Chapter 1

Taxonomy of *Macrophomina*—traditional to molecular approaches

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1.1 Introduction

The genus *Macrophomina* accommodates globally distributed seed-borne and soil-borne plant pathogenic species, causing charcoal rot and dry root rot on more than 500 plant species. *Macrophomina* species are well-known necrotrophic plant pathogens, carrying a suite of phytotoxins that make them some of the most destructive pathogens of agricultural and horticultural crops worldwide (Islam et al., 2012). Symptoms vary from seed rot, seedling blight, and damping off to stem, crown and root rot, and plant death (Maholay & Sohi, 1983; Adorada et al., 2018). Due to the production of microsclerotia with the ability to survive in soil for long periods of time (Baggio et al., 2019; Short et al., 1980; Zveibil et al., 2012), *Macrophomina* species are notoriously difficult and expensive to manage in agricultural systems.

Despite their global importance and the plethora of genetic and genomic studies on *Macrophomina* species (Burkhardt et al., 2019; Poudel et al., 2022; Purushotham et al., 2020; Radadiya et al., 2021; TančićŽivanov et al., 2019; Viejobueno et al., 2022; Wingfield et al., 2022), many aspects of their biology and pathogenesis remain little understood. Until 2014, *Macrophomina* was considered as a monotypic genus, with *M. phaseolina* as the only known *Macrophomina* species. However, recent molecular studies have shed light on cryptic species within this genus occurring on the same host, with almost identical morphological features (Sarr et al., 2014; Poudel et al., 2021c).

Population genetic studies have so far mostly been focused on *M. phaseolina*, reporting unexpected high genotypic diversity and genetic heterogeneity. While some studies reported specialization of *M. phaseolina* genotypes on certain hosts or association with geographical locations, others failed to identify clear relationships between *M. phaseolina* genotypes and phenotypes or host of origin (Khan et al., 2017; TančićŽivanov et al., 2019; Poudel et al., 2021a, 2021b; Viejobueno et al., 2022). It is possible that some population genetic studies conducted before the molecular taxonomic resolution of the genus in 2014 included multiple cryptic *Macrophomina* species, where sub-clustering of isolates may have represented the unknown cryptic species. This chapter outlines the historical and modern taxonomy of the genus *Macrophomina*, current knowledge on their geographical distribution and host range, and implications for future research.

1.2 History of *Macrophomina phaseolina* (Tassi) Goid

Macrophomina belongs to the family Botryosphaeriaceae within the class Dothideomycetes, which is the largest and most diverse class of Ascomycetes. Until recently, *Macrophomina* was considered as a monotypic genus, with the type species *Macrophomina phaseolina* (Tassi) Goid. The genus *Macrophomina* was originally found by Petrak upon describing *M. philippinensis* with the type specimen obtained from stems of *Sesamum orientale* from the Philippines (Petrak, 1923). Subsequently, the taxonomy of *Macrophomina* was revised several times over the years.

Ashby (Ashby, 1927) examined the type specimen of *M. philippinensis* and several other species, namely, *Dothiorella cajani* Syd. and Butl., *Macrophoma cajani* Syd. and Butl., *Macrophoma corchori* Saw., *Macrophoma sesami* Saw., *Macrophoma phaseoli* Maubl., *Rhizoctonia bataticola* (Taub.) Butl., *Rhizoctonia lamellifera* Small., and *Sclerotium bataticola* Taub., and synonymized these under the name *M. phaseoli* (Maubl.) Ashby, designating *Macrophoma phaseoli*

Macrophomina Phaseolina. https://doi.org/10.1016/B978-0-443-15443-0.00022-X

Maubl. Maublanc (1905) as the basionym (Ashby, 1927). The name *M. phaseoli* was frequently used in literature until 1947, when Goidànich revised the taxonomy of the genus and indicated that *Macrophoma phaseolina* Tassi (Tassi, 1901) was an earlier basionym, thus, proposing the combination *M. phaseolina* (Tassi) Goid (Goidànich, 1947).

Later, the name *Tiarosporella phaseolina* (Tassi) van der Aa was introduced by Von Arx (1981), who reduced *Macrophomina* to a synonym of *Tiarosporella* Höhn (Crous et al., 2006). Crous et al. (2006) induced sporulation in several *M. phaseolina* strains on pine needle agar, confirming that *M. phaseolina* can produce conidiospores with apical mucoid appendages similar to the genus *Tiarosporella*. However, *M. phaseolina* was distinguished by percurrently proliferating conidiogenous cells and conidiospores that turn to dark brown in color at maturity. Therefore, the genus *Macrophomina* and the name *M. phaseolina* (Tassi) Goid. were retained, and an amended description was proposed by Crous et al. (2006), which was further supported by phylogenetic analysis of LSU sequences separating *Tiarosporella* from *Macrophomina* (Crous et al., 2006).

1.3 Molecular taxonomy of *Macrophomina* species

Due to the high level of genetic diversity and pathogenic variation observed in *M. phaseolina* populations globally, the presence of potential cryptic species within this genus had been hypothesized (Vandemark et al., 2000; Almeida et al., 2008). However, initial molecular phylogenetic studies of *Macrophomina* based on nuclear ribosomal DNA (nrDNA) sequences, although helpful in differentiating the genus from the other morphologically similar genera like *Tiarosporella* (Crous et al., 2006; Baird et al., 2010; Saleh et al., 2010), did not provide resolution at the species level. Subsequent molecular taxonomic studies based on phylogenetic analyses of concatenated sequences data, genealogical concordance phylogenetic species recognition (GCPSR), and coalescent-based approaches using additional housekeeping loci indicated the presence of more than one species within the genus *Macrophomina*.

In 2014, Sarr et al. (2014) conducted the first systematic phylogenetic investigation on a global set of 189 *Macrophomina* isolates from 23 host species in 15 countries, using sequences of the actin (*act*), calmodulin (*cmd*), translation elongation factor one-alpha (*tef1-α*), beta tubulin (*tub2*), and internal transcribed spacers and the 5.8S region of the nrDNA (ITS). This resulted in the designation of an epitype for *M. phaseolina s. str.* and description of a new species, *M. pseudophaseolina,* which formed a sister clade to *M. phaseolina,* separated with maximum bootstrap support.

Consequently, several studies conducted on *Macrophomina* species from different regions and hosts using the same set of genetic loci described three additional species, namely, *M. euphorbiicola* (Machado et al., 2019), *M. vaccinii* (Zhao et al., 2019), and *M. tecta* (Poudel et al., 2021c). As a result, currently five *Macrophomina* species are recognized (Fig. 1.1).

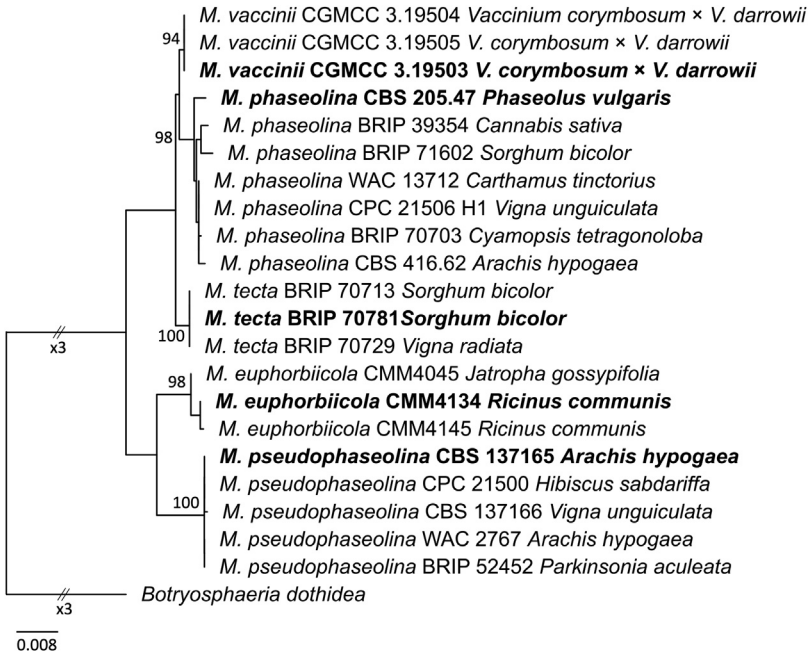

FIGURE 1.1 Phylogeny of *Macrophomina* species recognized to date. Maximum likelihood phylogeny of *Macrophomina* species based on the concatenated ITS, *cmd*, *tef1-α*, and *tub2* alignments constructed in RAxML v. 8.2.11 (Stamatakis, 2008) using the GTRGAMMA model of nucleotide substitution applied to individual partitions with 1000 pseudoreplicates. Ex-type strains are indicated in bold. Bootstrap values are given at the nodes. The tree was rooted to *Botryosphaeria dothidea* (Poudel et al., 2021c).

1.4 Host range and distribution of *Macrophomina* species

Of the five *Macrophomina* species recognized to date, *M. phaseolina* is the most widely distributed, displaying a cosmopolitan distribution on more than 500 plant species. While the cosmopolitan distribution and broad host range of this species has been confirmed in more recent molecular studies, some of the older reports of this species based on morphological studies may need to be treated with caution as this species is morphologically indistinguishable from more recently described species such as *M. tecta* (Poudel et al., 2021c) and can only be distinguished from *M. pseudophaseolina* based on morphology of the conidia (Sarr et al., 2014), which are not always readily formed in culture to allow for morphological characterization. As noted, recent molecular studies still point to the broad distribution of *M. phaseolina* on a board range of plant species. Of the 189 isolates studied by Sarr et al. (2014) in Senegal, 171 were recognized to be *M. phaseolina*. Likewise, of the 80 isolates from 28 plant species in Australia, the majority (88%) belonged to *M. phaseolina* (Poudel et al., 2021c).

Macrophomina pseudophaseolina has thus far been reported in association with 13 plant species and in six countries. These hosts include *Abelmoschus esculentus* (okra) in Senegal (Sarr et al., 2014), *Arachis hypogea* (peanut) in Australia, Brazil, and Senegal (Sarr et al., 2014; Machado et al., 2019; Poudel et al., 2021c), *Boerhavia diffusa* in Brazil (Negreiros et al., 2019), *Coleus forskohlii* in India (Mastan et al., 2019), *Gossypium hirsutum* (cotton) in Brazil (Machado et al., 2019), *Hibiscus sabdariffa* (roselle) in Senegal (Sarr et al., 2014), *Ipomoea batatas* (sweet potato) in Brazil (de Mello et al., 2021), *Jatropha curcas* in Brazil (Machado et al., 2019), *Lens culinaris* (lentil) in Algeria (Kouadri et al., 2021), *Manihot esculenta* (cassava) in Brazil (Brito et al., 2019), *Parkinsonia aculeate* a native plant species in Australia (Poudel et al., 2021c), *Phaseolus vulgaris* (bean) in Argentina (Viejobueno et al., 2022), *Ricinus communis* in Brazil (Machado et al., 2019), *Trianthema portulacastrum* in Brazil (Negreiros et al., 2019), and *Vigna unguiculata* (cowpea) in Senegal (Sarr et al., 2014).

In contrast, the remaining three species currently recognised within the genus have been recorded from a limited number of and host plants and geographical locations. *M. euphorbiicola* has thus far only been reported in Brazil on *I. batatas*, *Jatropha gossypiifolia,* and *R. communis* (Ayala-Armenta et al., 2020; de Mello et al., 2021; Machado et al., 2019). *M. vaccinii* has only been reported in China on *Pogostemon cablin* (Fang et al., 2022) and *Vaccinium* spp. (blueberry) (Ayala-Armenta et al., 2020; Zhao et al., 2019). *M. tecta* has only been recorded on *Zea mays* (corn) in Argentina (Viejobueno et al., 2022) and on *Sorghum bicolor* (sorghum) and *Vigna radiata* (mungbean) in Australia (Poudel et al., 2021c). The restricted host range could be due to the very recent recognition of these species, and further studies are warranted to investigate their potential host specialization.

1.5 Intraspecific genetic diversity and pathogenic variability

Understanding the genetic diversity and structure of pathogen populations is essential for better understanding their evolution in agricultural ecosystems to allow for sustainable disease management. Population genetic and genomic investigations provide contribution to better understanding the pathogen's biology, disease epidemiology, and co-evolution of host and pathogen, which may be used to improve breeding for disease resistance and deployment of disease mitigation strategies. Genotyping via a variety of molecular markers, such as amplified fragment length polymorphisms (AFLP), random amplified polymorphic DNA (RAPD), restriction fragment length polymorphisms (RFLP), simple sequence repeats (SSR) and single nucleotide polymorphisms (SNP), and subsequent cluster analyses have been applied to understand genetic diversity of *M. phaseolina* populations and detected substantial genetic heterogeneity in Argentina (Reznikov et al., 2019), Australia (Poudel et al., 2021a, 2021b), Brazil (Almeida et al., 2008; Sybuia et al., 2022), Europe (TančićŽivanov et al., 2019), Iran (Mahdizadeh et al., 2012), Mexico (Mayék-Pérez et al., 2001; Reyes-Franco et al., 2006) and the United States (Vandemark et al., 2000; Baird et al., 2010; Saleh et al., 2010). These studies reported separation of isolates into multiple subpopulations, with no clear association with either geographical location or host of origin.

In contrast, other studies have detected association of *M. phaseolina* genotypes and host (Su et al., 2001; Viejobueno et al., 2022). Pathogenicity and RAPD-based analysis of a collection of 45 isolates from cotton, corn, sorghum, and soybean from different geographical locations suggested an association between isolate clustering, pathogenicity, and cropping history, irrespective of geographical origin of isolates (Su et al., 2001). Similarly, in India, *M. phaseolina* isolates obtained from cotton and soybean clustered corresponding to their host of origin (Jana et al., 2005). Also, Jana et al. (2003) discovered RAPD, SSR, and URP-PCR (universal rice primer PCR) markers associated with *M. phaseolina* genotypes from certain hosts or geographical origins.

Lack of association of genotypes with pathogenicity/virulence profiles on different hosts is expected and has been reported in other fungal plant pathogens too (Barrès et al., 2008; Vaghefi et al., 2017, 2018). This is due to the fact that

phylogenetic and population genomic studies usually use neutral genetic markers for population characterization, which do not necessarily represent pathogenicity and virulence phenotypes, which are under selection pressure form host populations (Vaghefi et al., 2017). On the other hand, if loci used for population characterization are linked to pathogenicity and virulence genes, the association of genotypes, and different pathogenicity/virulence profiles may be expected.

Detection of high genetic diversity in *M. phaseolina* populations, in the absence of a known sexual form, is surprising and has been attributed to parasexuality, long-distance dispersal of the isolates (genotype flow) and/or host adaptation. Parasexuality is a nonmeiotic process that produces genetically diverse progeny and is an effective mechanism to enhance genotypic diversity in asexual fungi (Pontecorvo et al., 1953). A parasexual cycle starts with the formation of heterokaryons following fusion of two genetically compatible isolates. The two haploid nuclei may fuse and form a heterozygous diploid nucleus. Upon division of the diploid nuclei, mitotic nondisjunction or mitotic recombination may take place, giving rise to recombinant haploid nuclei containing novel allelic combinations (Pontecorvo et al., 1953). Recent discovery of heterokaryon formation in *M. phaseolina* (Pereira et al., 2018) and parasexual recombination in *M. pseudophaseolina* (Pereira et al., 2018; Sybuia et al., 2022) confirms genetic exchange between vegetatively compatible isolates as a result of which mitotic recombination can be a major source of genotypic diversity in the absence of sexual recombination in *Macrophomina* populations.

Another factor underlying the high genetic diversity in *M. phaseolina* populations could be the pathogen's ability to infect a diverse range of host crops. Almeida et al. (2008) investigated how crop rotation may affect the genetic diversity of *M. phaseolina* using 89 isolates obtained from a 4-year no-tillage crop rotation paddock and an uncropped paddock. RAPD genotyping results showed that genetic diversity was higher in *M. phaseolina* population from the crop rotation paddock compared to the uncropped paddock. This led the authors to conclude that the occurrence of different hosts with different levels of resistance may have exposed the pathogen population to diversifying selection pressure leading to an increase in genetic variability.

It should be noted that some population genetic studies conducted before 2014 may have included multiple cryptic *Macrophomina* species, which may have led to inflation of genetic diversity assuming all isolates belonged to *M. phaseolina*. Population studies conducted by Poudel et al. (2021a, 2021b) using restriction site-associated DNA (RAD) sequencing have shown that sympatric populations of *M. phaseolina* and *M. tecta* occur on all surveyed sorghum crops in Australia; therefore, raising the possibility that mixed populations of *Macrophomina* spp. can also exist on other crops and in previous population genetic studies. Therefore, results from some population genomics studies that precede resolution of cryptic *Macrophomina* spp. via molecular taxonomy should be treated with caution.

1.6 Conclusions

Molecular taxonomy of the genus *Macrophomina* was resolved only very recently; therefore, many aspects of biology and epidemiology of recently described *Macophomina* species that is, *M. euphorbiicola*, *M. pseudophaseolina*, *M. tecta*, and *M. vaccinii* remain little understood. On the other hand, the extensive morphological, pathogenicity, and epidemiological studies conducted on *M. phaseolina* may need to be treated with caution since different *Macrophomina* species occur sympatrically in agricultural ecosystems (Poudel et al., 2021a, 2021b); thus, the results from studies based on morphological identification of species may have been confounded by presence of two or more cryptic species.

The very first step in successful disease management is correct identification of the causal agent. Therefore, development of reliable molecular markers to differentiate *Macrophomina* species should be a priority. To the best of our knowledge, DNA-based assays capable of distinguishing all five species of *Macrophomina* have not yet been developed. Such molecular markers may be applied for extensive surveys of *Macrophomina* species on different crops and soils, enabling generation of predictive models to understand the impact of each of these species and their interactions in agricultural ecosystems.

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