Glomerella*) is one of the most significant members of the kingdom fungi in the division Ascomycota (Order: Glomerellales, Class: Sordariomycetes). Despite its asexual morphology, for which the genus is named, molecular phylogenetics place the species in the Ascomycota (Cai *et al.*, 2009). *Colletotrichum* species in legumes remain undefined in terms of the number and type of species exhibiting pathogenicity. Worldwide, many countries have reported at least one *Colletotrichum* species allied with one or more of the major legumes, such

Table 1. *Colletotrichum* species complexes* associated with anthracnose of legumes.

Hosts	Species*	Distribution (country)	GenBank accession number	References
Almond (*Prunus amygdalus* Batsch.), Apple (*Malus domestica* Borkh.), Avocado (*Persea americana* Mill.)	*Colletotrichum gloeosporioides*	Israel		Freeman *et al.*, (1996)
Banana (*Musa* spp.)	*C. gloeosporioides*	Ecuador	MG564348	Riera *et al.*, (2019)
Banana	*C. gloeosporioides*	Malaysia	JX163228	Intan Sakinah *et al.*, (2013)
Banana	*C. gloeosporioides*	Côte d'Ivoire	MG515233	Bele *et al.*, (2018)
Bean (*Phaseolus* sp.)	*C. lindemuthianum*	USA	AJ301958	Chen *et al.*, (2006)
Blackgram (*Vigna mungo* (L.) Hepper)	*C. lindemuthianum*	India	–	Aggarwal *et al.*, (2017)
Blackgram	*C. truncatum*	India	–	Chatak and Banyal, (2021)
Blackgram	*C. truncatum*	India	–	Bindra *et al.*, (2016)
Chili (*Capsicum annuum* L.)	*C. truncatum*	India	GU227880	Noor and Zakaria, (2018)
Chili	*C. truncatum*	China	–	Shi *et al.*, (2021b)
Chickpea (*Cicer arietinum* L.)	*C. truncatum*	Malaysia	JX971160	Mahmodi *et al.*, (2013)
Chili pepper (*Capsicum* sp.)	*C. truncatum*	Korea	MH085102	Oo and Oh, (2020)
Cocoa (*Theobroma cacao* L.)	*C. gloeosporioides*	Indonesia	–	Dwi *et al.*, (2014)
Common bean (*Phaseolus vulgaris* L.)	*C. lindemuthianum*	Mexico	–	Hernández-Álvarez *et al.*, (2013)
Common bean	*C. lindemuthianum*	United Kingdom	GU227800	Damm *et al.*, (2009)
Cowpea (*Vigna unguiculata* (L.) Walp.)	*C. lindemuthianum*	Nigeria	–	Adebanjo and Bankole, (2004)
Lentil (*Lens culinaris* Medik)	*C. truncatum*, *C. lentis*	Canada	NR_137781.1	Gossen *et al.*, (2009)
Lentil	*C. truncatum*	Bulgaria	–	Kaiser *et al.*, (1998)
Lentil	*C. truncatum*	North America	–	Tullu *et al.*, (2003)
White lupin (*Lupinus albus* L.)	*C. lupini*	Switzerland	MT741840	Alkemade *et al.*, (2021a)
Mango (*Mangifera indica* L.)	*C. gloeosporioides*	Southwestern Nigeria	–	Awa *et al.*, (2012)
Mungbean (*Vigna radiata* (L.) R. Wilczek)	*C. truncatum*	India	–	Roopadevi *et al.*, (2014)
Mungbean	*C. truncatum*	India	MT394500	Pandey *et al.*, (2021a)
Mungbean	*C. phaseolorum*	Japan	GU227896	Damm *et al.*, (2009)
Papaya (*Carica papaya* L.)	*C. truncatum*	Mexico	HQ287581	Rampersad *et al.*, (2013)
Papaya	*C. gloeosporioides*	Mexico	JF749805	Rampersad *et al.*, (2013)
Papaya fruit	*C. truncatum*	Brazil	MK135782	Santos Vieria *et al.*, (2020)
Pea (*Pisum sativum* L.)	*C. coccodes*	Brazil	HM171679	Bellé *et al.*, (2020)
Peanut (*Arachis hypogaea* L.)	*C. chlorophyti*	China	MN688797	Zhao *et al.*, (2021)
Peanut	*C. truncatum*	China	MN148631 and MN148632	Yu *et al.*, (2020)
Peanut	*C. dematium*	India	–	Ankur *et al.*, (2012)
Peanut	*C. gloeosporioides*	Korea	–	Kim *et al.*, (1998)
Red-fleshed dragon fruit (*Selenicereus costaricensis* (F.A.C. Weber) S. Arias & N. Korotkova)	*C. truncatum*	Malaysia	JX416096	Iskandar Vijaya *et al.*, (2015)
Soybean (*Glycine max* (L.) Merr.)	*C. cliviae*	Brazil	KT696282–87	Barbieri *et al.*, (2017); Dias *et al.*, (2018)
Soybean	*C. truncatum*	Brazil	KJ614294	Rogério *et al.*, (2017)
Soybean	*C. sojae*	USA	KC110830	Yang *et al.*, (2014)
Soybean	*C. chlorophyti*	USA	GU227894	Yang *et al.*, (2012)
Soybean	*C. gloeosporioides*	Malaysia	JX669450	Mahmodi *et al.*, (2013)
Soybean	*C. coccodes*	USA	–	Riccioni *et al.*, (1998)
Soybean	*C. plurivorum*	Germany	NR_160828.1	Damm *et al.*, (2019)
Soybean	*C. incanum*	USA	KC110788	Yang *et al.*, (2014)
Soybean	*C. musicola*	Brazil	WIGM00000000	Boufleur *et al.*, (2020)
Soybean	*C. destructivum*	USA	–	Manandhar, (1986)
Soybean	*C. brevisporum*	China	MT36107	Shi *et al.* (2021b)
Strawberry (*Fragaria* × *ananassa Duchesne*)	*C. gloeosporioides*	China	FJ608625	Xie *et al.*, (2010)
Strawberry	*C. gloeosporioides*	China	–	Zhang *et al.*, (2020)
Sunflower (*Helianthus annuus* L.)	*C. lindemuthianum*	Argentina	–	Anitha *et al.*, (2020)
Common vetch (*Vicia sativa* L.)	*C. lentis*	China	KY241666.1	Unpublished

*These pathogens can cause disease also on other plants than legumes.

as soybean, peanut, chickpea, common bean, pea, pigeon pea, lupins, lentil, blackgram, and mungbean. More than 15 European countries have already reported lupin anthracnose (Fischer *et al.*, 2015), at least eight European countries have reported anthracnose in lentils (Buchwaldt *et al.*, 2004), and *C. lindemuthianum* on common bean has been reported in several African countries (Adebitan and Olufajo, 1998). Countries like USA, China, India, Taiwan, and Brazil have greatest *Colletotrichum* species diversity, followed by Mediterranean countries, Canada, Myanmar, and other south Asian countries (da Silva *et al.*, 2020). Historically, *C. truncatum* and *C. lindemuthianum* are considered worldwide prevalent species of anthracnose in legumes causing 30–100% yield loss in cowpea (Enyiukwu *et al.*, 2014; Falade and Borisade, 2018), common bean (Adam-Blondon *et al.*, 1994), mungbean (Pandey *et al.*, 2021a), chickpea (Mahmodi *et al.*, 2013), soybean (Sharma *et al.*, 2011; Yang and Hartman, 2015), and blackgram (Aggarwal *et al.*, 2019).

The main *Colletotrichum* species affecting lentil production was formerly considered as *C. truncatum*, which has a wide host range (Altaf *et al.*, 2018). However, in view of the recent clear differentiation of *C. lentis* from *C. truncatum* (Damm *et al.*, 2014; Buchwaldt *et al.*, 2018), many plant species may be non-hosts of *C. lentis*. Therefore, while *C. lentis* appears to have a limited host range in the Fabaceae family, since 1987 it has seriously affected lentil cultivation in Canada (Morrall, 1988; Altaf *et al.*, 2018). In association with extensive lentil cultivation, it was also confirmed in China (Xu *et al.*, 2017), Bulgaria (Kaiser *et al.*, 1998), and the United States (Venette, 1994). Other than lentils, *C. lentis* causes anthracnose in faba bean, pea, chickpea (Gossen *et al.*, 2009), and in common vetch (*Vicia sativa* L.) in China (Xu *et al.*, 2017). Although this species does not currently infect lupins, dry bean (*Phaseolus vulgaris* L.), or alfalfa (Gossen *et al.*, 2009), this could change in the future with it becoming pathogenic across multiple legumes species, perhaps a consequence of expected environmental changes associated with future climates.

Colletotrichum boninense and *C. gigasporum* have been isolated from soybean, although isolations were made either from asymptomatic plant tissues or with no evidence of pathogenicity (da Silva *et al.*, 2020). In contrast, the pathogenicity of *C. gloeosporioides*, *C. dematium*, *C. truncatum*, and *C. magnum* has been demonstrated in soybean (da Silva *et al.*, 2020). Anthracnose caused by *C. destructivum* and *C. truncatum* is one of the most prevalent disease complexes of soybean in Argentina, the world's third largest soybean producer (Ramos *et al.*, 2010, 2013). However, since both species were only identified by conidial features, it remains unclear whether *C. destructivum* was truly associated with the disease (Ramos *et al.*, 2013). Despite this, the literature reports show that soybean anthracnose is caused by multiple *Colletotrichum* species whereas anthracnose on lentil, lupins, bean, mungbean, blackgram, and cowpea is caused by a single species (Boufleur *et al.*, 2022). Despite the importance of an accurate identification of the causal agent in effective disease management (Chen *et al.*, 2018), reliable pathogen diagnosis techniques for the disease complexes are currently lacking, and addressing this needs to be prioritized in future research.

The distribution of *C. truncatum*, *C. gloeosporioides*, *C. lindemuthianum*, *C. lupini*, and the more recently described *C. lentis*, shows a noteworthy correlation with both relative humidity and atmospheric temperature (Shi *et al.*, 2022). This is not surprising as these factors strongly influence pathogen infection, survival, and spread. Reports of anthracnose caused by *Colletotrichum* species in legumes and other crops on a global scale are presented in Table 1.

III. Disease symptoms

Colletotrichum-caused disease symptoms can be observed on legume crops at all growth stages. They include pre- and post-emergence damping-off that consists of seed rotting, seedling wilting, as well as dark, depressed, and irregular patches on petioles, stems, and pods in advanced growth stages leading to premature defoliation of plants (Pandey *et al.*, 2021a; Sharma *et al.*, 2011; Yang *et al.*, 2015). Yellow to brown lesions appear on the infected seeds, which may result in poor germination. Small, dark brown to black lesions can be seen on diseased cotyledons. Infected hypocotyls develop rust-colored specks that enlarge longitudinally, resulting in sunken lesions. Infected cotyledons senesce prematurely, resulting in stunted growth. Species, such as *C. coccodes*, *C. incanum*, *C. gloeosporioides*, *C. lindemuthianum*, *C. truncatum*, *C. musicola*, and *C. plurivorum* cause such symptoms (Riccioni *et al.*, 1998; Mahmodi *et al.*, 2013; Dias *et al.*, 2018; Boufleur *et al.*, 2020). Necrotic spots caused by *C. truncatum* on stems are hexagonal (e.g., on soybean, Yang *et al.*, 2014 and mungbean, Pandey *et al.*, 2018) while rounded to asymmetrical grayish spots surrounded with dark margins are often caused by *C. sojae* (Damm

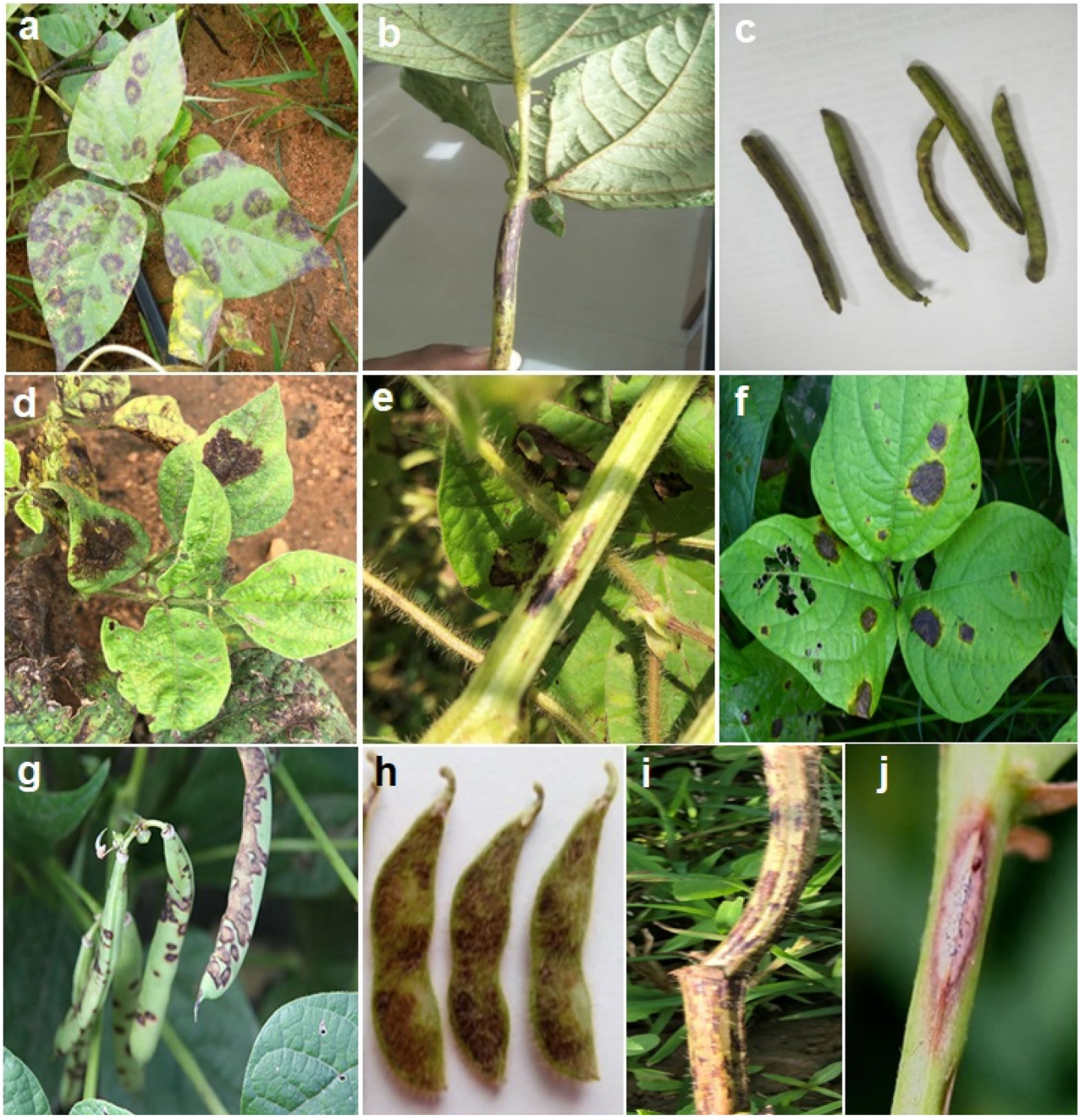

Figure 1. Typical anthracnose symptoms produced by *Colletotrichum* species on mungbean (a-leaf, b-stem, c-pods), blackgram (d-leaf, e-stem), common bean (f-leaf, g-pods), soybean (h-pods, i-stem), and lentil (stem-j).

et al., 2019). In contrast, *C. chlorophyti* causes intra- and inter-veinal necrotic spots bounded by slight chlorosis (Yang *et al.*, 2012). On blackgram, *C. truncatum* produces circular, black, sunken spots with dark center and bright red orange margins on leaves and pods, which later become horseshoe shaped in appearance. In severe infections, the affected parts wither. Symptoms on leaves, pods, and stem caused by *Colletotrichum* species on legumes are shown in Figure 1.

IV. Disease cycle

The disease cycle of *C. lindemuthianum*, *C. lentis*, *C. lupini*, and *C. truncatum* has been well-described in the literature (Adhikari *et al.*, 2009; Yang and Hartman, 2015; Padder *et al.*, 2017; Singh *et al.*, 2022) while that of other *Colletotrichum* spp. associated with legume anthracnose is still poorly documented. These four species are soil- and seed-borne, survive in infected crop debris and on wild plants, and can

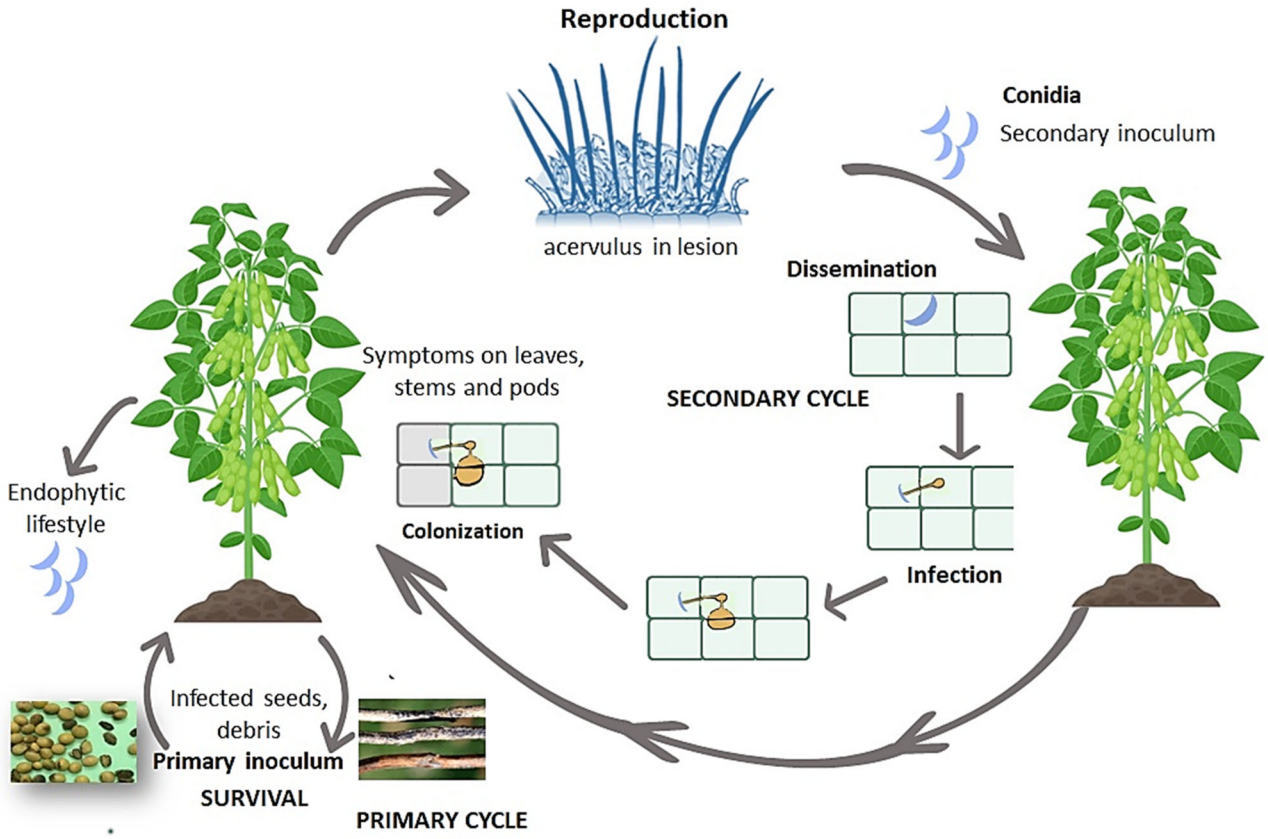

Figure 2. Disease cycle of anthracnose caused by *Colletotrichum truncatum* on soybean crop.

produce virulent microsclerotia (Iamsupasit *et al.*, 1993; Yang and Hartman, 2015; Padder *et al.*, 2017; Singh *et al.*, 2022). There is no evidence that weeds or alternative hosts play a role in the disease epidemiology. Infected seed is assumed to be the main source of primary inoculum allowing long-distance dissemination of these pathogens and global seed market and trade contribute to the introduction of aggressive pathogen isolates to new production areas (Chakraborty *et al.*, 1996; Singh *et al.*, 2022).

During the lifecycle, conidia germinate and form appressoria on the host plants after penetration of fungal hyphae on plant surfaces. All species, including *C. truncatum*, *C. lentis*, *C. lupini*, and *C. lindemuthianum*, infect and colonize leaf and/or stem surfaces in a similar manner (Khan, 1992; Cannon *et al.*, 2012; Rao *et al.*, 2020). The pathogen lives a hemibiotrophic lifecycle in the first stage of development whereby a primary hypha develops from the penetration peg. This is followed by biotrophic vesicles located between plasma membranes and cell walls. As the biotrophic phase ends, the necrotrophic phase begins with the development of secondary hyphae which colonize tissues intra- and inter-cellularly and kill the plant cells (Kavanashree *et al.*, 2022). Sometimes, the pathogen also has an endophytic lifestyle (Bhadauria *et al.*, 2013a) by colonizing internal plant tissues without showing any disease symptoms (Chen *et al.*, 2006; Luo and Jiang, 2022). Necrotrophic stages of anthracnose produce acervuli containing conidia, a typical symptom of anthracnose. Secondary infection cycles follow, with conidia dispersed by splashing water that dissolves the mucilage covering them and aids in short-range dispersal (Kaiser *et al.*, 1998). An example of *C. truncatum* lifecycle is presented in Figure 2.

Epidemiological studies significantly contribute toward effective disease management and require an understanding of the relative status of each species complex in its development. Several species associated with legume anthracnose are known to undergo sexual reproduction, including *C. sojae*, *C. gloeosporioides*, *C. plurivorum*, and *C. musicola* (Ramos *et al.*, 2013; Boufleur *et al.*, 2020). For example, in soybean, previously *Glomerella glycines* (=*C. sojae*) was considered as the sexual morph of three *Colletotrichum* species, creating taxonomic confusion that was later resolved by Damm *et al.* (2019). Similarly, *Glomerella cingulata* was considered as sexual morph of *C. gloeosporioides*, an anthracnose pathogen of mungbean (Chaudhari and Gohel, 2016) and forage legumes (Iamsupasit

et al., 1993). However, some species like *C. destructivum, C. incanum*, and *C. truncatum* possess only the asexual stage (Cannon *et al.*, 2012). Nonetheless, a few concerns regarding the epidemiology of pathogens still need to be addressed, as they directly affect disease management. For example, pathogens with a sexual stage in their lifecycle often have greater survival on alternate hosts. Genetic recombination plays an important role in *Colletotrichum* species variability and pathogen survival. While sexual ascospores can spread the disease over wide distances and can infect the plants in different way compared to conidia, most of the infection processes are generally similar (Cannon *et al.*, 2012). Moreover, the infection process of *C. lupini* was recently visualized in *Lupinus mutabilis* (Guilengue *et al.*, 2022), where it was found that the pathogen penetration occurred from melanized appressoria and then a switch to necrotrophy was observed after 3 days after pathogen inoculation. A recent study revealed that *C. lupini* reproduces clonally through four independent lineages (Alkemade *et al.*, 2023). Differences in morphology and virulence patterns have been reported among the *C. lupini* isolates on Andrean lupin and white lupin between and within the clonal lineages. Isolates from lineage II contained a minichromosome, and while it was partially present in lineages III and IV it was not present in isolates belonging to lineage I (Alkemade *et al.*, 2023). Variations in the presence of this minichromosome suggest it could have a possible role in host-pathogen interactions.

V. Variability of *Colletotrichum* isolates in legumes and causes of variability

Species of *Colletotrichum* are exceedingly variable in terms of toxin production and their morphological and genetic features (Hyde *et al.*, 2009; Trabanco *et al.*, 2015). There are various explanations for the high level of genetic variation in the genus *Colletotrichum*, including the occurrence of natural mutation (O'Connell *et al.*, 1993; Bhadauria *et al.*, 2013a) and heterokaryosis (O'Connell *et al.*, 1993; Chacko *et al.*, 1994; Souza-Paccola *et al.*, 2003). In addition to natural mutation, asexual recombination, and heterokaryosis, the so-called parasexual cycle, has been proposed as more vital in causing genetic difference in imperfect fungi, *viz.*, *C. truncatum*, *C. lindemuthianum*, and *C. gloeosporioides* (O'Connell *et al.*, 1993; Bhadauria *et al.*, 2013a). There is also evidence that in nature, heterokaryon incompatibility appears to inhibit parasexuality. In this section, we discuss the extent to which variability exists at different levels.

A. Morpho-cultural variability

Species of *Colletotrichum* that infect legumes are highly variable in their cultural (colony color, growth pattern) and morphological features, such as hyphal morphology; shape and size of conidia, and sporulation. For example, the presence of boat-shaped conidia can discriminate *C. truncatum* from other species of *Colletotrichum* but not between closely related/parallel species (Pandey *et al.*, 2021a). The length and width of conidia and conidiophores are other morphological features that can be considered in the differentiation of species (da Silva *et al.*, 2020). Another test to measure variability among isolates is the vegetative compatibility test (Liu *et al.*, 2021). For instance, two genetic groups (I and II) have been identified within *C. lupini* based on their vegetative compatibility (Shivas *et al.*, 1998). Historically, phenotypic variability was considered for the classification and nomenclature of species within the genus *Colletotrichum*. However, morphological features alone were inaccurate parameters in species discrimination as their growth was influenced by many factors, including the composition of culture media, intensity of light, and temperature (Cai *et al.*, 2009; Liu *et al.*, 2014, 2016). For instance, *C. truncatum* and *C. gloeosporioides* conidial length and width varied when both species were grown on different culture media (Mahmodi *et al.*, 2013; Pandey *et al.*, 2021a). Based on these morphological differences, host specialization has become more acceptable for species discrimination in *Colletotrichum* (Chongo *et al.*, 2002; Gossen *et al.*, 2009; Reveglia *et al.*, 2023). The diagnostic value based morphological features, however, should not be overlooked. For instance, host specialization may not be a suitable diagnostic measure in cases where a *Colletotrichum* isolate can infect more than one host or when different species of the pathogen are involved as a disease complex.

B. Variability at the molecular level

Since 1980, molecular markers have enabled the investigation of genetic variation at the molecular level along with molecular taxonomy and phylogeny. Genetic variability among isolates of *C. truncatum*, *C. gloeosporioides*, *C. lindemuthianum*, and other *Colletotrichum* species has been widely investigated using diverse molecular markers. These include the

following: random amplified polymorphic DNA (RAPD, Adam-Blondon *et al.*, 1994; Sant'Anna *et al.*, 2010); restriction fragment length polymorphism (RFLP, Tullu *et al.*, 2006); amplified fragment length polymorphism (Tullu *et al.*, 2006); random amplified microsatellites (Rogério *et al.*, 2019); inter simple sequence repeat (Mahmodi *et al.*, 2014; Basandrai *et al.*, 2016); simple-sequence repeats (Rogério *et al.*, 2019); and nuclear internal transcribed spacers (Nirenberg *et al.*, 2002; Ford *et al.*, 2004; Padder *et al.*, 2008; Fontenelle *et al.*, 2017; Pandey *et al.*, 2021a). Various molecular markers have allowed identification of high levels of genetic variability among isolates of *C. truncatum* and *C. lentis* from lentil (Ford *et al.*, 2004; Xu *et al.*, 2017), soybean (Rogério *et al.*, 2017), blackgram (Basandrai *et al.*, 2016), and other hosts (Vasconcelos *et al.*, 1994; Sharma, 2009; Sant'Anna *et al.*, 2010). This highlights the extensive genetic variation among *Colletotrichum* isolates worldwide despite genetically homogeneous regional populations and suggests a restricted geographical dispersal range of *Colletotrichum* species (Rogério *et al.*, 2019). However, despite these molecular investigations, the molecular phylogeny and taxonomy of the genus *Colletotrichum* remain unclear.

C. Variability in toxin production

Colletotrichum species produce a highly variable range of host-specific toxins (García-Pajón and Collado, 2003), such as for isolates of *C. truncatum* on soybean (Masi *et al.*, 2022). To date, more than 14 *Colletotrichum* species complexes have been identified (Bhunjun *et al.*, 2021). Some of these cannot be discriminated from saprophytic or hemibiotrophic species like *C. gloeosporioides*, *C. lindemuthianum*, and *C. truncatum* based on morphological features, but they can be differentiated based on their unique pathogenicity (Chongo *et al.*, 2002; Chakraborty *et al.*, 2019) which is strictly dependent on the specific toxins (Masi *et al.*, 2022). Despite this variability, there is no scientific consensus in classifying *Colletotrichum* species according to their pathotypes (Chongo *et al.*, 2002; Banniza *et al.*, 2018).

VI. Mechanisms of pathogenicity

A. Enzymatic reactions

The pathogenicity of *Colletotrichum* species in legumes has not been well-studied despite recent advances in omics technology (Rogério *et al.*, 2019). However, research has shown that conidia germinate in both susceptible and resistant cultivars after successful infection, producing germ tubes, which build up in intercellular spaces in the leaf epidermal layer (Khan and Sinclair, 1991; Pandey *et al.*, 2021a). In bean, the biotrophic stage of *C. lindemuthianum* develops into numerous cortical and epidermal cells, whereas in cowpea this stage is always limited to a single epidermal cell (O'Connell *et al.*, 1985; Bailey *et al.*, 1990). Pathogen penetration and movement in this process most likely occur through enzymatic action. Fungal phytopathogens also transude various cell wall degrading enzymes that permit them to successfully infect plants (O'Connell *et al.*, 2012; Faisal Peeran *et al.*, 2014). For example, *Colletotrichum* species produce cellulase enzymes that catalyze the host's cell wall degradation (Anand *et al.*, 2008; Faisal Peeran *et al.*, 2014). While *C. truncatum* (Ramos *et al.*, 2010), *C. gloeosporioides* (Faisal Peeran *et al.*, 2014), and *C. lindemuthianum* (O'Connell *et al.*, 1985; Sharma *et al.*, 2007) have shown potential *in vitro* pectinolytic and cellulase activity, a significant variation in cellulase activity has been reported under field conditions (O'Connell *et al.*, 1985; Ramos *et al.*, 2010). Other enzymes produced by *Colletotrichum* species during pathogenesis include chitinase, pectinolytic enzyme, glucanase, protein kinases, and endopolygalacturonases (Anand *et al.*, 2008; Faisal Peeran *et al.*, 2014). Considering the limited information available, no conclusion can be drawn regarding the role of enzymes in *Colletotrichum* pathogenicity.

B. Toxin production

Colletotrichum species produce low molecular weight compounds called phytotoxins that may cause histological and physiological alterations in legumes. For example, hemibiotrophic infection of *Pisum sativum* by *C. truncatum* caused significant histological and physiological changes in hosts (O'Connell *et al.*, 1993). Phytotoxins produced by fungi may be host-specific (selective, non-toxic to other hosts) or non-specific (non-selective, toxic for a broader range of plant species). Hence, production of toxins is a key part of pathogenesis (Banniza *et al.*, 2018). Toxins produced by the pathogen can have unexplainable effects on pathogenesis, elicitor production, and enzymatic reactions (Katoch *et al.*, 2017). Therefore, it can be difficult to study the mechanisms of pathogenicity when these factors are interconnected (Amusa, 1994). *Colletotrichum* produces non-host-specific toxins, such as colletopyrone by *C. nicotianae* and colletotin by *C. fuscum* (Amusa, 1994). Likewise,

C. truncatum produces meso- and D (−)-butane2,3-diol, colletruncoic acid, methyl ester, and 2-hydroxymethylhexa-2,4-dienol in soybean (García-Pajón and Collado, 2003). The presence of numerous other metabolites and non-host specific compounds in culture filtrates of *C. lindemuthianum* and *C. truncatum* have been reported (Amusa, 1994). In addition, while García-Pajón and Collado (2003) also studied metabolites isolated from various *Colletotrichum* species, including *C. gloeosporioides* and *C. truncatum*, it is evident that their actual pathogenesis role in legumes remains unclear and needs resolution. Further, the role of toxins in anthracnose disease development remains poorly investigated. Parthasarathy *et al.* (2015) showed that culture filtrates of *C. gloeosporioides* produce a non-host selective toxic metabolite that shows inhibitory effects on seed germination of various crops like maize, sorghum, tobacco, tomato, and chili. Recently, using the OSMAC–metabolomics approach, Reveglia *et al.* (2023) studied secondary metabolites compounds produced by *C. truncatum* and *C. trifolii* that are accountable for phytotoxic activities in lentil, soybean, and red clover. Cultural filtrates produced colletopyrone, and higginsianin B, compounds reported to have phytotoxic and cytotoxic activities (Reveglia *et al.*, 2023). Further, colletopyrone also contributed toward discriminating between fungal pathogens, being highly produced by *C. truncatum* (Reveglia *et al.*, 2023). However, further analysis of the structure and function of the active component(s) of these toxins still needs to be investigated. Clearly, while *Colletotrichum* species can synthesize numerous toxins, their isolation, purification, and characterization need further research.

Various host-specific toxins are also produced by *Colletotrichum* species infecting legumes. For example, Liang *et al.* (2021) identified a novel host-specific pathogenicity gene *CgNPG1* of *C. gloeosporioides*. Likewise, *CgDN3*, a pathogenicity gene from *C. gloeosporioides* infecting tropical legumes, has been identified (Stephenson *et al.*, 2000). Bhadauria *et al.* (2015) identified ClToxB, a host-specific toxin in *C. truncatum* and *C. lentis* infecting lentil that is responsible for virulence differentiation, seemingly contributing quantitatively to virulence differences between *C. lentis* races 0 and 1 (Bhadauria *et al.*, 2015). This indicates that these genes encode a novel pathogenicity determinant necessary to avert a hypersensitive reaction in a compatible host during the biotrophic phase of primary infection. However, no such studies have been conducted in relation to the interaction between *C. truncatum* and *C. lindemuthianum* with other legumes like chickpea, mungbean, blackgram, common bean and peanut, and this warrants future investigation.

VII. Impact of climate change on disease development

Disease outbreaks in legumes are influenced by multiple factors. The development of virulent strains within a diverse pathogen population, weather conditions, level of resistance in host plants against emerging aggressive strains of the pathogen, uniformity of cropping system, plant architecture, and limited antagonistic activities of microbial biocontrol agents can all play a crucial and interrelated role in disease outbreaks (Pangga *et al.*, 2013). Under climate change, several previously reported minor diseases have become much more important worldwide, especially in Asian and European countries (Pande *et al.*, 2010; Pathak *et al.*, 2018; Pszczółkowska *et al.*, 2019). South Asia and southern Africa are particularly vulnerable to the effects of climate change, resulting in more severe disease in grain legumes (Bahl, 2015). Various climatic conditions affect plant disease progress, including light, temperature maxima and minima, water availability, wind speed, and concentrations of atmospheric gases, *viz.*, methane, ozone, and CO_2 (Varanasi *et al.*, 2016). These can have negative, neutral, or positive effects on disease progression, as each disease may respond differently to these agro-climatic variations (Elad and Pertot, 2014; Velásquez *et al.*, 2018). As occurs with other crop diseases, anthracnose diseases of legumes seem similarly triggered by climate change (Thomas, 2010). For instance, climate change can affect anthracnose disease complex by replacing or predominating one species within the complex by another. In lentils, *C. truncatum* was previously considered as the main anthracnose pathogen but *C. lentis* has recently predominated disease epidemics in this crop (Buchwaldt *et al.*, 2018).

Plant resistance traits may be affected in a positive or negative way by climate change. Elevated CO_2 coupled with elevated temperatures and humidity increased anthracnose incidence in shrubby *Stylosanthes* in Australia (Pangga *et al.*, 2004) and in chickpea in India (Sharma *et al.*, 2011). Further, Sozen and Karadavut (2018) reported anthracnose emergence and epidemic development, especially with heavy spring rains, led to huge production losses of chickpea in Turkey. In 2019, a field survey conducted by Girma

et al. (2022) to determine anthracnose epidemics in major common bean-growing areas of Ethiopia highlighted that anthracnose intensity was strongly influenced by regional zone and by altitude (i.e., by differences in rainfall, temperature, and humidity) emphasizing a need for climate change resilient agronomic practices. Climate change can alter host tolerance and/or resistance with consequent heightened risk of more serious epidemic development and greater crop losses. For example, in Australia, Thomas *et al.* (2008) reported that Wanga, a resistant cv. of lupin, became susceptible to anthracnose when the temperature increased from 12 to 18 °C and again increased further at 26 °C. White lupin resistant Australian genotype P27174 was susceptible when cultivated in Switzerland, putatively due to difference in growing conditions (higher temperature in Switzerland, where lupin is sown as a spring crop as compared to Australia, where lupin is sown as a winter crop (Alkemade *et al.*, 2021a). Similarly, mungbean genotype VI000203 B-Br found anthracnose-resistant in 2016 and 2017, became susceptible in 2018 possibly due to increased temperature (Pandey *et al.*, 2021a). The anthracnose severity of mungbean and blackgram in India increased with an increase in temperature and relative humidity whereas rainfall had little effect (Kulkarni, 2019; Gupta, 2021; Pandey *et al.*, 2021a). Likewise, increased soybean anthracnose severity was related to an increase in temperature and relative humidity in India (Nataraj *et al.*, 2020), Brazil (Júnior *et al.*, 2021), and Argentina (Dias *et al.*, 2019). Similarly, elevated temperature and relative humidity significantly reduced lentil production in Canada (Buchwaldt *et al.*, 2018), common bean production in Africa (Mukankusi *et al.*, 2019), and cowpea production in Nigeria (Falade and Borisade, 2018), in each case a consequence of increased anthracnose severity. Climate change not only alters disease epidemics and associated host resistance responses, but fosters emergence of new pathotypes, ultimately leading to changes in disease management practices (Boadi and Owusu, 2019), as discussed further in the following section. Due to all these factors, it is difficult to speculate on future effects of climate change, particularly when the long-term datasets from the past needed to develop and test predictive models for the future are lacking (Lamichhane *et al.*, 2015). However, there is growing interest in studies on the temperature requirements of *Colletotrichum* spp., as reflected by an increase in the number of papers published per year evaluating the effect of temperature on mycelial growth, conidial germination, conidial infection, and sporulation (Salotti *et al.*, 2022).

VIII. Integrated management of legume anthracnose

As for all disease complexes, a single solution to a single problem, as used in the past, generally has not been an effective approach for sustainable anthracnose management. Several potential non-genetic approaches are used for legume anthracnose management, but these strategies individually are not anticipated to offer sustainable disease management in the future, for the reasons as discussed below. For effective anthracnose management in legumes, it needs to be based on the principles of integrated disease management (Barzman *et al.*, 2015; Pandey *et al.*, 2018) and agroecological crop protection (Deguine *et al.*, 2023) by combing all available levers.

A. Cultural practices

This method aims to reduce or even eliminate the introduction of pathogen inoculum from nearby disease infected fields, minimize the rate of infection, and generate unfavorable conditions for disease spread and development (Mohammed, 2013). As the pathogen is seed-borne, hot water emersion treatment at 52–55 °C is efficient in reducing seed-borne anthracnose in mungbean, blackgram, and white lupin (Rana *et al.*, 2016; Pandey *et al.*, 2018; Alkemade *et al.*, 2022a). Unfortunately, hot water treatment also reduces seed germination and viability limiting the possibility of its adoption for anthracnose management. Alkemade *et al.* (2022a) reported that vinegar may also reduce white lupin anthracnose incidence under on-farm field conditions. Another cultural practice is soil solarization that, to some extent, can reduce the incidence of common bean anthracnose given the soilborne nature of the pathogen (Yousef, 2021). However, some *Colletotrichum* species, such as *C. dematium*, *C. gloeosporioides*, *C. truncatum*, and *C. destructivum* are likely to survive at temperatures higher than those achieved with soil solarization (Pandey *et al.*, 2018; Salotti *et al.*, 2022). However, soil solarization is not practical for large broadacre cropping situations. Other specific cultural practices used to manage legume anthracnose include crop rotation with a non-host crop, sowing of non-infected seeds, and reducing and/or eliminating sources of anthracnose from infected crop debris in which pathogen survives during winter and subsequently produce massive amounts of spores at the beginning of a new growing season (Mohammed, 2013). Failure to reduce/eliminate infected crop debris greatly increases the risk of

serious anthracnose epidemics in nearby leguminous crops in the subsequent year.

B. Use of synthetic fungicides

Applications of synthetic fungicides are the most common approach for the management of fungal diseases in legumes (Pandey *et al.*, 2018). Traditionally, broad-spectrum fungicides have been used in legumes as seed treatments and foliar sprays to manage diseases (Lamichhane *et al.*, 2020). Both protectant and systemic fungicides have been included in chemical management. Systemic fungicides are applied before or during disease development, whereas protectant fungicides are applied before or during disease initiation. Currently, legume anthracnose is controlled by a mixture of fungicides designed to slow its progression. Fungicides commonly used as prophylactic treatments to control mungbean, blackgram, soybean, and beans anthracnose include methyl benzimidazole carbamate fungicides, such as carbendazim and thiophanate-methyl, that inhibit mitosis (β-tubulin assembly) in fungi, inhibiting their further growth and multiplication (Gupta *et al.*, 2005; Mohammed 2013; Kale and Barhate, 2016; Kumar *et al.*, 2020; Chatak and Banyal, 2021).

A mixture of fungicides is often used in-field as foliar sprays to slow the anthracnose progress in legumes, including beans (Mohammed, 2013; Sileshi *et al.*, 2014; Ayana and Fininsa, 2018), mungbean (Chaudhari and Gohel, 2016; Jaiganesh *et al.*, 2019; Kulkarni 2019; Misal *et al.*, 2019), soybean (Kale and Barhate, 2016; Subedi *et al.*, 2016), blackgram (Kumar *et al.*, 2020; Chatak and Banyal, 2021), common bean (Amin *et al.*, 2014), and chickpea (Benzohra *et al.*, 2020). These include various combinations of fungicides like methyl benzimidazole carbamate, demethylation inhibitors, such as triazoles, dithiocarbamates, such as mancozeb, and quinone outside inhibitors, such as azoxystrobin. However, unfortunately multiple fungicide resistance in *C. truncatum* (Poti *et al.*, 2020; Shi *et al.* 2021a), *C. gloeosporioides* (Han *et al.*, 2018), and *C. lindemuthianum* (Lokya Naik and Anilkumar, 1991) populations appeared as early as 1991. In natural populations of *Colletotrichum* species, resistance to fungicides is controlled by a single, incompletely dominant gene present at a low level. Other limits of synthetic fungicides include their relatively high costs, toxicity to human health and the environment, and the need for their application at the right time (Mishra *et al.*, 2018). Fortunately, fungicide application rates and frequency can be significantly reduced by using cultivar resistance or tolerance if available, especially where combined with accurate disease forecasting to ensure the best timing of application (Pandey *et al.*, 2018).

C. Use of natural agents

Biological seed treatment is one of the sustainable levers to improve legumes productivity. A recent global meta-analysis showed that the yield gain potential due to biological seed treatment is higher in legumes compared to other field crops (Lamichhane *et al.*, 2022). Combinations of different biological agents have shown the most promise in legume anthracnose management (Kumar *et al.*, 2016). For example, seeds inoculated with *Trichoderma* species and *Pseudomonas fluorescens* reduced anthracnose incidence in-field by up to 80% in common bean (Amin *et al.*, 2014; Sileshi *et al.*, 2014) and blackgram (Chatak and Banyal, 2021). Similarly, biological control of three *C. lindemuthianum* races has been reported using *P. chlororaphis* with *P. fluorescens* (Bardas *et al.*, 2009). Combined *Rhizobium leguminosarum* RPN5 + *Bacillus* sp. BPR7 + *Pseudomonas* sp. PPR8 has shown potential against a *Colletotrichum* sp. associated with anthracnose in common bean (Kumar *et al.*, 2016). Foliar application of *Trichoderma* biocides also reduced anthracnose severity in soybean (Kale and Barhate, 2016), common bean (Padder *et al.*, 2010; Amin *et al.*, 2014), and cowpea (Adebanjo and Bankole, 2004) by up to 75%. The critical approaches needed for developing plant growth promoting rhizobacteria mixtures with improved biocontrol efficacy and stability under field conditions have been recently highlighted (Wang *et al.*, 2021). Although *Serratia marcescens* has proved a promising against *C. lindemuthianum*, its validation under field conditions is required before recommendation (Papitha *et al.*, 2020). Furthermore, aqueous extract of *Lawsonia inermis* L. (Kale and Barhate, 2016), *Melia azedarach* L. (Sharma *et al.*, 2022), and *Eucalyptus* sp. (Chatak and Banyal, 2021) reduced anthracnose severity in soybean, bean, and blackgram up to 75–80%. Nevertheless, while low field efficacy and inconsistency have generally limited the adoption of microbial agents and natural products by legume growers, these constraints should be overcome in the future. Overall, next generation "fungicides" including those derived from active ingredients of plants offer significant potential toward more ecologically safe, efficient and minimal dose beneficial possibilities in combatting legume anthracnose diseases.

IX. Genetic approaches for anthracnose management

Reducing economic losses in legumes due to anthracnose through developing resistant cultivars offers the most cost-effective and efficient long term mitigation strategy (Boufleur *et al.*, 2020). Several genetic approaches have been used to develop legume varieties resistant to anthracnose.

A. Search for genetic sources of resistance

Methods available for screening of legume germplasm against anthracnose include detached leaves, various glasshouse/greenhouse artificial inoculation methodologies, and evaluation under natural disease pressure. Disease screening can be particularly successful under field conditions with high disease pressure, or artificial inoculation with virulent pathogen isolates. Relative disease severities using these screening methods have been assessed using qualitative and quantitative disease rating scales (Pandey *et al.*, 2021a).

The sources of genetic resistance identified against anthracnose in legumes are presented in Table 2. Anthracnose resistance in legumes has been identified mainly in cowpea, lentil, mungbean, lupins, blackgram, common bean, and soybean. However, research on sources of genetic resistance to anthracnose associated with chickpea, peanut, and pigeon pea has not yet been performed. Field/bush types of cowpeas have various levels of resistance to anthracnose compared to the vegetable/trailing types that are highly susceptible (Pradhan *et al.*, 2018). Anthracnose resistant sources in cowpea were mainly from Nigeria and India and were also resistant against multiple foliar diseases, including Cercospora leaf spot, rust, bacterial pustule, and target spot (Williams, 1977). Cowpea genotype, IAR7/180-4-5 was also resistant against scab, and bacterial blight (Adebitan and Olufajo, 1998).

Sources of anthracnose resistance in mungbean and blackgram were mostly identified from India (Table 2). In contrast, no breeding programs for varieties resistance to anthracnose were developed in other blackgram producing countries, such as Pakistan or Myanmar, despite large yield losses reported in these countries from *Colletotrichum* species. In such situations, the deployment of resistant varieties would greatly reduce production costs and allow reduced reliance on synthetic fungicides (Talhinhas *et al.*, 2016). Therefore, the genetic diversity of mungbean presents significant opportunities for identifying anthracnose resistance sources within breeding programs. In the case of lentils, most screening programs have been conducted in Canada against specific and multiple races of *Colletotrichum*. Although India is the second largest lentil producer, its breeding program has not focused on anthracnose resistance. Perhaps this is due to anthracnose being a disease of relatively minor concern in India (Roy *et al.*, 2022).

Few studies have been undertaken to identify sources of resistance to soybean. By inoculating 16 soybean accessions with *C. truncatum* isolates in Brazil, Dias *et al.* (2019) found that while some soybean accessions had a high level of resistance in stems these same lines were highly susceptible to cotyledon infection. They hypothesized that stems and cotyledons likely had distinctly different genetic resistances with independent mechanisms of resistance. While different searches for sources of resistance in soybean against *C. truncatum* have been conducted (Costa *et al.*, 2009; Nagaraj *et al.*, 2014; Yang and Hartman, 2015; Dias *et al.*, 2019), there has been no research to date on sources of resistance against other *Colletotrichum* species associated with soybean anthracnose. In contrast, many studies have been carried out to identify race specific sources of anthracnose resistance in common bean worldwide (Table 2). These genotypes represent significant potential donors of resistance genes in marker-assisted selection programs for transferring anthracnose resistance gene(s) into agronomically desirable susceptible genotypes.

Lupins offer great potential as an alternative protein source to soybeans since they have a similar protein content and better digestibility (Lucas *et al.*, 2015). In Australia, New Zealand, Chile, and Germany, breeding efforts for lupins anthracnose resistance have been primarily conducted in the field (Cowling *et al.*, 2000; Adhikari *et al.*, 2009; Baer *et al.*, 2009; Jacob *et al.*, 2017). These efforts have identified anthracnose resistant genotypes, namely Ethiopian landraces P27174 and P27175 (Cowling *et al.*, 2000; Adhikari *et al.*, 2009). These two Ethiopian landraces form a distinct genetic group within white lupin (Raman *et al.*, 2014). An F3-derived single-plant selection of a cross between an anthracnose-resistant landrace P27175 from Ethiopia and a well-adapted but highly susceptible Western Australian breeding line 89B10A-14 has led to the development of anthracnose resistant commercial white lupin cultivars. While studying anthracnose resistance in white lupin, Alkemade *et al.* (2021a) found that under controlled conditions, stem inoculation-based disease phenotyping is a time-effective and appropriate method to identify field-relevant resistance. Further identification

Table 2. Resistant genotypes of legumes against anthracnose.*)

Legumes	Pathogens	Investigators	Country	No. of genotypes evaluated	Anthracnose resistant genotypes#)
Blackgram	*Colletotrichum truncatum*	Basandrai *et al.*, (1999)	India	100	TEU95-1, UPU95-1, P44, KU305, WVG110, Pusa3, and UPU91-7
Blackgram	*C. truncatum*	Basandrai *et al.*, (2003)	India	250	LU 1129, PLU 117.PLU 1077, UG 218, UG 786, UG 1120, HPBU 16, HPBU 124, UG 937, LU 6, LU 27, LU 89, UG 331, UG 353, UG 697, UG 931, LU 1125, LU 5-2, LU 1014, PU 19, PLU 791, and UL 251
Blackgram	*C. truncatum*	Sharma *et al.*, (2014)	India	240	44
Blackgram	*C. truncatum*	Kaushal and Singh, (1988)	India	48	13
Blackgram	*C. truncatum*	Aggarwal *et al.*, (2019)	India	–	PU-30 and PU-31 MDR
Common bean	*C. lindemuthianum*	Méndez-Vigo *et al.*, (2005)	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
Common bean	*C. lindemuthianum*	Alzate-Marin *et al.*, (1997); Gonçalves-Vidigal *et al.*, (2013)	Brazil	–	Ouro Negro (Honduras 35), a Meso-American common bean that contains a *Co-10* resistant gene
Common bean	*C. lindemuthianum*	Campa *et al.*, (2009)	Spain	–	TU (resistant to races, 3, 6, 7, 31, 38, 39, 102, and 449) and Michigan Dark Red Kidney (MDRK) (resistant to races, 449, and 1545)
Common bean	*C. lindemuthianum*	Campa *et al.*, (2011)	Spain	–	Kaboon against above eight anthracnose races
Common bean	*C. lindemuthianum*	Alzate-Marin *et al.*, (2007)	Brazil	–	Tlalnepantla 64 (PI 207262)
Common bean	*C. lindemuthianum*	Alzate-Marin *et al.*, (2007); Gonçalves-Vidigal and Kelly, (2006)	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* (Mexico 222), *Co-4* (TO), *Co-42* (SEL 1308), *Co-5* (SEL1360), *Co-6* (AB 136),
Common bean	*C. lindemuthianum*	Alzate-Marin *et al.*, (2001)	Brazil	–	G2333 was demonstrated to possess resistance against 14 specific races
Common bean	*C. lindemuthianum*	Young *et al.*, (1998)	USA, Brazil	–	SEL1360, SEL 1308 derived from G2333), K13, K10, BRS Esteio, and Widusa
Common bean	*C. lindemuthianum*	Lima Castro *et al.*, (2017)	Brazil	–	The Andean cultivar, Paloma was resistant to Mesoamerican and Andean races
Common bean	*C. lindemuthianum*	Chen *et al.*, (2017)	China	–	Andean cultivars Hongyundou
Common bean	*C. lindemuthianum*	Gonçalves-Vidigal *et al.*, (2020)	Brazil	–	CDRK
Common bean	*C. lindemuthianum*	Gonçalves-Vidigal *et al.*, (2016)	Brazil	–	Pitanga (*Co-14*)
Common bean	*C. lindemuthianum*	Gonçalves-Vidigal *et al.*, (2007)	Brazil	–	Michelite (*Co-11*)
Common bean	*C. lindemuthianum*	Lacanallo and Gonçalves-Vidigal, (2015)	Brazil	–	Jalo Listras Pretas landrace (*Co-11*)
Common bean	*C. lindemuthianum*	Zuiderveen, (2015)	Tanzania	226 Andean Diversity Panel	28 lines were resistant against six races, and Uyole98, a yellow bean variety was resistant against all the eight races
Common bean	*C. lindemuthianum*	Hegay *et al.*, (2014)	Kyrgyzstan	–	Vaillant and Flagrano carrying the *Co-2* gene resistance to races 23 and 102 of pathogen
Common bean	*C. lindemuthianum*	Vazin *et al.*, (2015)	Canada	–	Bolt
Common bean	*C. lindemuthianum*	Coimbra-Gonçalves *et al.*, (2016)	Brazil	–	Crioulo 159, Awauna UEM, Flor Diniz UEM, Pitanga, and Corinthiano
Common bean	*C. lindemuthianum*	Costa Lara Fioreze *et al.*, (2018)	Brazil	–	Ten lines had moderate/resistant landraces
Common bean	*C. lindemuthianum*	Marcon *et al.*, (2020)	Brazil	–	Beija Flor
Common bean	*C. lindemuthianum*	Almeida *et al.*, (2021)	Brazil	–	18 Mesoamerican accessions were resistant
Common bean	*C. lindemuthianum*	Banoo *et al.*, (2020)	India	188	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.
Common bean	*C. lindemuthianum*	Gupta *et al.*, (2021)	India	87	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
Common bean	*C. lindemuthianum*	Palacıoğlu *et al.*, (2021)	Turkey	–	Zulbiye, Akin, Onceler, and Karacasehir 90

(*Continued*)

Table 2. Continued

Cowpea	*Colletotrichum lindemuthianum*	Williams, (1977)	Nigeria	5,000	28 lines
Cowpea	*C. lindemuthianum*	Amusa, (1994)	Nigeria	14	5 MDR
Cowpea	*C. lindemuthianum*	Adebitan and Olufajo, (1998)	Nigeria	12 varieties	IAR7/180-4-5
Cowpea	*C. lindemuthianum*	Ganesh *et al.*, (2022)	India	–	VBN3
Cowpea	*C. lindemuthianum*	Shiny *et al.*, (2015)	India	–	Arimbra local
Cowpea	*C. lindemuthianum*	Pradhan *et al.*, (2018)	India	–	Kanakamony
Lentil	*C. lentis*	Barilli *et al.*, (2020)	Spain	250	PI572330, PI572334, and PI572338
Lentil	*C. lentis*	Bawa *et al.*, (2022)	Canada		LR-66-528, a RIL
Lentil	*C. lentis*	Tullu *et al.*, (2006); Fiala *et al.*, (2009); Bhadauria *et al.*, (2017b); Gela *et al.*, (2020)	Canada	–	L-01-8271A, LR-59-81, and IG72815 against multiple races of pathogen
Lentil	*C. lentis*	Buchwaldt *et al.*, (2004)	USA and Germany	1,771	16 accessions were resistant
Lentil	*C. lentis*	Vandenberg *et al.*, (2002)	USA and Germany	–	Partial resistance: CDC Robin, CDC Redberry: Resistant
Lentil	*C. lentis*	Gela *et al.*, (2021a)	Canada	–	LR-01 (ILL 1704 × CDC Robin) and LR-18 (CDC Robin × 964a-46) resistant to race 1
Lentil	*C. lentis*	Shaikh *et al.*, (2013)	Canada	–	VIR-2633 resistant to both races
Lentil	*C. lentis*	Gela *et al.*, (2020), (2021b)	Canada	–	Few sublines (12) of VIR-2633 possess resistance to race 1 but not race 0
White lupin	*C. lupini*	Adhikari *et al.*, (2009); Cowling *et al.*, (2000)	Australia	–	P27174 and P27175 in the Ethiopian landraces
White lupin	*C. lupini*	Alkemade *et al.*, (2021a)	Germany and Switzerland	40	Leb01, Eth01, Ares, NL01, Blu-25, Frieda, Eth02, and Kiev Mutant
Narrow-leafed lupin	*C. lupini*	Yang *et al.*, (2004)	Australia	–	Tanjil, Wonga, 83A:476 (gene Lanr1)
		Yang *et al.*, (2008)	Australia	–	Mandelup (gene *AnMan*)
		Fischer *et al.*, (2015)	Germany	–	Bo7212 (gene *LanrBo*)
White lupin	*C. lupini*	Alkemade *et al.*, (2022b)	Switzerland	–	Rumbo Baer
Yellow lupin	*C. lupini*	Lichtin *et al.*, (2020)	Chile	–	Core 98 (PI385149)
		Adhikari *et al.*, (2011)	Australia	–	Several lines
Mungbean	*C. truncatum*	Bhattacharjee and Bhattacharjee, (2019); Kulkarni et al. (2009)	India	101	42
Mungbean	*C. truncatum*	Kulkarni, (2009)	India	30	TARM-18 and TM-96-2
Mungbean	*C. truncatum*	Kaur *et al.*, (2011)	India	–	ML1464, 1486, 1349, and 1194
Mungbean	*C. truncatum*	Marak *et al.*, (2018)	India	41	TARM-18, CZNK-1, PM-D5, and Sukumar 34 MDR
Mungbean	*C. truncatum*	Pandey *et al.*, (2021a)	India	296	MC-24, MC-51, MC-127, MC-207, MC-208, and MC-292
Soybean	*C. truncatum*	Amusa *et al.*, (1994)	India	14	PI-17144 and TGM236
Soybean	*C. truncatum*	Nataraj *et al.*, (2020)	India	225	EC538828, EC34372, EC4572541, AKSS67, and Karune-HR and 21 resistant genotypes
Soybean	*C. truncatum*	Dias *et al.*, (2019)	Brazil	16	BRS Pintado and W877
Soybean	*C. truncatum*	Costa *et al.*, (2009)	Brazil	48	Tabarana, Cometa, and Emgopa 316 were susceptible and remaining were resistant
Soybean	*C. truncatum*	Bhatt *et al.*, (2022)	India	40	None of the genotypes were resistant, Shivalik, JS 9305, and JS 335 were susceptible
Soybean	*C. truncatum*	Yang and Hartman, (2015)	USA	15	Mandarin
Soybean	*C. truncatum*	Yang and Hartman, (2015)	USA	28	Mandarin 507

*Most of the trials were conducted under natural disease pressure, except few in greenhouse/detached leaf method (Alkemade *et al.*, (2021a)).
#Genotypes includes cultivars, landraces, wild relatives, breeding lines, mutant lines, and germplasm.

of resistance sources and their genetic components can now be achieved using this approach. However, blue lupin cultivars, such as Tanjil and Mandelup with strong anthracnose resistance under Australian conditions (Yang *et al.*, 2008) proved susceptible in Germany (Fischer *et al.*, 2015). Expression of plant resistance can vary widely across different inoculation methods, from environmental variation, and from difference in *C. lupini* strain-specific virulence (Rychel-Bielska *et al.*, 2020). Further, variations in disease response in lupins and other legumes depend on several factors, including the source of pathogen isolation and virulence on different genotypes, and/or the nature of host resistance itself including whether it is governed by single or multiple genes.

B. Inheritance studies and genetic mapping

Studies on anthracnose inheritance have mainly focused on cowpea and common bean with much lower emphasis on lentil, blackgram, soybean, lupin and there have not been any studies on mungbean, chickpea, peanut, or pigeon pea. In general, anthracnose resistance in legumes is not governed by gene-for-gene hypothesis of qualitative/vertical resistance (Flor, 1971) where host resistance specificity is determined by the respective host *R* gene and pathogen *avr* gene interactions. Furthermore, anthracnose resistance in legumes has not been associated with a hypersensitive response. Rather, legume anthracnose is considered a complex quantitative trait controlled by multiple gene interactions that are highly influenced by environmental factors (Pradhan *et al.*, 2018).

1. Cowpea, blackgram, and soybean

In cowpea, only one study showed that resistance is either dominant or polygenic in nature (Pradhan *et al.*, 2018). A RAPD marker, OPAO2, and two ISSR markers (UBC810 and UBC811) co-segregated with anthracnose resistance genes in cowpea (Pradhan *et al.*, 2018). In blackgram, resistance was controlled by a single dominant gene which was non-allelic (Kaushal and Singh, 1988; Bindra *et al.*, 2016). Resistance to soybean anthracnose was governed by two major genes that interact in a complementary way (Nataraj *et al.*, 2020). Transgenic soybean plants expressing the *NmDef02* defensin gene were reported as having enhanced resistance against *C. truncatum* (Soto *et al.*, 2020).

2. Common bean and lentil

In lentil, resistance to race 1 and race 0 of *C. lentis* was polygenic or oligogenic in nature (Bhadauria *et al.*, 2017a). In common bean, most of the genes resistant to anthracnose are dominant except the *Co-8* gene which is recessive (Kelly and Vallejo, 2004; Gonçalves-Vidigal *et al.*, 2020). Over 20 anthracnose-independent resistance genes with multiple loci belonging to either the Mesoamerican or Andean gene pools have been identified in common bean (Vidigal Filho *et al.*, 2020). The genes/QTLs and/or markers associated with anthracnose resistance in lentil and common bean have been summarized in Table 3. A few partially dominant genes (*1-3*) with an additive gene action conditioning resistance to anthracnose were also reported (Nkalubo, 2006). In a resistant cultivar JaloEEP558, an additional gene (*KTR2/3*) in the *Co-x* locus confers anthracnose resistance (Richard *et al.*, 2021) as this gene encodes a truncated and chimeric CRINKLY4 kinase (CR4) located within a CRINKLY kinase cluster and its expression in leaves occurs following pathogen infection (Richard *et al.*, 2018).

Several single nucleotide polymorphisms (SNPs) associated with anthracnose resistance to races 3, 87, and 503 were located on Pv04 that encode leucine-rich repeat (LRR) and have typical NB-ARC domains (Banoo *et al.*, 2020). A gene, *Phvul.004G023900* encodes a methyltransferase for quantitative resistance against race 503 of pathogen on Chromosome (Chr) Pv04. Another SNP for resistance to race 503 was found on Chr Pv09 within gene model *Phvul.009G169600*, which encodes a zinc finger protein (Banoo *et al.*, 2020). Quantitative resistance loci (QRLs) linked with race 73 were reported on linkage group Pv08 overlapping with the *Co-4* gene. Additionally, the SNP within the gene *Phvul.011G202300*, which encodes a LRR within the NB-ARC domain, is also associated with resistance to race 73. For race 2047, different genomic regions on linkage groups Pv03, Pv09, and Pv11 were found to be linked with resistance in common bean (Banoo *et al.*, 2020).

In the Andean Diversity Panel (ADP), major QTLs for anthracnose resistance were discovered on linkage groups Pv01 (races 65, 73, and 3481), Pv02 (races 39 and 55), and Pv04 (races 7, 109) and minor QTLs on Pv10 (race 7) and Pv11 (race 7) (Zuiderveen, 2015). Resistance on linkage group Pv01 to aforesaid races was associated with SNP ss715645251 within the gene *Phvul.001G243800*, which encodes for a LRR receptor-like protein kinase. On linkage group Pv02, resistance was significantly associated with SNP ss715648451

Table 3. Anthracnose related QTLs/markers in common bean and lentil.

Gene/QTL	Markers	Linkage group	References
Lentil			
Ctr1, Ctr2, CtR3, CtR4, and *CtR5*	–	–	Fiala *et al.*, (2009); Buchwaldt *et al.*, (2013); Gela *et al.*, (2021a)
LCt-2	$OPEO6_{1250}$, UBC-704_{700}, $EMCTAAAG_{175}$, $EMCTTAGG_{375}$, and $EMCTTACA_{350}$	–	Tar'an *et al.*, (2003); Tullu *et al.*, (2003)
ANTH0-5.1	Lc23518	5	Bawa *et al.*, (2022)
qANTH0-2	Lc09295	2	Bawa *et al.*, (2022)
qANTH0-2	Contig354334p19115	2	Bhadauria *et al.*, (2017b)
qANTH0-3	Contig119649p37483		
qANTH0-5.1	Contig27270p11193	5	
qANTH0-5.2	Contig23853p125770	5	
qANTH0-7	Contig454980p46332	7	
qANTH1-2.1	Contig31239p30315	2	
qANTH1-2.2	Contig54235p29611	2	
qANTH1-3.1	Contig177849p8723	3	
qANTH1-3.2	Contig142466p23623	3	
qANTH1-5.1	Contig590995p19537	5	
qANTH1-5.2	Contig141093p18277	5	
qAnt1.Lc-3	Lcu.2RBY.Chr3.33827173, Lcu.2RBY.Chr3.33827185, Lcu.2RBY.Chr3.34117023, Lcu.2RBY.Chr3.35384298, Lcu.2RBY.Chr3.341261994, Lcu.2RBY.Chr3.417940994	3	Gela *et al.*, (2021b)
qANTH-3	Lcu.2RBY.Chr3_308775097	3	Gela *et al.*, (2021a)
qANTH-7	Lcu.2RBY. Chr7_521279838	7	
Common bean			
Co-1 (Co-1^2, Co-1^3, Co-1^4, Co-1^{HY})	$OF10_{530}$, SE_{ACT}/M_{CCA}, TF1/Clp-N1, PvSNP8p1922017/ PvSNP8p1574781, TGA1.1, ATA3, ATA03, PvM97, CV542014	B1	Young and Kelly, (1997); Kelly and Vallejo, (2004); Gonçalves-Vidigal *et al.*, (2011); Trabanco *et al.*, (2015); Vazin *et al.*, (2015); Chen *et al.*, (2017); Mahiya-Farooq *et al.*, (2019)
Co-u	NDSU_IND_2_40.3966, NDSU_IND_2_ 40.4411, *I* gene, SW13	B2	Melotto *et al.*, (1996); Geffroy *et al.*, (2008); Trabanco *et al.*, (2015)
Co-2	PV-ag001, $OQ4_{1440}$, $B355_{1000}$, SCH20, SCAreoli, $OH13_{480}$, SH13b	B11	Adam-Blondon *et al.*, (1994); Young and Kelly, (1996); Geffroy *et al.*, (1999); Rodríguez-Suárez *et al.*, (2008); Trabanco *et al.*, (2015)
Co-3/9	SW12, g1375, SB12, Pv-ctt001, ss715649427/ss715642306, SB10, BM161, $OAH18_{1100/600}$, SB12	B4	Méndez-Vigo *et al.*, (2005); Campa *et al.*, (2009), (2011); Trabanco *et al.*, (2015); Almeida *et al.*, (2021)
Co-4^2	OH 18, OBB14, SHI8, SBB14, SAS13, $OPY20_{830}$, SY20	B8	Young *et al.*, (1998); Trabanco *et al.*, (2015)
Co-5	SAB3, $OAB3_{450}$, BM210, SCARAZ20, g1233, Phs	B7	Young and Kelly, (1997); Campa *et al.*, (2009); Sousa *et al.*, (2015)
Co-6	$OAH1_{780}$, $OAK20_{890}$	B7	Young and Kelly, (1997)
Co-v	–	B7	Meziadi *et al.*, (2016)
Co-8	OPAZ20	–	Alzate-Marin *et al.*, (2001)
Co-3 and Co-3 2	–	B4	David *et al.*, (2008)
Co-10	F10, g2303	B4	Gonçalves-Vidigal *et al.*, (2013)
Co-13	OPV20680	B3	Gonçalves-Vidigal *et al.*, (2008); Trabanco *et al.*, (2015)
Co-15	–	B4	Sousa *et al.*, (2015)
Co-16	$g2467_{900/800}$	B4	Coimbra-Gonçalves *et al.*, (2016)
Co-y	–	B4	Geffroy *et al.*, (1999)
Co-z	–	B4	Geffroy *et al.*, (1999)
Co-17	–	B3	Trabanco *et al.*, (2015)
CoPv01^{CDRK}/PhgPv01^{CDRK}	ss715645251/ss715645248	B1	Gonçalves-Vidigal *et al.*, (2020)
Co-Pa	SS82/SS83	B1	Lima Castro *et al.*, (2017)
Co-14	–	B1	Gonçalves-Vidigal *et al.*, 2015
Co-w	–	B1	Geffroy *et al.*, (2008)
Co-x	–	B1	Geffroy *et al.*, (2008)
CoPv02	–	B2	Kelly and Vallejo, (2004); Geffroy *et al.*, (2008)
Co-AC	SS102/SS165	B1	Gilio *et al.*, (2020)

within gene *Phvul.002G328300* which encodes a mitogen-activated protein kinase (MAPK). On linkage group Pv04, resistance was associated with SNPs ss715642306 (within gene *Phvul.004G005800*) and ss715649432 (within gene *Phvul.004G006300*), respectively. Both genes encode for cytochrome P450. The minor QTLs on Pv10 (race 7) for moderate resistance were linked to SNP ss715648754 within gene

Phvul.010G025500, and on linkage group Pv11 (race 7) resistance was linked to SNP ss715645476 within gene *Phvul.011G021500* (Zuiderveen, 2015). More recently, using recombinant inbred lines derived from Ruda × AND277 crossing, Lima *et al.* (2023) mapped *Co-1*^{4} allele in the cultivar AND277 using markers ss715645251 and BARCPVSSR01356 and reported two resistant genes, namely *Phvul.001G243800* and *Phvul.001G243900* within *Co-1*^{4}. Therefore, the linkage between *Co-1*^{4} allele and markers ss715645351 and BARCPVSSR01356 will be essential for plant breeding programs to enable resistance genes to be transferred to elite cultivars via marker-assisted selection. Identifying and functionally analyzing candidate resistance genes in this region will help to develop accurate markers for anthracnose resistance, allowing for more efficient marker-assisted selection (Garzón *et al.*, 2007; Ferreira *et al.*, 2013; Vieira *et al.*, 2018).

SNPs or SSRs (simple-sequence repeat) markers were discovered using genome wide association studies (GWAS) on 10 common bean chromosomes associated with anthracnose resistance (Perseguini *et al.*, 2016; Zuiderveen *et al.*, 2016). Using NBS (nucleotide-binding site)-SSR markers, Wu *et al.* (2017) identified nine disease resistance loci for anthracnose, of which NSSR73, NSSR24, and NSSR265 were located at new Chr regions for anthracnose resistance. In addition, two markers NSSR271 and NSSR281 located on Chr 11, and NSSR24 on Chr 2 linked with resistance against anthracnose. Among these associated markers, in previous studies, NSSR65, NSSR8, NSSR234, NSSR117, NSSR281, and NSSR271 discovered for anthracnose resistance may be located at the same regions of the Chr (Campa *et al.*, 2014; González *et al.*, 2015; Perseguini *et al.*, 2016; Zuiderveen *et al.*, 2016).

In a meta-QTL (MQTL) investigation, information is assembled from numerous studies, and the confidence intervals are narrowed and better correlated with the results of individual studies. In several crops, MQTL analyses have been conducted for several traits, such as yield-related traits. In common bean, Shafi *et al.* (2022) identified 11 MQTLs located in Chr 06, and 10 hotspots QTLs each including many QTLs from a specific study on Chr 07 against anthracnose. The same study identified 1,251 genes, including multiple *R* genes, such as those encoding for protein kinases and NBS-LRR domain-containing proteins, and various other defense related genes (Shafi *et al.*, 2022). These MQTLs, hotspot QTLs, and potential candidate genes can be useful in marker-assisted breeding programs of common bean, in gene mapping, and in cloning of anthracnose resistance genomic regions.

3. Lupins

Inheritance studies involving lupin have been mainly conducted in Europe and Australia. Resistance is controlled by polygenic factors in a recombinant inbred line population of between P27174 and the susceptible cultivar Kiev Mutant (Phan *et al.*, 2007; Yang *et al.*, 2010). A similar case was reported for yellow lupin (Adhikari *et al.*, 2011), while anthracnose resistance in blue lupin is governed by single dominant genes *LanrBo*, *Lanr1*, and *AnMan* (Yang *et al.*, 2004, 2008; Fischer *et al.*, 2015). The development of resistant cultivars was facilitated through marker-assisted selection using *AnManM1* [later improved with Restriction-site Associated DNA (RAD) markers that are tightly linked to *Larn1*] (Yang *et al.*, 2008). This *AnManM1* marker is now being used for marker-assisted selection in the Australian lupin breeding program. Further, another anthracnose resistance gene, *Llur*, in yellow lupin has been reported (Haase and Ruge-Wehling, 2019). Based on linkage groups ALB10 (LG2), ALB02 (LG4), and ALB04 (LG17), QTL mapping of the recombinant inbred line population between P27174 and Kiev Mutant revealed three QTLs, antr04/05_1, antr04/05_2, and antr05_3, associated with resistance to anthracnose, which together accounted for 49% of the phenotypic variation observed in Western Australia in 2004 and 2005 (Phan *et al.*, 2007; Yang *et al.*, 2010).

With greater precision, using many SNP markers, Książkiewicz *et al.* (2017) identified the same QTLs from genotyping-by-sequencing (Elshire *et al.*, 2011). Even though white lupin and blue lupin share high synteny, anthracnose resistance QTLs in white lupin did not match with those in blue lupin (Książkiewicz *et al.*, 2017). In addition to facilitating QTL mapping, genotyping-by-sequencing provided many markers that could be used for genomic selection. This is a method for constructing a statistical model of phenotypic and genotypic data of representative populations to envisage breeding ethos for a trait (polygenic) found in genetic resources/inbred lines (Heffner *et al.*, 2009). According to a genomic prediction model, based on recombinant inbred line populations used to identify major QTLs, anthracnose resistance was predicted with a probability of 0.56, after considering variation not explained by the QTLs (Rychel-Bielska *et al.*, 2020).

In Chile, by mapping major QTLs in syntenic regions, Lichtin *et al.* (2020) found that alleles from

the wild parent (CGNA's Core 98 × Alu*Prot*-CGNA), explained phenotypic variation of 75% for anthracnose resistance. The marker sca82470 was highly linked with anthracnose resistance in yellow lupin and produced a hit of 90.9% identity on pseudo-Chr 11, 3,376,319–4,744,591 bp, where anthracnose resistance gene *Lanr1* was localized. Accessions selected based on these QTLs failed to show enhanced resistance under either controlled or field conditions (Alkemade *et al.*, 2021b). A high-throughput phenotypic system for field-relevant anthracnose resistance, as well as the availability of a reference genome for white lupin, allows in-depth genomic studies. A GWAS study with 181 white lupin accessions revealed two SNPs (Lalb_Chr05_2957940 and Lalb_Chr05_2957601) linked with resistance to anthracnose on SNP Lalb_Chr05_g021616 encoding a RING zinc-finger E3 ubiquitin ligase (Alkemade *et al.*, 2022b). These genes can be tagged with allele sequences and PCR-markers in marker-assisted selection programs.

X. Omics approaches for anthracnose management

Many potential omics approaches can help unravel the molecular mechanisms of legume responses to *Colletotrichum* species thereby improving the detection and diagnosis of the causal agents (Figure 3). The genome in each *Colletotrichum* species contains a unique set of genes from which numerous fungal phenotypes with varying virulence can be elucidated genetically by population genomic studies of a large number of loci (Sarrocco *et al.*, 2020). Fungal pathogen genes involved in host-specific interactions can be identified by utilizing techniques, such as GWAS, QTL mapping, and genome scans for selective sweeps and selection signatures (Plissonneau *et al.*, 2017).

A transcriptome is composed of all the coding and non-coding RNAs, whereas a proteome is composed of the proteins derived from a genome (Pandey *et al.*, 2021b). Conversely, the metabolome is all the metabolites existing in the plant/microbe system. Through transcriptomic and genomics methods, it is not possible to study the defense systems of leguminous plants against anthracnose pathogens. This is because these defense systems not only involve the expression of multiple genes but also the accumulation of post-translational modifications or metabolites affecting the expression of the final gene products. However, data from genomes and transcriptomes can be used in conjunction with proteomics and metabolomics to gain insight into gene expressions by proteins and metabolites. Even though these approaches are complex, they can be used to understand how plants respond to fungal pathogens and also to associated beneficial microbes. In addition, metagenomics approaches enable a deeper understanding of the microorganisms associated with plants, potentially opening up the way for new possibilities for large-scale legume production.

A. Genomics studies of hosts and pathogens

To date, draft genomes of *Colletotrichum* species causing soybean anthracnose (Rogério *et al.*, 2020) have been sequenced. These include the following species: *C. plurivorum* (IMI 507127), *C. truncatum* (IMI 507125), *C. sojae* (IMI 507126), and *C. musicola* (IMI 507128). A draft genome of two isolates of *C. lindemuthianum* infecting common bean with a genome size of 97.4 Mbp is also available (Queiroz *et al.*, 2017). Furthermore, the genome of two other *C. truncatum* strains, *viz.* TYU (*Taxus cuspidate*) and MTCC 3114 (*Capsicum annuum*), are available in the GenBank database (Gan *et al.*, 2017; Rao and Nandineni, 2017; Rogério *et al.*, 2020). Concerning *C. gloeosporioides*, a draft genome is available from the hosts Chinese fir (QFRH00000000, PRJNA471237, and SAMN09205517; Huang *et al.*, 2019) and avocado (Alkan *et al.*, 2013), with genome size 61.9 and 53.2 Mbp, respectively. The genome of *C. lentis* is 56.10 Mb in size and consists of 10 cores and two minichromosomes (Bhadauria *et al.*, 2019). Besides, the full genome sequence of *C. lupini* is 63.41 Mb in size (Baroncelli *et al.*, 2021). The genome assembly data of *Colletotrichum* species causing anthracnose in legumes is provided in Table 4. With the availability of genome sequences, numerous studies can be conducted, including comparative genomic analyses that characterize effector repertoires, which likely play a role in host-pathogen interactions and directly influence several disease management strategies (de Queiroz *et al.*, 2017).

A significant number of legume species have sequenced genomes available in GenBank database, and here we summarize a few of these resources based on their genome sizes. Whole genome sequences are available for mungbean (Kang *et al.*, 2014; Ha *et al.*, 2021; ~431 Mb), blackgram (Jegadeesan *et al.*, 2021, ~475 Mb), soybean (Schmutz *et al.*, 2010, 1,115 Mb), chickpea (Varshney *et al.*, 2013, ~738 Mb), pigeon pea (Varshney *et al.*, 2011; ~605.78 Mb), lentil (Arumuganathan and Earle, 1991; ~4 Gbp), peanut (Bertioli *et al.*, 2019; ~2.54 Gb), narrow-leafed lupin

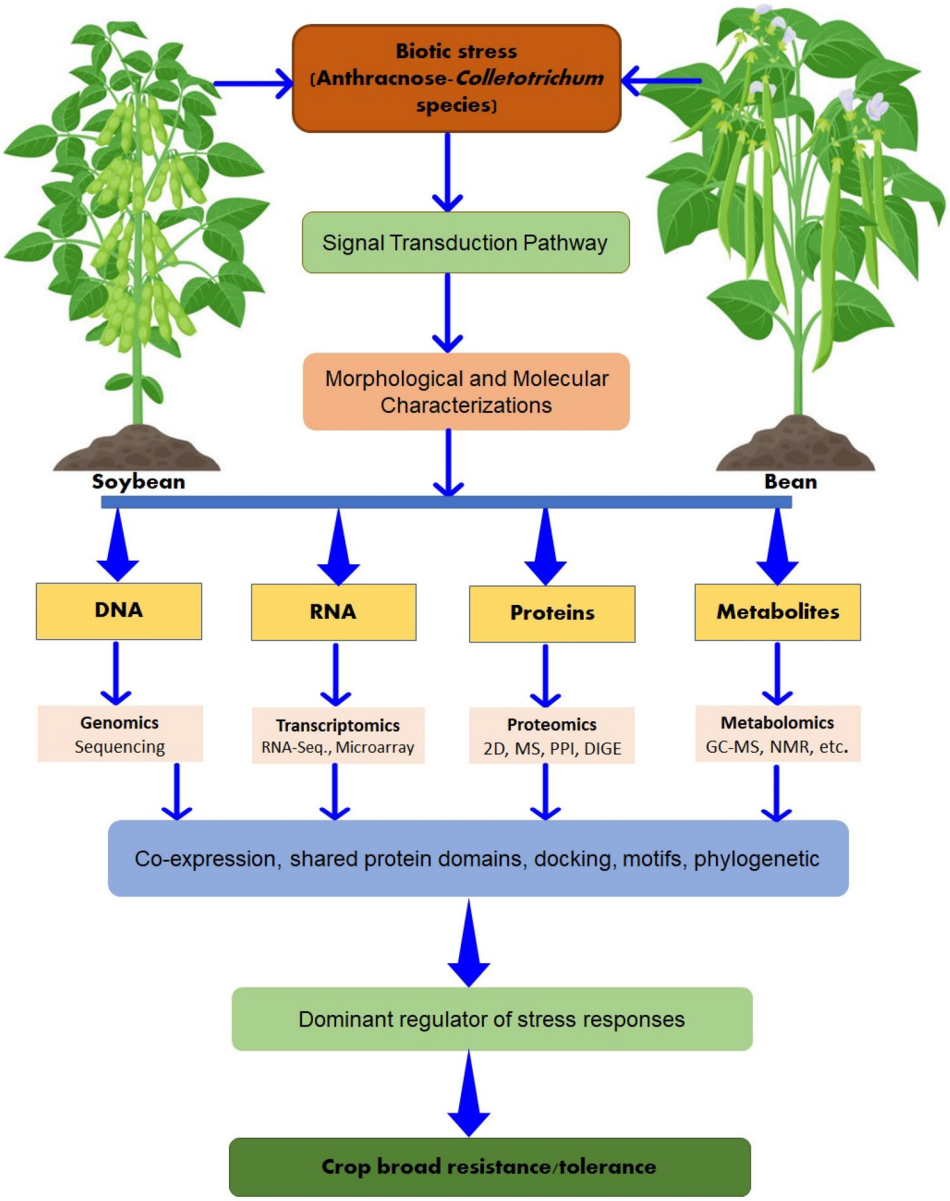

Figure 3. Schematic explanation of omics approaches used in future projects in the improvement of resistance/tolerant to legume anthracnose (PPI: protein–protein interaction; DIGE: differential gel electrophoresis; GC-MS: gas chromatography-mass spectrometry).

Table 4. Summary of *Colletotrichum* spp. pathogenic to legumes and other crop that have whole genome sequences.

Host	Species	Country	Accession number	Assembly length (Mbp)	References
Avocado	*Colletotrichum gloeosporioides*	Israel	GSE41844	53.20	Alkan *et al.*, (2013)
Capsicum annum	*C. truncatum*	India	NBAU00000000	55.30	Rao and Nandineni, (2017)
Chinese fir	*C. gloeosporioides*	China	QFRH00000000, PRJNA471237, SAMN09205517	61.90	Huang *et al.*, (2019)
Common bean	*C. lindemuthianum*	Brazil	MASO00000000 MASP00000000	97.40	Queiroz *et al.*, (2017)
White lupin	*C. lupini*	Italy	CP019471–CP019482		Baroncelli *et al.*, (2021)
Solanum lycopersicon L.	*C. chlorophyti*	Japan	MPGH00000000	52.40	Gan *et al.*, (2017)
Soybean	*C. truncatum*	Brazil	VUJX00000000	56.10	Rogério *et al.*, (2020)
Soybean	*C. truncatum* (19 strains)	Brazil	SRX7095338–SRX7095355	–	Rogério *et al.*, (2019)
Soybean	*C. musicola*	Brazil	WIGM00000000	52.73	Rogério *et al.*, (2020)
Soybean	*C. plurivorum*	Brazil	WIGO00000000	49.70	Rogério *et al.*, (2020)
Soybean	*C. sojae*	Brazil	WIGN00000000	49.35	Rogério *et al.*, (2020)
Taxus cuspidata Siebold & Zucc.	*C. truncatum* (19 strains)	South Korea	NOWE00000000	53.00	Unpublished

(Hane *et al.*, 2017; ~609 Mb), white lupin (Hufnagel *et al.*, 2020, ~451 mm), and cowpea (Lonardi *et al.*, 2019; ~519 Mb). In addition, pan genome sequences are also available for narrow-leafed lupin (Garg *et al.*, 2022, ~975 Mb, Xu *et al.*, 2020, ~559 Mb), white lupin (Hufnagel *et al.*, 2021; ~14.9 Gb), and 26 wild and cultivated soybeans (Liu *et al.*, 2020; ranging ~992.3–1059.8 Mb). The genome sequences of these legumes are useful in unraveling the plant defense system against *Colletotrichum* species. It effectively identifies candidate genes accountable for the virulence of *Colletotrichum* species and allows targeting of potential genes in legumes that confer resistance. The available genomes of both legumes and *Colletotrichum* species will together be useful for legume breeders in developing new cultivars with durable anthracnose resistance through either alteration in the pathogen's virulence genes or through selection of defense-related genes in the host crop.

Despite the lack of breeding programs on anthracnose resistance in mungbean, blackgram, soybean, cowpea, peanut, pigeon pea, or chickpea, the available genomic resources should still support development of future breeding programs. However, the availability of the whole genome sequences of *Colletotrichum* species affecting legumes will not only be very useful for developing diagnostic tools for an early and accurate detection of *Colletotrichum* species (Klosterman *et al.*, 2016), but they will also enable new insights into pathogenesis processes at the molecular level. Together, they will contribute to the development of more efficient and innovative approaches to combat the pathogen in the legume–anthracnose pathosystem along with enlightening our knowledge of host–fungal interactions.

B. Transcriptomics studies

Multi-omics methods allow the discovery of resistant genes and analysis of molecular defense mechanisms for legume diseases including anthracnose. Plant pathogen interactions can be studied by RNA sequencing, allowing the recognition of genes and pathways involved in various phases of plant defense (Ranathunge *et al.*, 2009). For instance, an integrated analysis of metabolomics and transcriptomics revealed the regulation of primary metabolism in soybean crops in response to anthracnose (Zhu *et al.*, 2022). The R genes, *RPP13*, *PTI1*, *RGA2*, *ULP2B*, *RPS6*, and PR genes, such as *PR14* (lipid transfer proteins) and *CHI* (chitinase), provide enhanced resistance in cultivar ZC-2 than cultivar ZC-3 (Zhechun No. 3) to *C. truncatum* (Zhu *et al.*, 2022). The gene *RGA2* also confers partial resistance to common bean anthracnose (López *et al.*, 2003). Among these genes, *RPS6* provides resistance in *Arabidopsis* by regulating the MAPK signaling pathway (Takagi *et al.*, 2020). However, the role of the *ULP2B* gene, which was differentially expressed in resistant soybean cultivar ZC-2, remains still unclear that needs future investigation.

Other factors enhancing resistance in soybean cultivar ZC-2 against anthracnose include transcription factors (TFs), such as *WRKY* and *bHLH*, signal transduction mediated through auxin (AUX), jasmonic acid (JA), MAPK, and Ca^{2+} signaling, and strong terpenoid metabolism at the right time (Zhu *et al.*, 2022). JA, MAPK, AUX, and Ca^{2+} signaling have been identified as plant defense response regulators (Aldon *et al.*, 2018; Fan *et al.*, 2020). In a resistant soybean mutant where pods are challenged with *C. truncatum*, an overexpression of Ca^{2+} fluctuation and plant hormone signaling genes was also reported (Boufleur *et al.*, 2022; Zhu *et al.*, 2022). Further, there was extensive cross-talk between these signaling pathways, including examples of MAPK-*WRKY* (Wang *et al.*, 2018), MAPK and JA signaling (Liu *et al.*, 2011), AUX and JA signaling (Kazan and Manners, 2009; Naseem *et al.*, 2015), as well as Ca^{2+} and JA and signaling (Lv *et al.*, 2019). These signaling pathways interact synergistically to mediate plant defense responses. The cross-talk between *WRKY* TFs and AUX signaling as well as Ca^{2+} signaling and *WRKY* TFs may occur during the interaction of soybean–*C. truncatum*, although the underlying mechanism is not yet clear.

In particular, a plant's response to pathogen infection is regulated by *WRKY* TFs by modulating the expression of camalexin and resistance-associated gene synthesis (Jiang *et al.*, 2017). Thus, several *WRKY* TFs contribute to the positive regulation of the expression of presumed defense genes during infection by pathogens as reported in case of soybean. For example, Boufleur *et al.* (2022) identified seven *WRKY* TFs overexpressed only in the more resistant soybean genotypes *Gm*1-1080; *Gm*2-1059; two of them, *WRKY23* and *WRKY12,* were time-specific. The *WRKY12* encoding gene has been found down- and upregulated in more resistant and susceptible soybean genotypes, respectively, at the same time interval following *C. truncatum* infection (Zhu *et al.*, 2022). In soybean, the biosynthesis of glyceollin (phytoalexin) is positively regulated by *Gm*NAC42, a defensive metabolite that is involved in systemic acquired resistance (Jahan *et al.*, 2019). Further, overexpression of *Gm*NAC42 in

soybean pods has been observed following *C. truncatum* infection (Zhu *et al.*, 2022).

In a susceptible bean genotype, four *WRKY* TFs were upregulated and the pattern of expression increased over the time during *C. lindemuthianum* infection (Padder *et al.*, 2016). A few *WRKY* TFs have been associated with negative regulation of defense signaling thereby increasing the hosts' susceptibility toward anthracnose (Kim *et al.*, 2006; Pandey and Somssich, 2009), corroborating the findings by Padder *et al.* (2016). Tissue specific expression of *WRKY* TFs has been reported in common bean, and while these are dispersed across all chromosomes of bean the expression of most of these was found in roots, with few in leaves, over different time courses (Wang *et al.*, 2016). Taken together, the up-regulation of *WRKY* TFs may account for the host's susceptibility.

The importance of many signaling hormones, such as JA, indole acetic acid (IAA), ethylene, and salicylic acid (SA), in disease resistance activation is well-studied (Verma *et al.*, 2016). Zhu *et al.* (2022) found that in a more resistant soybean genotype both JA and IAA hormones responded more strongly and were associated with enhanced resistance of a more susceptible cultivar to *C. truncatum* following its treatment with these hormones (Zhu *et al.*, 2022). Similarly, up-regulation of the AP2 and ethylene responsive TFs were reported in an anthracnose susceptible common bean genotype (Padder *et al.*, 2016). This suggests that TFs play a key role in JA and SA mediated pathways that contribute to acquired resistance, as shown by this suppression of resistance due to pattern-triggered immunity in more susceptible bean genotypes. Other TFs, such as *bZIPs* and *kinase* defense genes, have shown potential response toward increased anthracnose resistance in common bean (Padder *et al.*, 2016).

The role of more than 50 NBS genes in disease resistance in legumes has been identified (Sekhwal *et al.*, 2015). Among 171 NBS genes reported in common bean, 67 genes showed differential expression levels for anthracnose between resistant and susceptible genotypes. More upregulated (48) than downregulated genes (19) were found in susceptible common bean genotype Jingdou as compared with the resistant genotype Hongyundou (Wu *et al.*, 2017). While gene *Phvul.010G054400* normally shows higher expression in a resistant cultivar, gene expression sharply declined following infection by pathogen race 81. In contrast, there was no change in expression in the susceptible genotype, confirming that this gene may act as a negative regulator of anthracnose resistance during host-pathogen interaction, thus enhancing the host's susceptibility. These studies have contributed significant new understanding of common bean NBS genes, especially in relation to diseases.

Padder *et al.* (2016) identified 3,250 DEGs with and between the near isogenic lines of common bean, with more DEGs upregulated in resistant lines during necrotrophic phase than biotrophic phase. The genes that help in the regulation of anthracnose in common bean include those encoding peroxidase, lipoxygenases, and PR proteins. In another study, *PvPR1*, *NPR1*, *FLS2*, and *β-GLUC* genes overexpressed in a resistant common bean genotype after inoculation with race 65 of *C. lindemuthianum*, suggesting that these genes have a crucial role in the common bean defense system against this pathogen (da Silva *et al.*, 2021). Another regulator gene, *pacCl* which encodes the TF PacC of *C. lindemuthianum*, also showed a differential response in biotrophic as compared with the necrotrophic phase (Soares *et al.*, 2014).

In lentil, a complex interaction between effector genes and resistance has been found for the development of anthracnose disease (Bhadauria *et al.*, 2017b). Overall, 26 resistance genes have been identified in this host including *dirigent* (a resistance response protein) and a suppressor of *npr1-1*, *constitutive 1* (NBS-LRR) following infection by a *C. lentis* virulent isolate of race 0 (Bhadauria *et al.*, 2017b). Several anthracnose resistance genes in lentil are also antagonistic defense signaling pathway markers, including PR5 (SA), PR1, and PR4 (JA) (Bhadauria *et al.*, 2013a). In anthracnose resistance, these genes can be positive or negative regulators of plant immunity. Cross-talk between signaling pathways permits plants to activate defense responses common to tackling diverse groups of pathogens, including biotrophic and necrotrophic pathogens. A resistance gene encoding a CC-NBS-LRR R protein was differentially expressed in a partial resistance lentil genotype, CDC Robin race 1 during infection. This gene is involved in host resistance after invasion (Bhadauria *et al.*, 2013a). By analyzing ESTs, Bhadauria *et al.* (2013b) discovered two effectors, *CtToxB* and *CtNUDIX*, and showed that *CtToxB* amplifies cell death signals to accommodate colonization of *C. lentis* whereas induction of *CtNUDIX* results in abrupt cell death (Bhadauria *et al.*, 2015). Defense response against anthracnose in narrow-leafed lupin was linked with upregulation of *CC-NBS-LRR*, *TIR-NBS,* and *NBS-LRR* genes, and 10 pathogenesis-related proteins, glucan endo-1,3-beta-glucosidases, lipid transfer proteins, genes from ROS pathway and

glycine-rich cell wall proteins (Książkiewicz *et al.*, 2022).

The pathogenicity mechanism in *C. lupini* infecting white lupin has been identified by using transcriptomic and proteomic approaches (Dubrulle *et al.*, 2020). That study revealed 897 genes in white lupin that were differentially expressed within 24–84 h following *C. lupini* inoculation. Of these, 520 genes had putative roles in coding for "pathogenicity factors" like effectors, enzyme-biosynthetic genes, and transporters. In addition, more than 300 putative pathogenesis-related proteins were identified by mass spectrometry (Dubrulle *et al.*, 2020). Despite such progress in pathogenicity characterization, little is known about the exact molecular pathway and this constitutes an area needing further research (Dubrulle *et al.*, 2020).

C. Metabolomics and proteomics studies

While several studies characterized a subset of metabolites in response to anthracnose, comprehensive metabolomic studies that are applied to disease and pest resistance are still lacking. Pathways involving flavonoid, phenylpropanoid, amino acid, isoflavonoid, terpenoid metabolism, and carbohydrate were adjusted in response to soybean infection by *C. truncatum* (Zhu *et al.*, 2022). The soybean resistance mechanism after infection with *C. truncatum* might be influenced by flavonoids, phenylpropanoids, and isoflavonoids where, at all-time points, cultivars ZC-2 and ZC3 were highly enriched in the "flavonoid biosynthesis," "phenylpropanoid biosynthesis," and "isoflavonoid biosynthesis" pathways. Additionally, other studies demonstrated that these pathways increase host resistance to anthracnose (Wang *et al.*, 2016, 2020; Chakraborty *et al.*, 2019; Botero *et al.*, 2021; Jiang *et al.*, 2021). While these roles were likely determined by amino acid and carbohydrate metabolism during soybean–*C. truncatum* interaction, more focused studies are needed to clarify their specific roles. Numerous studies have investigated the phenylpropanoid pathway and biosynthesis of isoflavonoids. The latter contains numerous defense-related compounds, strongly indicating that flavonoid-related compounds are prominently involved in the defense mechanisms of narrow-leafed lupin × *C. lupini* (Muth *et al.*, 2009; Wojakowska *et al.*, 2013, 2015), soybean × *C. gloeosporioides* (Lee *et al.*, 2013), and *Stylosanthes* × *C. gloeosporioides* (Jiang *et al.*, 2021), with several examples demonstrating their potential to increase disease resistance levels by genetic transformation (Lozovaya *et al.*, 2005). A TF called RAP2-7 regulates the biosynthesis of quinolizidine alkaloids in narrow-leafed lupin (Czepiel *et al.*, 2021). The flavor of soybean products is derived from glycitein that exhibited antibacterial and fungicidal effects in studies with *C. gloeosporioides* (Lee *et al.*, 2013). Taken together, all these studies highlight how secondary metabolites act as defense agents in legumes against anthracnose.

To date, only a single study has provided proteomic data on the legume-*Colletotrichum* pathosystem. By using two-dimensional electrophoresis and mass spectrometry, infected common beans were found to accumulate 17 proteins that were related to the following cellular processes: photosynthesis, antioxidants, carbon metabolism, defense, genetics, protein folding, stress response, and biosynthesis of phenylpropanoid and flavonoid compounds (Borges *et al.*, 2015). The accumulation of PR1 protein and antioxidant proteins in infected plants confirms the findings of transcriptomic studies. In addition, chalcone isomerase, an enzyme involved in generating cell wall compounds, was over-accumulated at the beginning of the necrotrophic phase (>48 h post-inoculation). Results at the transcript level are similar to those reported in the previous study of Oblessuc *et al.* (2012). A combination of transcriptomic and comparative proteomic approach to legume resistance in the future will allow a much better understanding of how protein activity is regulated in response to biotic stress, which will be essential for identifying resistance proteins. Consequently, metabolomics will play an increasingly important role in legume breeding programs in the coming years, as a tool for selection and validation to increase the breeding efficiency and shorten the time needed to develop new varieties.

XI. Conclusion and future remarks

Anthracnose is a very destructive disease of legumes worldwide. Unlike many other legume diseases, developing genetic resistance or determining the underlying mechanisms of host resistance to anthracnose are both challenging and complex as disease resistance in legumes does not follow the gene-for-gene interaction model. Except for a few legumes like the common bean, lentil, lupins, blackgram, and soybean, in the majority of anthracnose-affected legumes, no major resistance gene and QTLs have been identified and there is no race specificity among the pathogen populations. Further, many factors, such as plant type, plant physiological maturity, growth habit, and pod load affect the host response to anthracnose. Sources

of genetic resistance to anthracnose have been identified worldwide within the common bean, cowpea, mungbean, blackgram, soybean, lentil, and lupins, and have been exploited in classical breeding programs. However, there remains much scope and need for further investigation into genetic resistance to anthracnose in chickpea, peanut, and pigeon pea. The limited success of traditional breeding for improved anthracnose resistance is due to many factors, including various *Colletotrichum* species disease complexes, the polygenic nature of the resistance, the complex interactions between expression of resistance with other physiological and morphological features, the pathogen variability, the difficulties in maintaining resistance through successive generations of backcrossing, the lack of sufficient correlation between glasshouse and field screenings, the inability to directly identify and select for resistance genes, as well as the confounding effects of other foliar diseases during phenotypic screening.

From a taxonomic, biological, and ecological perspective, it is crucial to know the exact identities and diversity of different pathogens within an anthracnose complex and the diversity within each individual pathogen population. Accurate pathogen identity has major and direct implications for disease resistance breeding programs as well as the management of diseases by cultural and chemical approaches. This equally helps distinguishing between emerging and established fungal populations associated with legumes, to detect, limit the spread of, and effectively manage new *Colletotrichum* species. *C. truncatum*, *C. lindemuthianum*, and *C. lentis* are the most prevalent species infecting the majority of legumes. This review highlights at least 11 *Colletotrichum* lineages associated with soybean, with *C. truncatum* and *C. orchidearum* species complex having the broadest distribution worldwide and the greatest impact. Most of the available literature on soybean, mungbean, and blackgram anthracnose until now has been limited to *C. truncatum*, on common bean to *C. lindemuthianum*, on lentil to *C. lentis*, and on lupins to *C. lupini*. Considering all the *Colletotrichum* species that cause anthracnose, there remains a significant paucity of knowledge about critical aspects of their epidemiology, worldwide distribution, identification, control measures, fungicide efficiency, and genetic resistance. There remains a critical need for robust genomic sampling to fully understand relationships within and between taxa in the genus *Colletotrichum*, as well as to distinguish species-within-species complexes. While genome data are now available for several *Colletotrichum* species associated with anthracnose in legumes, there remains a need for phylogenomic studies of the genus to be conducted. Through population genomics and comparative genomics, we can identify genes that contribute to pathogenicity, virulence (or aggression), host specialization, fungicide resistance, and adaptability to different environments, with increased precision, enabling us to gain a deeper understanding of all aspects of *Colletotrichum* species dynamics, including within the various agroecosystems where anthracnose-susceptible legumes are deployed.

Among the available mitigation approaches, resistance breeding is the most effective, inexpensive, farmer friendly, and ecologically sound approach. Improved crop resistance is vital for sustainable legume production, and can be achieved through many different approaches ranging from traditional breeding to omics interventions. Recently, new sources of anthracnose resistance have been identified within legumes, which have been utilized extensively for identifying resistance QTLs and developing cultivars with improved resistance. The preliminary results from these studies have been encouraging, suggesting the possibility of developing commercially acceptable cultivars with good levels of anthracnose resistance. However, there is a need to further validate and refine these identified genetic bases to enable their wider more effective use in marker-assisted breeding of legumes. To improve breeding efficiency, a more detailed understanding of host-pathogen interactions, particularly of the operation and efficiencies of resistance mechanisms at genetic and molecular levels by implementing the omics interventions, is required.

Although the development of genomic resources in legumes against anthracnose has been relatively slow compared to other food crops, such as vegetables, oilseeds, and cereals, the extensive applicability of marker assisted selection has already been established in common bean, lentil, and soybean, and to a much lesser extent in cowpea, lupins, and pea, but they are still in an early infancy stage for most other legumes prone to anthracnose. Nevertheless, it is encouraging that potential research progress has already been made in engendering sufficient genomic resources in all the major legumes prone to anthracnose. The recent progress of phenotyping at larger scale, sequencing of the whole genome, genetic analysis, and expression of metabolites and proteins, will be helpful in further deciphering legumes-*Colletotrichum* interactions and recognizing potential resistance elements in economically important legume crops prone to anthracnose.

In recent years, the CRISPR/Cas approach has been used to enhance disease resistance among different crops through genome editing of hosts, a broad range of related necrotrophic fungi, and particularly *C. truncatum* (Mishra *et al.*, 2021). However, to the best of our knowledge, CRISPR/Cas has not been used in legumes against anthracnose by legume breeders. This approach can be utilized to engender a wide range of genetic diversity for legume breeding that can more easily enable plant breeders to develop advanced cultivars resistant to anthracnose. However, the potential application of these new genome editing tools including CRISPR/Cas in legumes may be impeded in some instances by a lack of an efficient plant regeneration protocol from callus culture. As the world faces synchronized challenges of climate change and rapidly increasing population, there is an urgent need to use a range of breeding and biotechnological tools to develop climate-resilient cultivars. To this aim, this review has made a first attempt to convey current knowledge gaps and has highlighted critical research needs based on previous and ongoing efforts in the study of anthracnose resistance in legumes across various disciplines, especially fields of genomics, transcriptomics, metabolomics, proteomics, and genome editing.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

Funding for this research was provided by the Australian Center for International Agricultural Research (ACIAR) for the International Mungbean Improvement Network Project (project no. CROP/2019/144).

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