

CHALLENGES AND PROSPECTS FOR MANAGEMENT OF ANTHRACNOSE CAUSED BY *COLLETOTRICHUM* SPECIES IN TROPICAL AFRICA

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ABSTRACT

Colletotrichum is a fungal genus comprising several pathogenic species that cause anthracnose in an array of key cash and food crops in the world's tropical, subtropical, and temperate regions. Considerable losses in various crops due to anthracnose in the African tropics have been reported despite the efforts to curb the disease. Several options are used to manage the disease in the region with little success. The challenges in managing *Colletotrichum* species include toxicity, high cost, inadequate farmers' knowledge of applying synthetic fungicides, variable and cross-infection nature of pathogenic species, physiological variability of pathogens, and unavailability of biological control agents to farmers in rural areas in tropical Africa. Several species of *Colletotrichum* are also known to develop mechanisms that allow them to counter immunity factors of the host plants. Consolidated information on the species prevalent, losses, and evaluation of the current control methods for anthracnose in the African tropics are essential for developing and adopting sustainable management strategies for anthracnose. This review discusses the key pathogenic *Colletotrichum* species in Africa, infection mechanisms, colonisation in several hosts, and the plant-pathogen interaction and losses due to the disease. Pathogen identification methods, disease management options, challenges, and prospects for the management of anthracnose in tropical Africa are also discussed.

Keywords: Anthracnose, pathogen, cross-infection, races, botanicals

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INTRODUCTION

The genus *Colletotrichum* includes several species that are pathogenic to crop plants ranging from woody to herbaceous. Species in this genus survive favourably in the tropical and subtropical regions, with a few exceptions where some species are known to affect temperate crops (Cannon *et al.*, 2012). Pathogens of this fungal genus are known to cause destructive diseases in many important crops. Owing to its economic and scientific importance, *Colletotrichum* ranks the 8th group of pathogenic fungi globally (Dean *et al.*, 2012).

The following groups of crops are affected by this group of fungi cereals like maize, sugarcane, rice, and sorghum legumes, including cowpeas, common beans, and pigeon peas. Fruits including mango, citrus, banana, coffee berries, strawberries, and avocado are also affected by this group of fungi (Dean *et al.*, 2012). Studies show that isolates of the pathogen from one host are capable of causing infection in other different host plant species (Lakshmi *et al.*, 2011), and there is a possibility of a single plant species hosting several species of *Colletotrichum* (Eaton *et al.* 2021).

Pathogenic *Colletotrichum* species cause diseases that are collectively called anthracnose with only

a few exceptions (Lenné, 2002). These diseases are characterised by seedling blight, stem, crown and fruit, flower rots, and sunken necrotic lesions on leaves, among other symptoms (Waller *et al.*, 2002; Agrios, 2005). Most of the species are seed-borne, though some are also soil-borne, capable of surviving as saprophytes on dead crop residues. This group of fungi is spread by air transmission of spores or water splashes of the conidia during the rainy season (Nicholson and Moraes, 1980). Some species can survive well in the soil for a maximum of one year (Freeman *et al.*, 2002).

Common management options for anthracnose include: use of resistant varieties (Bhagwat *et al.*, 2015; Gupta *et al.*, 2015), use of synthetic fungicides (Mohammed, 2013; Amin *et al.*, 2014), use of biocontrol agents (Palaniyandi *et al.*, 2011; Kamble *et al.*, 2015), cultural practices (Fokunang *et al.*, 2001; Oo and Oh, 2016) and little but growing attention has recently been on the use of botanicals (Masangwa *et al.*, 2013). Despite using these available methods, the management of *Colletotrichum* species remains a challenge, especially in tropical Africa. Knowledge of the mechanisms for invasion and colonisation employed by pathogenic *Colletotrichum* species and evaluating the challenges and prospects for management is vital for planning effective

control measures for anthracnose diseases. This review, therefore, discusses the key *Colletotrichum* species reported in Africa mechanisms and strategies used by *Colletotrichum* species to invade and colonise host plants and the methods currently used to manage anthracnose in African tropics. The review also critically evaluates the challenges in managing *Colletotrichum* species and prospects in tropical Africa. The information presented in this review is vital for breeders, plant pathologists, and other agricultural stakeholders to plan, set and adopt strategies to manage anthracnose in the African tropics.

Key species in the genus *Colletotrichum*: *Colletotrichum* is one of the most studied groups of the kingdom fungi, with several reviews in species classification. The taxonomy of this genus has been changing, and there are several revisions on the naming and identification of new species (Weir *et al.*, 2012). Managing anthracnose, therefore, requires precise classification and identification of the species responsible for causing the disease in question. Jayawardena *et al.* (2016) reported more than 190 species worldwide, with 11 occurring as complexes while 23 exist as singletons. Some of these species have been reported to occur and affect key crops in the African tropics (Table 1). Some of these species complexes have also been studied, with some previous species being renamed and new species named. A thorough study of the Gloeosporioides species complex by Weir *et al.* (2012) is among the extensive works on the *Colletotrichum* taxonomy.

Identification of *Colletotrichum* species: Proper identification of pathogenic species is critical for designing management strategies. Identification of *Colletotrichum* species is achieved using both morphological and molecular approaches. Morphological features used for the identity of these species include the colony colour, conidia size and shape, and the rate of growth. Because most species, especially in the same complex, share such characteristics, and these characteristics depend on the incubation temperature, light, type, and nature of the medium, they are not reliable for identification (Lee *et al.* 2020). This weakness, therefore, necessitated molecular approaches to identify species in the genus. The most common molecular tool is sequencing the nuclear ribosomal ITS (internal transcribed spacer) region. Recently, a combination of morphological characteristics, pathogenicity, and partial DNA sequencing of β -tubulin, glyceraldehyde-3-phosphate dehydrogenase, actin, and calmodulin genes have also been valuable tools for the identification of species (Liu *et al.* 2020). Other markers which have been identified and sequenced as barcodes for identification of *Colletotrichum* species include histone-3 (HIS3), the intergenic spacer between DNA lyase and the mating-type locus MAT1-2-1 (APN2/MAT IGS), the intergenic spacer between GAPDH and a hypothetical

protein (GAP2-IGS), chitin synthase (CHS-1), glutamine synthetase (GS), manganese superoxide dismutase (SOD2), mating-type gene (MAT1-2-1) and DNA lyase (APN2) (dos Santos Vieira *et al.* 2020).

Mechanism and strategies for invasion and colonisation of hosts: Pathogenic *Colletotrichum* species employ two main strategies to invade and colonise host plants, and it is on this basis, these pathogens are grouped into two groups: subcuticular intramural colonisation and intracellular colonisation. In both cases, the preliminary processes of spore adhesion, germ tube and appressorium formation and penetration are similar. The invasion begins with the adhesion of an asexual spore called conidium to the surface of the host, which in most cases is transmitted by air or rainwater splashes (Nicholson, 1996). After adhesion and under favourable environmental conditions, conidium germinates and forms an outgrowth called germ tube, which develops into a penetration structure, appressorium. This appressorium penetrates the cuticle directly and colonises the epidermis by forming infection hyphae inside the epidermal cells. The hyphae then develop into infection vesicles which later develop into a network of primary hyphae (Bailey *et al.*, 1992). In many *Colletotrichum* species, there is evidence of the production of cellulase enzymes that catalyse degradation of the host cell wall enabling penetration of the pathogen (Anand *et al.*, 2008; Peeran *et al.*, 2014).

Subcuticular intramural colonisation: Upon successful penetration of the appressorium into the cuticle, pathogens that employ this strategy develop an intramural network of hyphae below the cuticle and inside the epidermis. These hyphae develop rapidly in the surrounding cells and eventually kill these cells (Bailey *et al.*, 1992). In this strategy, the biotrophic phase is not evident though some studies have reported the possibility of the existence of a short form of this phase before the hyphae start destroying the colonised tissues of the host (Arroyo *et al.*, 2005; Diéguez-Uribeondo *et al.*, 2005; Peres *et al.*, 2005). Species like *Colletotrichum capsici* that infect cowpea and cotton, *C. circinans* on onion (Roberts and Snow, 1984; Bailey *et al.*, 1992; Pring *et al.*, 1995) are known to exhibit this strategy invading and colonising their hosts.

Intracellular colonisation: Most *Colletotrichum* species employ this strategy to colonise their hosts. Here, the hyphae grow between the cell walls of the host and plasma membranes after successful penetration. Most *Colletotrichum* species switch to the necrotrophic phase by transforming the primary infective hyphae into necrotrophic secondary hyphae, which invade the surrounding cells by secreting cellulose enzymes and ultimately killing these cells. This leads to the development of visible necrotic lesions, a typical

symptom of anthracnose (Perfect *et al.*, 1999; Barimani *et al.*, 2013). All the fungal species which exhibit two phases of biotrophy and necrotrophy are called facultative biotrophs or hemibiotrophs, and the length of these phases is dependent on environmental conditions and the developmental stage of the host. Examples of pathogens in this group include *C. truncatum*, *C. lindemuthianum*, *C. graminicola*, *C. orbiculare*, *C. destructivum*, *C. trifolii*, *C. gloeosporioides*, and *C. sublineolum* (Bailey *et al.*, 1992). So, for intracellular hemibiotrophic pathogens; the biotrophic phase does not cause symptoms to the hosts and live by absorbing nutrients from the living cells of the hosts whereas, in the necrotrophic phase, the pathogens kill the host cells, obtain nutrients from them and cause visible symptoms (O'Connell *et al.*, 2012).

There have been exceptions in the infection and colonisation strategies in the genus *Colletotrichum* as some species can employ both subcuticular intramural and intracellular strategies. This scenario has been reported in *C. gloeosporioides* on *Stylosanthes* species (Bailey *et al.*, 1992). A generalised *Colletotrichum* infection process is illustrated in Figure 1.

Factors that facilitate infection and colonisation of hosts by *Colletotrichum* species and plant-pathogens interaction: Several factors, including physical and exogenous chemicals, are involved in stimulating or

inhibiting germ tube formation and elongation and appressorium formation in *Colletotrichum* species (Podila *et al.*, 1993; Manandhar *et al.*, 1995). These signals from plant hosts trigger germination and formation of appressoria and are very pathogen-host specific. For instance, the wax produced on the surface of avocado triggers the spore germination as well as the formation of appressorium in *Colletotrichum gloeosporioides* (Podila *et al.*, 1993). Ethylene hormone also has been reported to activate spore germination and formation of appressorium in *C. musae* and *C. gloeosporioides* (Podila *et al.*, 1993; Kolattukudy *et al.*, 1995). The pathogens secrete effector proteins that suppress the host's immune responses to colonise the host tissues successfully. The secretion of cellulase enzymes by the pathogens has also been associated with degradation of the host's cell wall, facilitating penetration into the cell (Dou and Zhou, 2012; O'Connell *et al.*, 2012; Gan *et al.*, 2013; Guyon *et al.*, 2014). Polygalacturonase enzymes are also produced by several *Colletotrichum* species, which aid them in the degradation of polysaccharide-rich cell walls (Shivashankar *et al.*, 2010). This scenario brings a challenge in managing most of the *Colletotrichum* species in many important crops. These scenarios explain the compatible host-pathogen interaction where the pathogen completes its life cycle in the host plant, causing diseases.

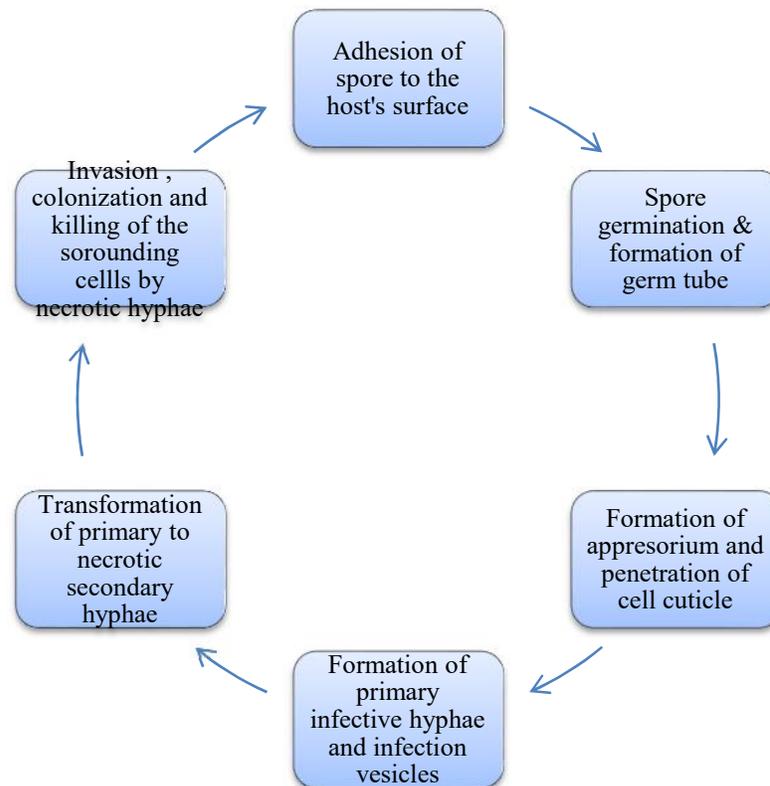


Figure 1: Generalised infection process for *Colletotrichum* species

Table 1: Colletotrichum species pathogenic to crops in Africa.

Species Complex	Species	Host	Country	Reference
Gloeosporioides species complex	<i>C. kahawae</i> ssp. <i>Kahawae</i>	<i>Coffea arabica</i>	Kenya, Burundi, Congo DRC, Malawi, Angola, Cameroon	UK, 1996; Batista <i>et al.</i> , 2017; Weir <i>et al.</i> , 2012
	<i>C. asianum</i>	<i>Mangifera indica</i>	South Africa, Ghana	Sharma <i>et al.</i> , 2015; Honger <i>et al.</i> 2014
	<i>C. gloeosporioides</i>	<i>M. indica</i> , <i>Persea americana</i> , <i>Manihot escalenta</i> , <i>Alium cepa</i>	South Africa, Kenya, Ghana	Weir <i>et al.</i> , 2012; Honger <i>et al.</i> 2014; Darvas and Kotze, 1987; Hindorf, 1999; Hillocks, 2002; Gyempeh <i>et al.</i> , 2015; Fokunang <i>et al.</i> , 2001; Wasilwa <i>et al.</i> , 2005
	<i>C. musae</i>	<i>Musa</i> sp.	Ethiopia, South Africa, Cameroon, Malawi, Zambia, Nigeria, Tanzania, Kenya, Cote d'Ivoire, Mozambique, Zimbabwe,	Weir <i>et al.</i> , 2012; CABI, 2001
	<i>C. siamense</i>	<i>Dioscorea rotundata</i> ,	Nigeria, South Africa	Weir <i>et al.</i> , 2012;
	<i>C. alatae</i>	<i>Carica papaya</i>	Ghana	Honger <i>et al.</i> , 2016
graminicola species complex	<i>Dioscorea alata</i>	<i>Dioscorea alata</i>	Nigeria	Weir <i>et al.</i> , 2012
	<i>C. sublineolum</i>	<i>Sorghum bicolor</i>	Mali, Nigeria, Sudan, Guinea, Tanzania, Uganda, Ghana, Togo, Ethiopia	Crouch <i>et al.</i> 2009; Marley <i>et al.</i> , 2005; Crouch & Tomaso-Peterson, 2012; Njoroge <i>et al.</i> , 2018; Mengistu <i>et al.</i> , 2019
Acutatum species complex	<i>C. lupini</i>	<i>Lupinus</i> sp., <i>Manihot utilissima</i>	South Africa, Rwanda	Lotter & Berger, 2005; Damm <i>et al.</i> , 2012; Jayawardena <i>et al.</i> , 2016
	<i>C. nymphaeae</i>	<i>Capsicum</i> sp., <i>Fragaria ananassa</i>	Zimbabwe, South Africa	Damm <i>et al.</i> , 2012
Destructivum species complex	<i>C. destructivum</i>	<i>Medicago sativa</i>	South Africa	Thompson and van der Westhuizen, 1985
	<i>C. tabacum</i>	<i>Nicotiana</i> sp.	Zimbabwe	Damm <i>et al.</i> , 2014
Obiculare species complex	<i>C. vignae</i>	<i>V. unguiculata</i>	Nigeria	Damm <i>et al.</i> 2014
	<i>C. lindemuthianum</i>	<i>Phaseolus vulgaris</i>	Tanzania, Burundi, Ethiopia, Sudan, Kenya, Uganda, Congo DRC, Rwanda, Zambia, Malawi	Mohammed, 2013; Batureine, 2009; Kachapulula <i>et al.</i> , 2010
Dematium species complex	<i>C. dematium</i>	<i>Vitis vinifera</i> , <i>V. unguiculata</i>	South Africa	Damm <i>et al.</i> , 2012; Smith and Aveling, 1997
	Singleton	<i>C. coccodes</i>	South Africa	Denner and Marais, 1989
Unknown	<i>C. capsici</i>	<i>Capsicum frutescens</i>	Nigeria	Amusa <i>et al.</i> , 2004

On the other hand, various studies show that plants respond to infection by *Colletotrichum* species in several ways. These include chemical, structural, and protein defence mechanisms. Shivashankar *et al.* (2010) reported that, following the production of polygalacturonase enzymes by *Colletotrichum* species, plant species produce polygalacturonase inhibitory proteins to inhibit the action of such enzymes at the early

stage of pathogen attack. Thickening of cuticle and cell wall and production of an enzyme, phenylalanine ammonia-lyase, are among the plant responses due to contact between the host and pathogen. Some studies also show that plant species produce defensive compounds, including pisatin, phaseolin, phytoalexins, kievitone, and phaseolinisoflavan (Joshi, 2018). Volatile organic compounds (VOCs), including methyl salicylate, methyl

jasmonates, limonene, and nonanal produced by common bean after pathogen attack, induce resistance against *C. lindemuthianum* (Quintana-Rodriguez *et al.* 2015). Apart from VOCs, plants also respond to *Colletotrichum* infection by producing reactive oxygen species (ROSs). For instance, studies show that hydrogen peroxide is an important factor in resistance against various *Colletotrichum* species, including *C. cocoides*, *C. acutatum* (Miles and Schilder, 2013). Such responses, therefore, present incompatible interactions between the host and pathogen.

Anthraxnose of key crops in the African tropics: The main food crops in tropical Africa include cassava, banana, maize, common bean, sorghum, groundnut, yams, finger millet, and coffee as a cash crop (Ramirez-Villegas and Thornton., 2015). Production of most of these crops is hampered by anthracnose, and tremendous losses have been reported in this region. This section discusses anthracnose of essential food and cash crop in tropical Africa.

Bean anthracnose: Bean anthracnose is caused by *Colletotrichum lindemuthianum* and has been reported as one of the significant biotic factors conflicting with bean production worldwide. In Africa, the disease has been

reported in almost all bean growing countries as among the devastating diseases of the crop. Tropical Africa is not exceptional as the disease has been reported in almost all bean growing areas, including Tanzania, Uganda, Burundi, Ethiopia, Kenya, Rwanda, Sudan, and the Democratic Republic of Congo (Batureine, 2009; Mohammed, 2013), which are the leading producers of common beans in Africa. Other countries include Zambia and Malawi (Kachapulula *et al.*, 2010).

The disease symptoms are most evident on leaves and bean pods, whereas infected leaves are characterised by brown, brick-red to black lesions on leaf veins and the lower surface of the leaf (Fig. 2b) though similar symptoms may be apparent on both leaf sides. As the disease advances, discoloration develops on the upper surface of the leaf. However, these leaf symptoms are mostly not very obvious and may not be very useful when evaluating the disease in the field (Kelly and Vallejo, 2004). On the other hand, Infected pods are characterised by small circular, reddish-brown sunken lesions (Fig. 2a & c). If severely infected, the pods shrivel, and the fungus may infect the seeds that usually bear sunken lesions (Kelly and Vallejo, 2004). Sometimes early infected pods abort, and seed development is interfered.

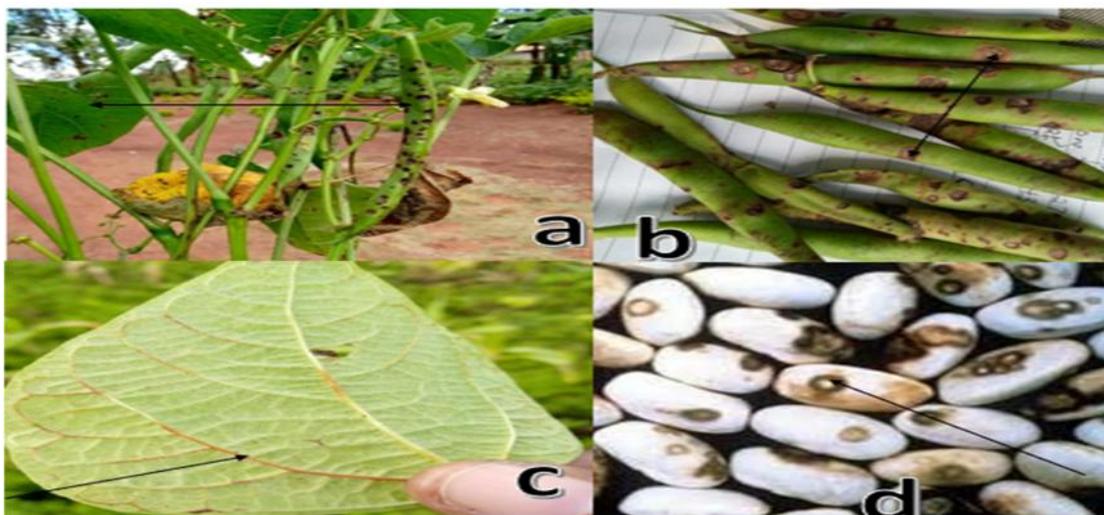


Figure 2: Symptoms of bean anthracnose. a) infected plant, b) sunken lesions on pods, c) leaf symptoms, and d) Infected seeds.

Bean anthracnose has been reported to cause significant losses in many African tropical regions, calling upon immediate attention. Reports on losses due to the disease are available for some individual countries, though current information is missing in some countries. An early study by Shao and Teri (1985) reported losses of up to 100% of the crop if susceptible cultivars are grown in Tanzania. However, a later study by Mohammed (2013) reported losses of between 40-80% in the same country. Reports from Uganda estimate the losses due to

bean anthracnose at 45% (Nkalubo *et al.*, 2007), whereas, under favourable climatic conditions, up to 90% have been noticed in Sudan (Mohammed, 2013). Mogita *et al.* (2017) reported an incidence of up to 53% in Western Kenya. Tesfaye (1997) estimated yield loss due to the disease in Ethiopia to be 63%. Despite the prevalence of the disease in the region and the massive losses, it causes, current information on the losses caused by bean anthracnose is lacking for most countries.

Anthracnose of sorghum: Sorghum (*Sorghum bicolor*) is an essential crop in most African countries, particularly in tropical and subtropical regions. It has been reported as a very important crop in the sub-Saharan African region due to its good adaptation to harsh climatic conditions. It is believed to be of African origin, particularly in Ethiopia (Dicko *et al.*, 2006).

Sorghum anthracnose is a fungal disease caused by *Colletotrichum sublineolum*. The disease was for the first time reported in Togo, West Africa, in 1902 but has so far spread in many countries around the world. In tropical Africa, the disease has been reported in West and Central African countries (Marley *et al.*, 2005), East Africa (Hulluka and Esele, 1992), and other countries in the tropics.

The disease occurs in various phases, including foliar, panicle, grain, and stalk rot phases. However, the foliar phase is the most common and can occur at any stage of plant growth, though in most cases, it is more evident to plants aged 30 to 40 days. The phase is characterised by circular and small spots which may be elongated or elliptical. These spots begin as purple to red dots under favourable humidity conditions, and high rainfall increase in number and merge to cover a large portion of the plant leaf. This ultimately kills the large

portion of the leaf or whole leaf. In its severe form, anthracnose of sorghum results in premature defoliation and reduced growth or sometimes premature death of the plants (anonymous, 2018).

Although current information on yield losses due to anthracnose in most countries is lacking, it has been reported to be more than 50% (Ngugi *et al.*, 2000) in most tropical African countries. A study by Mengistu *et al.* (2019) reported losses of up to 70% in sorghum in Ethiopia, and the incidence of 100% is common in the country (Tsedaley *et al.*, 2016), the comparable incidence of 100% has also been reported in Uganda (Sserumaga *et al.*, 2013). They also noted it as an important disease in all sorghum-growing areas of the country. In Kenya, no recent information on the losses, but it has been estimated at higher than 50% with an incidence of 65% (Ngugi *et al.*, 2000; 2002). Old studies in West and Central Africa report anthracnose as a threat to sorghum production (Marley *et al.*, 2005). Losses of up to 67% were reported in Mali and other West African countries (Thomas *et al.*, 1996). Data on the disease's current status for most countries has not been captured, thus not presented in this section. Therefore, assessing the current situation of the disease in tropical Africa is vital.



Figure 3: Foliar symptoms of sorghum anthracnose. Source: <https://www.greenbook.net/field-guide/diseases/anthracnose-leaf-blight>.

Yam anthracnose: Yam constitutes an essential portion of staple food in the tropics, and a large portion of world production (about 95%) comes from West Africa (FAO, 2002). Despite its importance as the primary food crop for most tropical African countries, especially in West Africa, anthracnose caused by *Colletotrichum alatae* (Weir *et al.*, 2012) remains a problem in yam production.

This disease is characterised by leaf necrosis and die-back of the yam vines, leading to the reduced photosynthetic area and the ability of the tuber to store food reserve (Abang *et al.*, 2003). These symptoms lead to reduced yield and thus food insecurity for smallholder farmers who depend on yam as their main food crop.



Figure 4: Leaf symptoms of yam anthracnose. Source: <https://africayam.org/download/screening-resistance-yam-anthracnose-disease/>

The disease has been reported in most West African countries, including Nigeria, Cameroon, Benin, Ghana, Togo, and Cote d'Ivoire. It is destructive, capable of causing yield reduction of up to 80% in high quality in West Africa (Akem, 1999). This considerable loss contributes to food insecurity in countries that heavily depend on the crop as their staple food, for instance, Nigeria.

Although yam is an important food crop in the African tropics and anthracnose has been reported as one of the primary diseases of the crop, little attention in terms of research has been paid in the region. This has led to limited information regarding the progress in managing and status of the disease is limited.

Anthracnose of coffee (coffee berry disease): Coffeeberry disease (CBD) is caused by *C. kahawae* ssp. *kahawae* (Weir *et al.*, 2012). The disease is destructive to coffee berries and is most common in African countries though it has also been reported in other parts (Waller *et al.*, 2007, Nguyen, 2010).

In tropical Africa, the disease was reported in Kenya for the first time, and since then, it has spread to other countries. So far, it has been reported in Angola, Congo DRC, Tanzania, Uganda, Malawi, Ethiopia, Cameroon, Zambia, and Zimbabwe (Belachew and Teferi, 2015). It is known to affect the plant at all stages of coffee berry, from flower setting to ripening of fruit, though infection of green berries is known to cause maximum losses (Belachew and Teferi, 2015).

Anthracnose of banana: Banana anthracnose is caused by *Colletotrichum musae* (Weir *et al.*, 2012) and has been reported as an important disease of bananas in many countries. The pathogen is known to infect mature fruits, especially in storage, and thus, anthracnose of banana is a postharvest disease. However, the infection has also been

reported to occur to immature fruits in the field, though symptoms of the disease appear at a ripening stage after germination of the fungal appressoria forming infection hyphae. Symptoms of the disease include black and sunken lesions with spore masses on the fruit (Chillet *et al.*, 2005).



Figure 5: Coffeeberry disease symptoms (Source: <https://www.cirad.fr/en/news/all-news-items/articles/2010/science/coffee-berry-disease>).

Studies show that Coffeeberry disease reduces the coffee yield significantly in different countries in the African tropics, affecting the economy of these countries, which partly depend on coffee export. Yield losses exceeding 80% in most countries in this region are common under favourable growth conditions for the pathogen (Silva, 2010). Waller *et al.* (2007) reported losses reaching 80% in Cameroon, whereas up to 90% of the crop has been reported to be destroyed by the disease in Tanzania (Ngulu *et al.*, 1998). Comparable losses have also been reported in other countries, including Kenya, 80% (Kebati *et al.*, 2016). In Ethiopia, complete yield loss due to coffeeberry disease is possible if susceptible landraces are grown (Belachew and Teferi, 2015). Although estimated losses due to the disease could not be captured for some countries, it remains a significant disease in Malawi (Phiri *et al.*, 2001) and Angola (Manuel *et al.*, 2010). However, a low incidence of the disease has been reported in Uganda, and the disease is considered minor in Rwanda but with the potential to cause significant economic loss in the future (Matovu *et al.*, 2013; Bigirimana *et al.*, 2012). Because the economies of most of the countries in the African tropics depend partly on coffee, and such huge losses have been a result of CBD, joint efforts to reduce such losses and increase the return from such an important crop are urgently recommended.



Figure 6: Banana anthracnose symptoms (Source: https://plantvillage.psu.edu/topics/banana/infos/diseases_and_pests_description_uses_propagation).

In tropical Africa, the disease has been reported in Kenya, Ethiopia, Tanzania, Uganda, Cote d'Ivoire, Zambia, Nigeria, Malawi, and Mozambique (CABI, 2001). Little information is available on estimated losses due to the disease in these countries. The fact that the ripe banana business is practised locally and subsistent in most of these countries compared to cooking banana which is the main food for many societies may be one of the reasons for little research efforts devoted by researchers to the disease in the region.

Cassava anthracnose: Cassava is one of the staple food crops in Africa, especially in the tropics. Its production is, however, constrained by anthracnose, among other diseases. Cassava anthracnose disease (CAD) was noticed for the first time in Tanzania in 1903 but spread to other countries where cassava is grown. In tropical Africa, the disease has been reported in East, West, and Central Africa (Fokunang *et al.*, 2001). It is a fungal disease caused by *Colletotrichum gloeosporioides* f.sp. *manihotis*. The available literature shows that this pathogen's identity is not resolved (Weir *et al.*, 2012). Necrotic lesions characterise the disease on leaves ranging from irregular to regular, and yellowing of leaves ultimately detach from the stem (William *et al.*, 2011) (Figure 7).

The development and severity of the disease are favoured by high humidity; hence it is severe in areas that receive heavy rains. A closed canopy facilitates humid retention and favourable conditions for the pathogen's survival and disease development (Fokunang *et al.*, 2001).

There is limited current information on the progress for disease management and yield losses caused by the disease in the African tropics. However, ancient studies reported severe infection and total crop failure when infected stems were used as cuttings in propagation (Ikotun and Hahn, 1991).



Figure 7: Leaf symptoms of CAD. Source: William *et al.*, (2011)

The lack of current information on the disease in the tropical African region as research outputs calls for more research to develop sustainable strategies to combat it, reducing losses and food insecurity in this region where cassava is a staple food crop.

Management options for anthracnose of *Colletotrichum* species in the tropics: Because anthracnose is a collection of diseases caused by *Colletotrichum* species, there is no single report on its management, but rather studies on the management of the disease have been done on specific species. However, management options for the disease in most cases include chemical, cultural, host resistance, biological control, and application of botanical fungicides (Mohammed 2013; Joshi, 2018).

Chemical methods: This method usually employs various synthetic or industrial fungicides in managing anthracnose. Several fungicides are available and currently used to manage anthracnose in various crops. For instance, Nuraini and Latiffah (2019) reported benomyl (benzimidazole) and difenoconazole as effective fungicides against *C. fructicola*, *C. siamense*, *C. truncatum*, *C. scovillei*, and *C. fiorinae*. Benlate, Mancozeb, Carbendazim and difenoconazole have been reported to inhibit the growth of *C. lindemuthianum* in beans (Amin *et al.*, 2014). Bavitin and Thiram effectively control several *Colletotrichum* species in the tropics (Choudhary *et al.*, 2013). Strobilurin, azoxystrobin, pyraclostrobin, and trifloxystrobin effectively manage anthracnose (Than *et al.*, 2008). Other fungicides which have been used to manage anthracnose in different crops include fludioxonil, propiconazole, benzovindiflupyr, azoxystrobin, thiophanate-methyl, difenoconazole, flusilazole, folpet, and Captan (Moral *et al.*, 2018)

Despite their effectiveness in managing anthracnose in many crops, fungicides are prone to resistance by *Colletotrichum* species in some cases, primarily when used for a long time (Staub, 1991). For instance, resistance of isolates of *C. gloeosporioides* from South Africa to benomyl has been reported (Farungsang and Farungsang, 1991; Sanders *et al.*, 2000). Further, there is evidence of the adverse effects of synthetic fungicides on human health and the ecosystem (Mwabulambo *et al.*, 2018). Therefore, alternative methods with less or no hazardous effects on the environment and human health must be considered to minimise the use and realised effects of synthetic fungicides.

Apart from synthetic fungicides, chemical plant defence activators have also shown potential to manage anthracnose in several crops. These chemicals activate the plant defence mechanisms upon application, including the expression of resistance genes (Edreva, 2004). Some of the activators that have shown potential to manage anthracnose include benzothiadiazole, Bion (2R,3R)-butanediol, salicylic acid (Jaiganesh *et al.* 2019), jasmonic acid (Alemu *et al.* 2019). Other activators with the potential to manage anthracnose include dibasic potassium phosphate (K₂HPO₄), acibenzolar-S-methyl (Benzo[1,2,3]thiadiazole-7-carbothioic acid-S-methyl

ester, ASM), and 2,6-dichloro-isonicotinic acid (DCINA) (Lopez and Lucas, 2002). Although these activators have shown potential to manage anthracnose in several crops, information on their availability and applications in the SSA region is still limited.

Host plant resistance: The use of resistant varieties/cultivars is the most reliable, cost-effective, environmentally and user-friendly, and stable strategy to manage most diseases in crops, including anthracnose (Miklas *et al.*, 2006; Tryphone *et al.*, 2013). Several crop varieties are known to possess genes that confer resistance against *Colletotrichum* species. For instance, Nguyen (2010) reported the availability of coffee cultivars resistant to *Colletotrichum kahawae* in Africa. Other important crops in the African tropics with resistant genes to *Colletotrichum* species include common bean (Kelly and Vallejo, 2004; Batureine, 2009; Gonçalves-Vidigal *et al.*, 2011), mango (Bhagwat *et al.*, 2015; Gupta *et al.*, 2015), banana (Zakaria *et al.*, 2009), chilli (Gupta *et al.*, 2018), sorghum (Prom *et al.*, 2012) and water yams (Egesi *et al.*, 2009). Even though host resistance is an economical approach, safe to farmers and the ecosystem, the pathogen populations are dynamic and evolving. Breeding programs, therefore, should focus on developing varieties with multiple resistance genes to avoid resistance breakdown due to the emergence of new pathogenic pathotypes.

Identification of resistance sources from local germplasm is a prerequisite for breeding for disease resistance. The availability of some cultivars with resistance to *Colletotrichum* species in the region provides an opportunity to combat this destructive disease. Regular screening of the cultivars is therefore recommended to identify such resistant genotypes. Multiplication and dissemination of the identified cultivars to farmers in the region are also imperative if sustainable disease management is to be achieved.

Host resistance is expected to reduce the use of synthetic fungicides in managing anthracnose in various crops. However, in the African tropics, particularly in rural areas where agriculture is mainly practised, developed resistant varieties may reluctantly not be adopted by farmers for cultivation due to unsatisfactory agronomic performance, availability, and accessibility, among other reasons. On this basis, farmers in most countries in tropical Africa still use local varieties, susceptible to diseases, and with little yield. Therefore, research institutions in the region should be empowered to devote more efforts to developing, disseminating, and promoting such disease-resistant varieties and ensuring their availability to farmers at affordable prices.

Cultural methods: This method involves the adherence of farmers to good farming practices both on-farm and postharvest. These practices may differ depending on the crop but generally include crop rotation for at least two

years with non-host crops, using pathogen-free planting material (seeds, cuttings, or seedlings), and destruction or burying of plant residues in infected fields. Because wet conditions favour the development of the disease, promoting dry conditions is also recommended as another management option for anthracnose. This is usually achieved using optimum spacing between plants (Fokunang *et al.*, 2001; Oo and Oh, 2016).

For perennial crops like avocado, coffee, and mango, removing fallen plant residues and annual pruning of the plants has been practised to manage anthracnose with success. Also, intercropping such crops with non-hosts crops of anthracnose has successfully reduced the disease epidemics (Arauz, 2000). All these practices aim to exclude the pathogen in the fields or create unfavourable conditions for the growth of the pathogen and/or disease development.

Adherence to these cultural practices is essential and the best option to minimise the effects and losses of anthracnose in key cash and food crops in the African tropics. Some studies have proved that cultural practices can significantly reduce disease effects. For instance, Marley *et al.* (2005) reported that cleaning the fields after harvest and before planting significantly reduced sorghum anthracnose disease severity and incidence in West and Central Africa. Using healthy planting materials significantly reduces anthracnose in yams (Green and Simons, 1994). Bedimo *et al.* (2007) also reported the efficacy of pruning of plants and mixed cropping in limiting the development of anthracnose of coffee berries in Cameroon. A good number of reports show similar evidence on the role of cultural practices in managing anthracnose in the African tropics. Therefore, through extension services, farmers should be educated on the importance of this method and how to practice these management measures efficiently.

Biological control: The application of biological agents in managing plant pathogens has recently attracted the attention of plant pathologists as it is one of the safe methods, environmentally friendly and causes no harm to humans (Palaniyandi *et al.*, 2011). Studies have shown promising prospects in managing anthracnose caused by *Colletotrichum* species in the tropics using biological agents. Several species of bacteria and fungi that inhibit the growth of *Colletotrichum* species and reduce anthracnose incidences have been identified. For instance, some species of *Trichoderma* have shown the ability to control anthracnose in various crops. Choudhary *et al.* (2013), Kamble *et al.* (2015), Musakhan and Zacharia (2017) reported the efficacy of *Trichoderma viride* and *Trichoderma polysporum* in managing *Colletotrichum* species in chilli. Also, Amin *et al.* (2014) recommended *Pseudomonas fluorescens* as a seed treatment to manage anthracnose in common beans. Some species of *Streptomyces* have also been reported as

potential biological control agents in managing anthracnose in yams (Palaniyandi *et al.*, 2011). *Candida membranifaciens*, *Brevundimonas diminuta*, and *Stenotrophomonas maltophilia* can reduce postharvest losses in mango (Kefalew and Ayalew, 2008). Hernandez-Montiel *et al.* (2018) reported *Debaryomyces hansenii* as the effective biocontrol agent in papaya fruit. Further, *Pichia guilliermondii*, *Candida musae*, *Issatchenkia orientalis*, and *Candida quercitrusa* reduced the incidence of anthracnose in chilli (Chanchaichaovivat *et al.* 2007).

These biological agents interfere with the growth cycle of the pathogen and hence limit disease development. Previous studies using *Trichoderma* species as the model biological agents suggest that these agents employ either of these mechanisms to achieve the biocontrol activity:

Induction of systemic resistance: Treatment of biological agents to plants in the root zone has shown relatively higher levels of chitinase, peroxidase, and pathogenesis-related proteins (Howell, 2003). These factors are essential in the plant defence against the attacking pathogens. Therefore, it is so that these biological control agents can protect crop plants against pathogens.

Parasitism and antibiotic production: One of the characteristics of bioagents, particularly of the genus *Trichoderma*, is that they are good parasites of other fungal species. It is on this ground that these species can parasitise and hence inhibit the growth of plant pathogens. Some species are also known to produce lethal compounds to plant pathogens (Howell, 2003). Availability of information from these studies on the potential of biological control agents in managing anthracnose diseases in tropical Africa calls for further efforts to formulate these agents on a large scale to be accessible to farmers and at relatively affordable costs. These bioagents are safe to farmers, consumers, and the ecosystems, suggesting their potential to save as an alternative to synthetic fungicides.

Botanical fungicides: Plants possess several secondary metabolites, including alkaloids, essential oils, saponins, phenols, flavonoids, steroids, and quinines. Some of these substances are known to have antimicrobial properties. Among them are glucosinolates, acetaldehydes, essential oils, and jasmonates which have shown potential as fungicides and alternatives to other methods that have not effectively managed plant pathogens (Tripathi and Shukla, 2010).

There are two forms of plant products that can be used to manage plant diseases, essential oils and plant extracts. These products are known to exert fungistatic or fungicidal effects on the phytopathogens, or they may maintain unfavourable conditions for the growth and establishment of the pathogens to the host (Scheuerell

and Mahaffee, 2002). Some studies also have reported that these products induce systemic resistance to susceptible host plants. A study by Hassan *et al.* (2009), among other studies, reported the increased activity of enzymes related to plant defence such as polyphenol oxidase, peroxidase, and phenylalanine ammonia-lyase following treating plant leaves with plant extracts.

The use of botanical fungicides in managing anthracnose in tropical Africa has not been extensively explored. Some studies have reported the potential of some plant species in the management of *Colletotrichum* species (Amadioha, 2003; Alemu *et al.*, 2014; Masangwa *et al.*, 2013; Bazie *et al.*, 2014; Gwa and Nwankiti, 2017; Musakhan and Zacharia, 2017) among others. Despite the availability of such information on the potential of using

plant products to curb anthracnose, little is known on the commercial availability of botanical formulations for application by farmers in tropical Africa. Smallholder farmers traditionally use this method on small plots. This, therefore, calls for more research on developing botanical formulations for the management of these diseases in the region. These formulations should be not only safe for humans but also affordable to farmers.

Limitations of management methods for anthracnose: Anthracnose management methods discussed here are facing limitations despite being effective in some ways (Table 2). In tropical Africa, the choice of the method is subject to its accessibility and affordability and not its effectiveness.

Table 2: Strengths and weaknesses of common management methods for anthracnose.

Management option	Strengths	Limitations
Chemical method	Proved effective against many species of <i>Colletotrichum</i> Available to farmers even in rural Setting Gives immediate results	Relatively expensive Limited by resistance from some of the species Cause adverse effects to the ecosystem and human health
Biological agents	Provide long term effect, no regular applications Safe to the environment and human health Mostly, it is specific to the target Pathogen	Not readily available to farmers in rural settings Relatively expensive to subsistence farmers It does not provide immediate results
Host resistance	Effective in managing many species	In most cases, it is a single gene the resistance, which can be easily broken down Pathogenic variability of some species renders resistant varieties susceptible
Cultural methods	Relatively less expensive and reliable Not associated with environmental or human adverse effects Eco-friendly method Relatively less expensive	Resistant varieties sometimes not accessible and adopted by farmers Smallholder farmers own small plots, rotation or fallowing is impractical Some farmers cannot afford to buy certified planting materials like seeds Maintaining unfavourable conditions to the pathogens in fields is laborious and not economical
Use of botanicals	Locally available and relatively Inexpensive Have fewer residual effects to the ecosystem and human health	Overexploitation of medicinal plant species may lead to their extinction Little scientific knowledge to farmers on the importance and effectiveness of botanicals

Challenges for managing *Colletotrichum* in tropical Africa: Several factors challenge the total management

of anthracnose caused by *Colletotrichum* species in various crops. These include:

Diversity, cross-infection nature, and broad host range of some species: *Colletotrichum* is among the most diverse groups of fungi, and recent studies have reported more than 190 species of this genus, with most of them being pathogenic to a wide range of crops in tropics and subtropics (Jayawardena *et al.*, 2016). In many cases, it has been reported that one species of *Colletotrichum* is capable of infecting and causing anthracnose symptoms to more than one host species, and different pathogen species can infect a single host and induce symptoms. Such species include *C. gloeosporioides* (Darvas and Kotze, 1987; Hindorf, 1999; Hillocks, 2002; Gyempeh *et al.*, 2015), *C. lindemuthianum* (Wortmann and Allen, 1994; Mohammed, 2013), *C. graminicola* (Marley *et al.*, 2005) and *C. capsici*. This lack of host specificity and cross-infection nature among species brings a challenge in managing these destructive pathogens. Also, in a situation where many species infect a single host, it is difficult to isolate and identify the species causing symptoms, thus impossible to target and manage it.

Pathogenic variability of some species: In some instances, several species of *Colletotrichum* exhibit pathogenic variation at race levels. For instance, the *Colletotrichum lindemuthianum* has been reported as one of the highly variable pathogens among other species of the genus. More than 182 physiological races of this species have been reported worldwide (Padder *et al.*, 2017), with the possibility of more races. These races differ in virulence, and therefore, one race may be virulent to one crop variety but not others. Similarly, resistance in some varieties can work only for some races, and the same suffer susceptibility to other races (Balardin *et al.*, 1997; Ansari *et al.*, 2004). Such variations have also been observed in other species, including *Colletotrichum gloeosporioides* (Palaniyandi *et al.*, 2011) and *C. sublineolum* (Marley *et al.*, 2001). This variation and emergence of new races bring another challenge in managing this pathogen, mainly using resistant varieties.

Adverse effects and resistance to synthetic fungicides: Despite their effectiveness in managing anthracnose in many crops, fungicides are prone to resistance by *Colletotrichum* species in some cases, especially when used for a long time (Staub, 1991). For instance, resistance of isolates of *C. gloeosporioides* from South Africa to benomyl has been reported (Farungsang and Farungsang, 1991; Sanders *et al.*, 2000). The use of synthetic fungicides has also been reported to pose adverse effects to the environment and health of farmers and consumers (Wightwick *et al.*, 2009; Komárek *et al.*, 2010). The risk is even worse in developing countries, mainly tropical Africa, where farmers spray these fungicides unprotected using risky and straightforward tools. A recent study in Tanzania revealed severe health

problems associated with exposure to these agrochemicals among farmers and applicators (Mwabulambo *et al.*, 2018). This calls for alternative management options that would minimise the effects of such chemicals on ecosystems and human health.

Prospects for managing *Colletotrichum* species in African tropics: Following the adverse effects on the ecosystem, farmers, consumers, and environment in general caused by synthetic chemicals, the world's focus is to reduce such chemicals by promoting alternative options. Pathogen exclusion in fields remains the best and recommended strategy to control *Colletotrichum* species in tropical Africa. Gene pyramiding in some cultivars with resistance to *Colletotrichum* species and desirable traits is also a promising strategy to curb the challenge of pathogen variability in some species, which develop into several pathotypes. In this case, cultivars with multiple resistance genes to several pathotypes need to be developed. Furthermore, the fact that African tropics are blessed with diverse plant species with medicinal properties, future research should focus on exploring the potential of botanical-based fungicides in managing *Colletotrichum* species in the region. Therefore, more efforts should be made on developing formulations from plants known to have antifungal compounds against *Colletotrichum* species. This would, in turn, reduce reliance on synthetic fungicides, which have been associated with environmental and human health side effects. In tropical Africa, the use of biological control options to manage anthracnose, among other plant diseases, has not been at a level that farmers in rural areas can access and afford. The availability of such agents to farmers is also still a challenge. In the future, investment in research and development of formulations on a large scale is expected to reduce the losses caused by anthracnose in tropical Africa. Investment in research, especially gene pyramiding to develop multi-resistant varieties, is also highly recommended.

Conclusion: Anthracnose caused by *Colletotrichum* species causes significant losses in various leading cash and food crops, especially in tropical regions of Africa. Total management of this devastating disease has not been achieved due to several factors, including variable and cross-infection nature of the pathogens, the ability of some species to evolve mechanisms that counter the host's immunity factors and ineffective management options currently available. More efforts are therefore needed to develop effective control strategies to curb this disease. There is limited current information on the management of anthracnose in the region. More studies are needed with a focus on developing new disease management strategies. Future studies should include exploiting and using botanical fungicides and developing crop varieties with multiple resistance genes to *Colletotrichum* species.

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