# *Colletotrichum*, naming, control, resistance, biocontrol of weeds and current challenges

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*Colletotrichum* is one of the most economically important fungal genera which causes anthracnose disease, affecting a wide range of hosts, especially tropical and subtropical crops, reducing yield and quality of the plant products. There has been a surge of interest in this genus and this paper reviews information on *Colletotrichum* from these studies. Most important for the study of *Colletotrichum* species is the need to understand species concepts and enable accurate identification based on morphology and molecular methods. A polyphasic approach for defining species include morphology, multigenes analysis physiology, symptoms on different hosts, pathogenicity and testing on a range of hosts. The disease life cycle, use in biological control and currently accepted names of *Colletotrichum* are discussed and updated as such information will support effective disease control management.

**Key words** – Anthracnose – Biocontrol – Disease resistance – Infection processes – Plant disease

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## General introduction to *Colletotrichum*

*Colletotrichum* is one of the most economically important plant pathogenic genera causing anthracnose of fruits and leaves of a wide range of hosts worldwide, and particularly in the tropics and subtropics (Sutton 1992, Hyde et al. 2009a, 2010). The above-ground parts of plants and fruit trees can be affected by *Colletotrichum* anthracnose and in the case of fruit infection results in reduction in quantity and/or quality and post harvest losses (Phoulivong et al. 2010a). *Colletotrichum* species have been reported to cause disease of many hosts in Thailand such as chili (*Capsicum* spp.), guava (*Psidium guajava*), jujube (*Zizyphus mauritiana*), mango (*Mangifera indica*), papaya (*Carica papaya*) and rose apple (*Eugenia javanica*) (Damm et al. 2009, Freeman et al. 1996, Kim et al. 2009).

*Colletotrichum* species are cosmopolitan and it has been shown that multiple species can infect a single host, while a single species can infect multiple hosts (Cai et al. 2009, Hyde et al. 2009). Fungus/host relationships are broad, imprecise and often overlapping (Freeman et al. 1996), although relationships are becoming more clearly defined of late. It is also believed that *Colletotrichum* species may adapt to new environments (Sanders & Korsten 2003), leading to serious cross infection problems in plant production. The study of pathogenic variability of *Colletotrichum* species is therefore important and the understanding of the host range of a particular pathogen may help in efficient disease control and management (Whitelaw-Weckert et al. 2007).

Previous studies have shown that anthracnose and fruit rot of tropical fruits is mainly caused by *C. gloeosporioides* and to a lesser extent *C. acutatum*. These results however, were based on morphological identification or if gene sequence data were used comparisons were often made with wrongly applied names (Cai et al. 2009). Epitypification of many important *Colletotrichum* species has now occurred (Table 1). In a recent paper of fungi from anthracnose disease of tropical fruits in Thailand (Phoulivong et al. 2010a), it was found that none of the *Colletotrichum* isolates were *C. acutatum* or *C. Gloeosporioides*. Thus, the previous understanding that anthracnose of most tropical fruits is caused by *C. acutatum* and *C. gloeosporioides* is incorrect.

Cultural, conidial and appressorial characters can be used to differentiate taxa into species complexes, but cannot easily separate species within a complex (Cai et al. 2009). Certain species however, have distinct morphological characters or growth rates. For example *Colletotrichum siamense* colonies are pale yellowish to pinkish with dense white-greyish aerial mycelium, and the growth rate is 9.12 ± 1.95 mm/day as compared to *Colletotrichum fructicola* with grey to dark grey colonies, dense pale grey aerial mycelium, and are fast growing (growth rate 10.72 ± 0.53 mm day, Prihastuti et al. 2009) that can be used in tandem with molecular data to distinguish species (Prihastuti et al. 2009, Yang et al. 2009).

The generally accepted bar-coding gene for fungi, the internal transcribed spacer (ITS) region, does not adequately resolve species in *Colletotrichum*, however, this gene can resolve species complexes (Cai et al. 2009). The six gene regions presently recommended for resolving *Colletotrichum* species are actin (ACT), β-tubulin (TUB2), calmodulin (CAL), glutamine synthetase (GS), glyceraldehyde-3-phosphate dehydrogenase (GPDH) genes and the complete rDNA-ITS (ITS) region (Cai et al. 2009, Phoulivong et al. 2010b). Prihastuti et al. (2009) were able to resolve *Colletotrichum asianum*, *C fructicola*, *C. horii*, *C. kahawae* and *C. gloeosporioides* in the "gloeosporioides" complex using these five genes. Another novel species in the "gloeosporioides" complex, i.e. *C. siamense*, however, received only moderate support and further genes are needed to resolve phylogenetic relationships of this species. Ideally a single housekeeping gene needs to be found that can readily differentiate between *Colletotrichum* species (Noireung et al. 2011).

## History of the study of *Colletotrichum*

*Colletotrichum* was first reported by Tode (1790) in *Vermicularia*, but was later redescribed as *Colletotrichum* (Corda 1837) in the order Melanconiales; class Coelomycetes; subdivision Deuteromycotina. *Colletotrichum* species comprise imperfect or asexual taxa which have a *Glomerella* teleomorph stage (Sutton 1992). *Colletotrichum* comprises

**Table 1** Reports of *Colletotrichum* species infecting tropical fruits.

| Fruit | *Colletotrichum* species | References |
|---|---|---|
| Avocado (*Persea americana*) | *C. acutatum*, *C. gloeosporioides* | Hindorf et al. 2000, Peres et al. 2002, Everett 2003, Giblin et al. 2010. |
| Banana (*Musa* spp.) | *C. musae* | Postmaster et al. 1997, Peres et al. 2002, Photita el al. 2004, Nuangmek et al. 2008. |
| Chili (*Capsicum annuum*) | *C. acutatum*, *C. capsici*, *C. gloeosporioides* | Kanchana-udomkarn et al. 2004, Than et al. 2008a, Kim et al. 2009, Ratanacherdchai et al. 2010. |
| *Citrus* spp. | *C. acutatum*, *C. gloeosporioides* | Hindorf et al. 2000, Chen et al. 2005, Fischer et al. 2009, MacKenzie et al. 2009. |
| Coffee (*Coffea arabica*) | *C. acutatum*, *C. asianum*, *C. boninense*, *C. capsici*, *C. fructicola*, *C. kahawae*, *C. gloeosporioides*, *C. siamense* | Nguyen et al. 2009, Prihastuti et al. 2009, Van der Vossen & Walyaro 2009. |
| Dragon fruit (*Hylocereus undatus*) | *C. gloeosporioides* | Masyahit et al. 2009. |
| Durian (*Durio zibethinus*) | *C. gloeosporioides* | Alahakoon & Brown 1994, Pongpisutta and Sangchote 1994, Freeman et al. 1996. |
| Guava (*Psidium guajava*) | *C. acutatum*, *C. gloeosporioides* | Hindorf et al. 2000, Alahakoon & Brown 1994, Peres et al. 2002, Amusa et al. 2006, Soares et al. 2008. |
| Jasmine | | |
| Mango (*Mangifera indica*) | *C. acutatum*, *C. gloeosporioides* | Peres et al. 2002, Alahakoon & Brown 1994, Kefialew & Ayalew 2008, Nelson 2008, Giblin et al. 2010. |
| Mangosteen (*Garcinia mangostana*) | *C. gloeosporioides* | Alahakoon & Brown 1994. |
| Passion fruit (*Passiflora* spp.) | *C. acutatum*, *C. gloeosporioides* | Hindorf et al. 2000, Peres et al. 2002. |
| Papaya (*Carica papaya*) | *C. acutatum*, *C. capsici* and *C. gloeosporioides* | Peres et al. 2002, Rahman et al. 2008. |
| Rose apple (*Syzygium jambos*) | *C. gloeosporioides* | Alahakoon & Brown 1994. |
| Rambutan (*Nephelium lappaceum*) | *C. gloeosporioides* | Farungsang et al. 1994, Sivakumar et al. 1997, Wijeratnam et al. 2008. |
| Strawberry (*Fragria frageriae*) | *C. acutatum*, *C. gloeosporioides*, *C. fragariae* | Schiller et al. 2006, Jelev et al. 2008, Hyde et al. 2009a, MacKenzie et al. 2009. |
| *Therbroma cacao*, | *Colletotrichum ignotum* | Rojas et al. 2010. |
| *Tetragastri panamensis* | *Colletotrichum tropicale* | Rojas et al. 2010. |

number of endophytic, saprobic and plant pathogenic species, the latter of worldwide importance on a wide range of economic crops and ornamentals (Cai et al. 2009, Hyde et al. 2009a,b, Prihastuti et al. 2009, Yang et al. 2009, Phoulivong et al. 2010b).

*Colletotrichum* is one of the most important plant pathogens worldwide causing anthracnose disease in a wide range of hosts including cereals and grasses, legumes, vegetables, perennial crops and tree fruits (Lubbe et al. 2006, Abang et al. 2009, Crouch et al. 2009, Kim et al. 2009, Masyahit et al. 2009, Ratanacherdchai et al. 2007, Ratanacherdchai et al. 2010). *Colletotrichum* species have also been found on wild fruits in Hong Kong (Tang

et al. 2000). *Colletotrichum acutatum*, *C. capsici* and *C. gloeosporioides* have been reported causing anthracnose disease on chili fruits in Thailand (Than et al. 2008a). *Colletotrichum* species that cause serious plant disease are also commonly isolated as endophytes from healthy plants and have been identified as saprobes on dead plant material (Photita et al. 2004, Cai et al. 2009, Hyde et al. 2009, Prihastuti et al. 2009, Phoulivong et al. 2010b). In addition to being plant pathogens, *Colletotrichum* strains have also been used as biological control agents against weeds (Templeton 1992).

The pathogenesis of *Colletotrichum* is diverse, arising from nutritional and ecological diversity within the genus, which varies from intracellular hemibiotrophy to subcuticular intramural or abiotrophic necrotrophy (Bailey & Jeger 1992, Pring et al. 1995). Specialized infection structures are produced by *Colletotrichum* species such as germ tubes, aprèssoria, intracellular hyphae and secondary necrotrophic hyphae (Perfect et al. 1999, Rojas et al. 2010). *Colletotrichum* infect hosts by either colonizing subcuticular tissues intramurally or being established intracellularly. The pre-infection stages of the both infection types in *Colletotrichum* are very similar, in which colonization of conidia of susceptible hosts include adhesion, germination, appressoria formation and penetration (Du et al. 2005).

The pathogens colonize the intramural region beneath the cuticle, invading in a necrotrophic manner and spread rapidly throughout the tissues (O′Connell et al. 1985). There is no detectable biotrophic stage of parasitism form. In contrast, most anthracnose pathogens exhibit abiotrophic infection strategy initially by colonizing the plasmalemma and cell wall intracellularly. The biotrophic stage which is generally short-lived includes all events in which infection develops without visible disruption of host systems. Subsequently, intracellular hyphae colonize one or two cells and produce secondary necrotrophic hyphae (Bailey et al. 1992). *Colletotrichum* are regarded as hemiobiotrophs or facultative biotrophs (Kim et al. 2004). An example of hemiobiotrophy is found in infection of avocado, chili and citrus by putatively named strains of *C. gloeosporioides* which produce both intracellular biotrophy at an early stage and later intramural necrotrophy. Though, the infection process in *Colletotrichum* species is apparently similar in the pre-penetration process, there are differences between species in the later process such as conidial adhesion, melanization and cutinization in penetration of the plant cuticle by the appressoria (Rojas et al. 2010).

**Symptoms of *Colletotrichum* diseases on leaves and fruits**

*Colletotrichum* species cause anthracnose of various hosts most frequently in humid and sub-humid tropical regions. Strains can often be isolated from disease tissues of stems, leaves, flowers and fruits of a wide range of crops and especially fruit trees (Freeman et al. 2001, Peres et al. 2002, Kim et al. 2009, Crouch et al. 2009, MacKenzie et al. 2009). Crop loss is a result of reduction in quantity and/or quality of total yield. The pathogen is capable of affecting various plant parts such as root, twigs, leaves, blooms and fruit, causing a range of symptoms such as crow root rot, defoliation, bloom blight and fruit rot (Lubbe et al. 2006). Symptoms on the fruit first appear as sunken, water-soaked lesions that expand rapidly on the fruit (Voorrips et al. 2004). Fully expanded lesions are soft, sunken and range in colour from dark red to tan to black, generally described as anthracnose disease (Wharton & Dieguezuribeondo 2004). *Colletotrichum acutatum* mainly affects fruits, but branches, twigs and leaves can occasionally be affected and severe defoliation of trees has been reported (Chen et al. 2005, MacKenzie et al. 2009). Moreover *C. acutatum* is a major pathogen of various disease complexes where more than on *Colletotrichum* species is associated with a single host (Than et al. 2008a,b). In the case of strawberry, *C. acutatum*, *C. gloeosporioides* and *C. fragariae* cause anthracnose with up to 80% plant death in nurseries and yield losses of over 50% (Sreenivasaprasad & Pedro 2005, Hyde et al. 2009b), *Colletotrichum acutatum* mainly causes fruit rots on strawberry, but can also infect various other parts. An unusual strawberry root necrosis was observed in Israel in 1995–1996 during a major anthracnose outbreak (Freeman et al. 2002). *Colletotrichum acutatum* isolates recovered from these plants did not differ from isolates from plants with

typical anthracnose symptoms (Freeman et al. 2000).

Fruit infections caused by *C. acutatum* can lead to economically import losses on various crops. For example, *Colletotrichum acutatum* cause major losses in strawberry production worldwide, and is frequently responsible for important yield losses (Mertely & Legard 2004). It is also responsible for poor olive oil quality (Rhouma et al. 2010). Post-blossom fruit drop of citrus (*Citrus* spp.) is caused by *C. acutatum* and was first identified in Belize an then found throughout the humid tropical citrus areas of the Americas (Chen et al. 2005, Sreenivasaprasad & Pedro 2005). Damage to tamarillo (*Cyphomandra betacea*) fruit occurred with yield loss of more than 50% in Colombia (Sreenivasaprasad & Pedro 2005).

During infection by *Colletotrichum codylinicola*, the first symptoms are multiple small lesions; these can rapidly cover most of the fruit (Roberts et al. 2001). As the infection progresses, the surface of the lesion becomes covered with wet, gelatinous, buff to salmon-coloured spores that exude from acervuli that may contain numerous black setae either scattered or in concentric rings within the lesions (Esquerré-Tugayé et al. 2000, Fig 1). The formation of setae gives the overall lesion its black colouration (Zitter 2004). Foliage and stem symptoms appear as small, irregularly-shaped gray-brown spots with dark brown edges (AVRDC 2004, Fig. 1).

### *Colletotrichum* and plant disease

*Colletotrichum* affects the leaves, flowers and fruits of many important crops (Sutton et al. 1992, Abang et al. 2009). Flower infection (blossom blight) can destroy flower and young fruit and cause complete crop failure (Adaskaveg & Förster 2000, Farungsang et al. 1994, Freeman et al. 1998, Jeger & Plumbley 1998). This may lead to an extended flowering period as the trees compensate for lowered fruit infection causing premature fruit drop (Hindorf et al. 2000). Major post harvest losses also occur during fruit ripening when quiescent infections break out and cause spreading black lesions (Than et al. 2008c, Phoulivong et al. 2010a). Heavy infection causes rapid rotting and even light infection which mainly causes cosmetic damage that may shorten the storage life of the fruit as (Kim et al. 2009, Ratanacherdchai et al. 2010, Fig. 1).

### Morphological characters

Morphological characterization used to identify *Colletotrichum* species are the shape and size of conidiomata (acervuli), conidia, conidiophores, setae, conidiophores, aprèssoria and setae in culture (Sutton 1992, Cai et al. 2009, Than et al. 2008c). The conidia of *Colletotrichum gloeosporioides* are oblong with obtuse ends, and are generally broader than conidia of *C. fragariae* and *C. acutatum* (Gunell & Gubler 1992). In general, conidia of *C. acutatum* are elliptic to fusiform, whereas conidia of *C. gloeosporioides* are oblong with obtuse ends (Freeman et al. 1998).

However morphological characters overlap between species and morphology alone does not provide sufficient information for a precise identification, especially for those species in the *C. gloeosporioides* and *C. dematium* complexes. Crouch et al. (2009) considered that conidial size and shape, along with conidial appressoria were taxonomically uninformative and of little use for species diagnosis in graminicolous *Colletotrichum* species. Species with similar morphological characteristics may have considerable variation at the physiological and pathogenic levels. Taxonomy based on morphology alone is likely to result in ambiguity and morphological characters should be used in conjunction with other characters to establish species relationships within *Colletotrichum* (Cai et al. 2009, Prihastuti et al. 2009).

### Disease cycle and epidemiology

The epidemiology of several anthracnose diseases of tropical fruits has been studied at various stages of crop development (Freeman et al. 1998, Jeger & Plumbley 1998, Kim et al. 2004). In most *Colletotrichum* disease, conidia are water-borne with the occurrence of quiescent infections being highest during the wettest periods of the growing season (Wharton & Deiguez-Uribeondo 2004). In avocado, citrus, papaya and mango it has been shown that infected leaves in the tree canopy are the main source of inoculum, with conidia being rain-splash dispersed to unripe fruit (Hindorf et al. 2000). However, in mango and citrus disease, infected flowers also contribute to the conidia

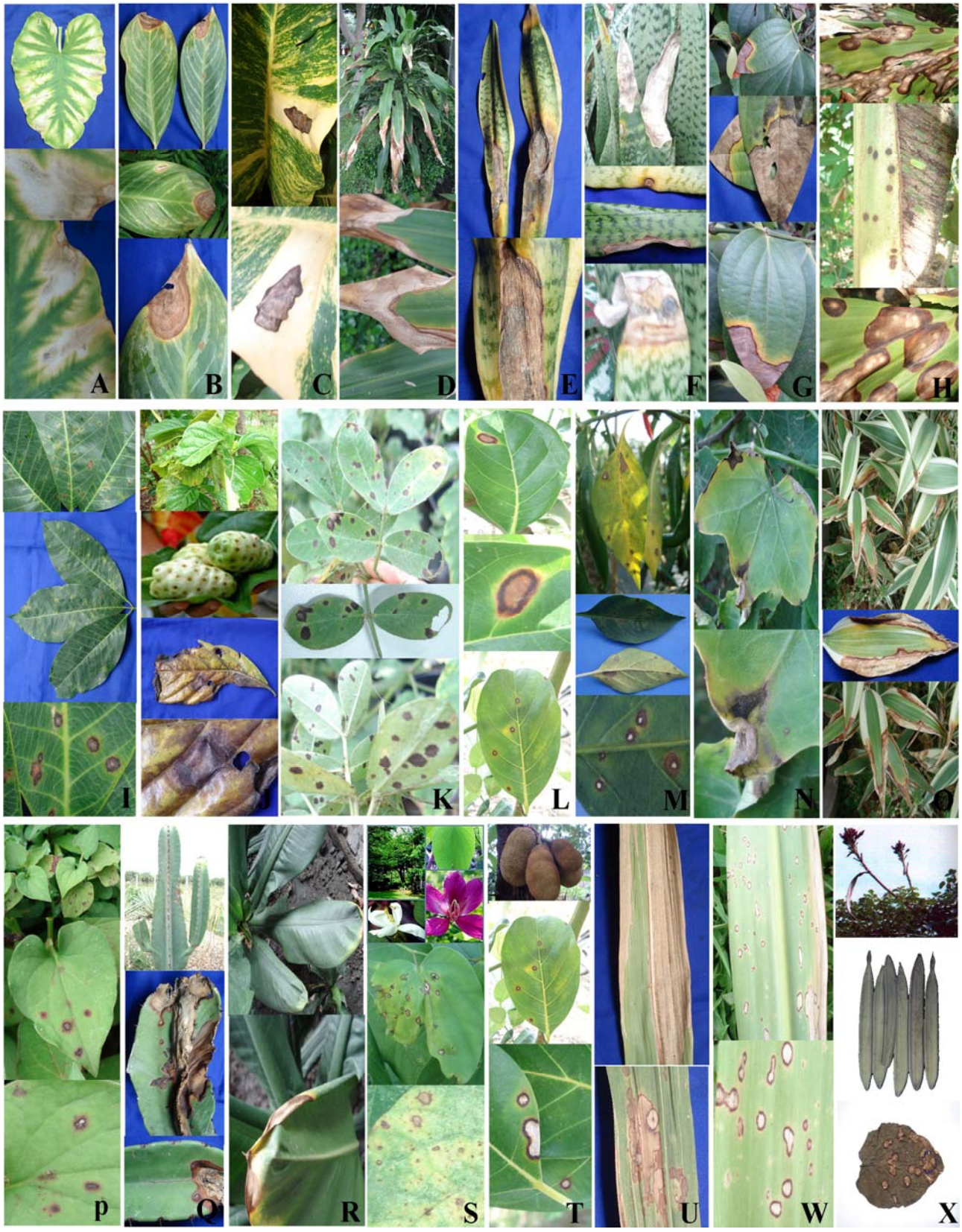


**Fig. 1(a–x)** – Symptoms of *Colletotrichum* sp causing anthracnose disease on leaves, **A** *Alocasia indica*, **B** *Aglaonema ssp*., **C** *Scindapsus aureus*, **D** *Dracaena fragrans*, **E,F** *Sansevieria spp*, **G** *Piper nigrum*, **H** *Caryota mitis*, **I** *Hevea brasiliensis*, **J** *Morinda Citriforia*, **K** *Arachis hypogaea*, **L** *Artocarpus heterophyllus*, **M** *Capsicum annuum*, **N** *Coccinia grandis*, **O** *Dracaena sanderiana*, **P** *Houttuynia cordata*, **Q** *Creus hexagonus*, **R** *Diffenbaschia sp*., **S** *Bauhinia saccocalyx*, **T** *Artocarpus heterophyllus*, **U** *Saccharum officinarum*, **W** *Saccharum* sp., **X** *Oroxylum indicum*.

inoculum source (Chen et al. 2005, Abang et al. 2009). Infection by *Colletotrichum* can take place at all stages of fruit development. In blueberry, the fungus is thought to over winter as mycelium in and on blighted twigs, which act as the main source of inocula in spring (Sutton 1992). However, recent data suggest that the primary source of overwintering inoculum may be from dormant flower buds (Van Der Vossen & Walyaro 2009). In studies carried out on the cultivar 'Blue crop' in New Jersey, flower buds accounted for 72% of overwintering infections (Wharton & Deiguez-Uribeondo 2004). In screening experiments carried out on the susceptible cultivar 'Jersey' in Michigan, 57% of healthy looking flower buds were found to be infected, and of those infected, 82% of the infections were caused by *C. acutatum* (Wharton & Deiguez-Uribeondo 2004). It was observed that flower buds broke dormancy, the fungus grew out of the buds and colonized the surrounding stem tissue, causing black lesions around the infected buds. These lesions gradually grow from small to large and cause the death of flower bud after about seven days to produce a pore on death tissue (Freeman et al. 2000). In the field, the fungus sporulates on infected tissue during periods of extended wetness in the spring, and conidia of *C. acutatum* are dispersed by rain splash. As in citrus and strawberry, secondary conidiation, may play a role in early-season dispersal of *C. acutatum* conidia on blueberries (Wharton & Deiguez-Uribeondo 2004).

*Colletotrichum* species survive in and on seeds as acervuli and micro-sclerotia (Pernezny et al. 2003). They may also persist on alternative hosts such as other solanaceous or legume crops. *Colletotrichum* may also be introduced into fields on infected transplants or it may survive between seasons in plant debris or on weed hosts (Peres et al. 2002). Microsclerotia are naturally produced by *Colletotrichum* species to allow the fungus to lie dormant in the soil during winter or under stressed conditions. However, this mode of survival has not been confirmed for all species. Micro-sclerotia can survive for many years even throughout a 2 or 3 years crop rotation although significant reductions in inoculum are quite likely.

Conidia from acervuli and microsclerotia can be dispersed in water splash and thus spread to the foliage and fruit (Bailey et al. 1992). Cuticular wax layers of plants are one of the first barriers to fungal infection. New spores which are produced within the infected tissue are then dispersed to other foliage or fruits (Pernezny et al. 2003). Adhe-sive appressoria serve as survival structure until an infection peg penetrates the surface (Ratanacherdchai et al. 2010).

*Colletotrichum capsici* is a sub-cuticular intramural pathogen, indicating that it grows entirely beneath the cuticle and within the peri-clinical walls of the epidermal cells, causing dissolution of the wall structure (Bailey et al. 1992, Pring et al. 1995). An intramural network of hyphae is then formed, which spreads rapidly throughout the tissue exhibiting.

**Host range of *Colletotrichum***

*Colletotrichum* can affect host ranges with a worldwide diffusion and having a severe impact on crops (Cai et al. 2009, Hyde et al. 2009, Phoulivong et al. 2010). It is common to find that a single species of *Colletotrichum* infects multiple hosts such as apple (*Malus pumila*), avocado (*Persea americanna*), banana (*Musa sapientum*), coffee (*Coffea arabica*), citrus (*Citrus* spp.), guava (*Psidium guajava*), jujube (*Zizyphus mauritiana*), lime (*Citrus aurentiforia*), longan (*Euphoria longana*), papaya (*Carica papaya*), mango (*Mangifera indica*, olive (*Olea eupea*), papaw (*Carica papaya*), strawberry (*Fragaria frageriae*), sugar apple (*Annona squamosa*), tomato (*Lycopersicon esculentum*) (Bailey & Jeger, 1992, Simmonds 1965, Wharton & Deiguez-Uribeondo 2004). *Colletotrichum falcatum* is however, host-specific on sugar cane (*Saccharum officinale*) (Kumar et al. 2010, Malathi et al. 2002).

Previous data on host ranges of *Colletotrichum* species must however be treated with caution (Freeman et al. 1996, 2000, Hyde et al. 2010, 2011). Recent studies have shown that the ubiquitous species, *C. gloeosporioides* is not as common in the tropics as thought. In a study of *Colletotrichum* species causing anthracnose in Laos and Thailand no fruits were infected by *C. gloeosporioides*. In fact, molecular data has revealed that *C. gloeosporioides*

is a species complex comprising between 20 and 50 species (Hyde et al. 2009) The study of host range of *Colletotrichum* species is therefore an area of research that needs in-depth study and most previous data must be treated with caution (Hyde et al. 2010, 2011).

**Pathogenicity testing**

Artificial inoculation methods *in vitro* are commonly used to test the pathogenicity of a fungal species, as it is easy to control environmental conditions (Photita et al. 2004). Common inoculation methods for pathogenicity testing include drop inoculation and wound /drop inoculation (Kanchana-udomkan et al. 2004, Lee et al. 2005), micro-injection, and spraying with high pressure guns (Freeman 1996, Lin et al. 2002, AVRDC 2003, Sharma et al. 2005, Than et al. 2008b, Cai et al. 2009). The drop inoculation method involves dropping a spore suspension on to the surface of a fruit and the wound/drop method involves wounding the surface of the fruit by pricking it with a pin and then placing a drop of fungal spore suspension on the wounded tissue (Ratanacherdchai et al. 2010). The wound/drop method is more favourable since wounding allows the pathogenic isolate internal access to the fruit and enhances infection (Cai et al. 2009). The wound/drop method has been shown to be useful to select resistant varieties of *Capsicum annuum* from susceptible varieties (Lin et al. 2002). However some researchers are of the opinion that the wound/drop method is paramount to damaging the plant so much, that infection is inevitable.

Different hosts and their stages of maturity are important for testing the expression of resistance to *Colletotrichum* species. The interaction between fruit maturity stage and infection of colonisation may depend on the species of *Colletotrichum* (AVRDC 2002). Pathogenicity testing can provide data on the resistance of crops to the fungal taxon and is useful in plant breeding programs. It is also important for integrated disease management programs because the use of resistant plant varieties can reduce the negative effects of chemical use on the environment (Peres et al. 2004, Wharton et al. 2004, Ratanacherdchai et al. 2010).

*Colletotrichum gloeosporioides sensu-lato* has previously been listed to cause disease of a very wide range of fruits and infect leaves of many hosts in Thailand and Laos (Ratanacherdchai et al. 2007, Than et al. 2008c, Phoulivong et al. 2010, Hyde et al. 2011). *Colletotrichum gloeosporioides* was epitypified in 2008 with a living strain that has been sequenced with sequence data deposited in GenBank (Cannon et al. 2008b). This has enabled researchers to compare their isolates of *Colletotrichum* with the *C. gloeosporioides* epitype. This has resulted in the description of several new species in the *C. gloeosporioides* species complex (Prihastuti et al. 2009, Yang et al. 2009, Phoulivong et al. 2010, Noireung et al. 2011). With the introduction of several new species it is important to establish whether they are host-specific or have a wide host range as this will have important implications in disease control and management (Freeman et al. 2000, Sanders & Korsten 2003, Ratanacherdchai et al. 2009).

**Disease control management**

Effective control of *Colletotrichum* diseases usually involves the use of one or a combination of the following practices: using resistant cultivars, cultural control, chemical control and biological control using antagonistic organisms. The applicability of control strategies much depends on the characteristics of the crops on which they are being used as on the disease at which they are targeted (Wharton & Deiguez-Uribeondo 2004).

***Cultural control of Colletotrichum diseases***

Cultural control is related to the range of methods use to control diseases, mostly using tactics aimed at disease avoidance through phytosanitation, manipulation of cropping patterns or by enhancing resistance and avoiding predisposition (Roberts et al. 2001, Agrios et al. 2005). The ubiquitous nature of inoculum sources of *Colletotrichum* under suitable conditions reduce the effectiveness of many pre-harvest general phytosanitary practices. However, general orchard hygiene has a place in integrated disease control, as removal of obvious inoculation sources such as diseased leaves and fruit can increase the efficiency of chemical control (Waller 1988).

Cultural control refers to tactics aimed at disease avoidance through phytosanitation,

manipulation of cropping patterns, or by enhancing resistance and avoiding predisposition. For chili peppers, only seeds and seedlings that are pathogen free should be planted (Pernezny et al. 2003). Otherwise, seeds should be disinfected with a 30 minute soak in water at 52°C followed by fungicide treatment (AVRDC 2002, 2003. Healthy transplants should be used and transplant flats should be sanitized if they are to be reused (Kefialew & Ayalew 2008, Sreenivasaprasad & Talhinhas 2005; Sutton 1992). Broad-spectrum fumigants may be used in soil to control the pathogens and soil solarization may also be effective (Bailey et al. 1992). Proper plant spacing should be maintained to provide adequate movement of air around plants which helps reduce the severity of foliar diseases (Abang et al. 2009). If disease was previously present, chili peppers should be rotated with crops other than potato, soybean, beans, tomato, eggplant and cucurbits for three years (Pernezny et al. 2003, AVRDC 2004).

Crop rotation is one of the best ways to promote healthy crops production, since it helps minimizing diseases especially those caused by soil borne pathogens (Bailey et al. 1992). Mulch should be provided to reduce soil splash onto fruit and lower leaves. Overhead irrigation should be minimized or avoided to reduce periods of wetness. The field should have good drainage and be free from infected plant debris. Insects should be controlled to reduce fruit wounds as they provide entry points for *Colletotrichum* species (Roberts et al. 2001, Agrios et al. 2005, Than et al. 2008c).

A crucial cultural control for minimizing disease is to harvest vegetables and fruits as soon as they ripen, as otherwise anthracnose develops very readily (Jeyalakshmi & Seetharaman 1998, Kefialew & Ayalew 2008). In addition, proper sanitation techniques during processing of the harvested fruit, transporttation, packaging and storage should be adopted to minimize the resumption of growth of the dormant infection of the pathogen (Abang et al. 2009).

Covering fruit with paper bags is common place in many parts of the word. This method not only excludes insects from the fruit but also excludes *Colletotrichum* infection. When fruits are young the bags are placed over individual fruits or if small, over many fruits and left until mature. The type of bag used is important as fruits will rot in plastic and soft paper bags will disintegrate in heavy rain. This method is particularly useful for avocado, banana, guava, longan, mango, rose apple, santol and star fruit. (Nakasone & Paul 1998).

***Biological control of Colletotrichum diseases***

Biological control methods for *Colletotrichum* diseases have not received much attention until recently even although as early as the potential of biological control through the use of phyllosphere antagonists was discussed. Jeger & Plumbley (1988) reviewed possibilities for biological control of postharvest fruit diseases caused by *C*, *gloeosporioides* (Robert & Nakasorn 1998) when they found that an isolate of *Pseudomonas fluorescens* was successful in significantly reducing anthracnose development on mango as compared to the control fruit. However, the mechanism by which the bacterium was able to reduce anthracnose development is still unknown. These positive results indicated that there was considerable potential for the development of a biological control agent for control of mango anthracnose.

Most biological control methods are still at the research stage but recent progress has resulted in a number of new commercial products which have been developed for postharvest applications as this situation offers more advantages for biological control strategies (Korsten et al. 1997).

Biological control of anthracnose fruit rot and die-back of chili peppers with plant products in laboratories and field trials showed that the crude extracts from rhizome, leaves and creeping branches of sweet flag (*Acorus calamus* L), palmorosa (*Cymbopogon martini*) oil, and neem (*Azadirachia indica*) oil could restrict growth of the anthracnose fungus (Jeyalakshmi & Seetharaman 1998). Sweet flag extract in ethyl acetate showed good inhibitory effect. However, this and other biocontrol method need further research and validation before being promoted at the commercial scale.

***Chemical control of Colletotrichum diseases***

Chemical control of anthracnose has widely been used for controlling anthracnose of

fruit crops because the increase in value of the product usually offsets the relatively expensive chemical inputs, in terms of pesticide cost, machinery, materials and labor, and transport-tation and storage. Moreover the availability and efficiency of chemical control is relatively greater than that of other control methods (Jeger & Plimbley 1998). Generally, *Colleto-trichum* disease can be controlled by a wide range of chemicals including copper com-pounds such as dithiocarbanates, benimidazole and triazole compounds, and other fungicides such as chlorothalonill, imazalil and prochloraz (Waller et al. 1993). Newer classes of fungi-cides such as the strobilurins are also proving highly effective against *Colletotrichum* species that infect fruits. However, the problem of fungicide tolerance may arise quickly if a single compound is relied upon too heavily (Wharton & Deiguez-Uribeondo 2004).

Chemical control involves the frequent applications of fungicides such as mancoceb, carbendazim, dipheconasol, dicolad and benomyl. However, there are negative effects on farmers income and health, particularly in developing countries (Voorrips et al. 2004) and even with the application of fungicides, pre- and post-harvest anthracnose fruit rot can cause severe loss (Hartman & Wang 1992). Farmers may get into the habit of over-spraying their crops with fungicides that may lead to other forms of damage and the chemical applications would become costly.

For successful chemical control, timing and placement are of critical significance. Application of registered protectant fungicides to plants starting when the first fruit are set may be recommended for the control of anthracnose when environmental conditions are less than optimum for disease development or when a low level of inoculum is present. This will prevent or minimize the occurrence of infections (AVRDC 2003). However, poorly timed fungicide applications may actually lead to an increase in the severity of disease due to the disturbance of natural biological control mechanisms and increased crop susceptibility. Although treatment with fungicides can significantly reduce the incidence and severity of disease, eradication cannot normally be achieved (Adaskaveg & Förster 2000). Thus, if treatments are stopped and conditions favor-able for disease re-occur, then the disease in the crop may subsequently increase. Applications prior to conductive conditions are thus required and rotation programs between fungicides of different classes are highly recommended (Adaskaveg & Förster 2000). Development of models to predict anthracnose risk due to environmental conditions can efficiently reduce the number of fungicide applications (Wharton & Diéguez-Uribeondo 2004).

***Resistance of Colletotrichum to fungicides***

Use of resistant cultivars is perhaps the most desirable aspect for disease control in agriculture crops (Than et al. 2008b,c, Wharton & Diéguez-Uribeondo 2004). Such an approach has been less exploited in fruit crops mainly due to the longer time frame required for breeding and selecting for resistance and the shorter-term advantages of chemical con-trol (Voorrips et al. 2004). Cultivar resistance in fruit crops is also complicated by the ability of most *Colletotrichum* fruit pathogens to form quiescent infections (Agrios 2005).

The resistance varieties can be elimi-nated crops losses and eliminated chemical and mechanical expenses of disease control (Agrios 2005, Than et al. 2008b,c) Resistance is consi-dered the most prudent means of disease control because of its effectiveness, ease of use, and lack of potential negative effects on the environment and its use is highly recommen-ded.

One area that has received much research attention is that of developing chili varieties that are resistant to *Colletotrichum* anthro-acnose (list 3−4 refs from below). Genetic control of resistance to anthracnose in chili peppers has been studied for over 10 years and several cultivars resistant to *Colletotrichum* species have been reported (AVRDC 2002, Agrios 2005, Kim et al. 2009). At present, research is underway to identify resistance sources, to evaluate these sources for purity of resistance, and to introgress the resistance traits into cultivated chili pepper ,*Capsicum annuum*. (Roberts et al. 2001).

AVRDC (2002) has identified five acces-sions of peppers (*Capsicum chinense*: CO4554, PBC932, *Capsicum baccatum*: PBC880, PBC81, PBC133) that are resistant to three species of *Colletotrichum*, *i.e*. *C. acutatum*, *C.*

*gloeosporioides* and *C. capsici* (Table 2). Resistance to all three pathogens is of great importance because it increases the likelihood that resistance will be expressed in the field where all three pathogens occur. However, breeding for resistance is complicated by the ability of most *Colletotrichum* species to form quiescent infections. AVRDC (2003) reported that not all accessions that express resistance in the green fruit stage express resistance at the ripe fruit stage, although accessions PBC 932 and PBC 81 express immune resistance at both stages of fruit development.

Characterization of resistance genes is being carried out to transfer and incorporate resistance into cultivars to develop anthracnose resistant *C. annuum* genotypes. AVRDC Pepper Breeding Unit has been introgressing resistance from PBC932 into advanced *C. annuum* chili lines and $BC_1F_5$ and $BC_3F_4$ lines resistant at both the green and ripe fruit stages have been identified. The $BC_3F_4$ lines are now being used as the resistant parent in the breeding program to develop advanced anthracnose resistant chili pepper lines, to generate populations to study inheritance of resistance studies and to develop molecular markers for use in marker-assisted breeding for anthracnose resistance (AVRDC 2003). The studies have recently become complicated due to changes in understanding of the species that infect chili (refs). However, as long as resistant is bred against those strains causing disease it should not present great problems.

In most host-pathogen interactions, resistance involves the triggering of host defense responses that prevent or retard pathogen growth and may be conditioned by a single gene pair, a host resistance gene and a pathogen a virulence gene (Flor 1971). However, the reports differ in the predictions of the number of genes involved in conferring resistance in *Capsicum* species. Some studies reported that resistance to *C. capsici* in *C. annuum* populations segregated in a Mendelian fashion and was likely to be controlled by a single dominant gene (Park et al. 1990, Lin et al. 2002) while resistance to *C. gloeosporioides* was reported to be partially dominant or over dominant (Park et al. 1990). Another study found that resistance to *C. gloeosporioides* in one cultivar was controlled by a single dominant gene, and in the other two cultivars was controlled by a pair of dominant genes (Fernandes & Ribeiro 1998). In addition, polygenic resistance has been reported (Ahmed et al. 1991). However, Cheema et al. (1984) found that resistance to *C. capsici* was inherited recessively, with significant epistatic interactions. The differences could have resulted from different cultivars being used in establishing the chili pepper population, different fungal strains used in the bioassays, difference in the level of resistance of the so called resistant lines and the different evaluation methods adopted (Pakdeevaraporn et al. 2005). However, Pakdeevaraporn et al. (2005) mentioned that none of the above mentioned resistant *C. annuum* cultivars were completely resistant. Resistance in *C. chinense* PBC932 was reported to be controlled by a single recessive gene, which has been designated '*co1*' (Pakdeevaraporn et al. 2005). The inheritance of resistance to *Colletotrichum capsici* and *C. gloeosporioides* in *C. chinense* (PRI95030) was studied using a quantitative trait locus mapping approach in an $F_2$ population derived from a cross between *C. chinense* and an Indonesian hot pepper variety (*C. annuum*). In laboratory tests where ripe fruits were artificially inoculated with either *C. gloeosporioides* or *C. capsici*, three resistance-related traits were scored, the infection frequency, the true lesion diameter (averaged over all lesions that actually developed), and the overall lesions diameter (averaged over all inoculation points, including those that did not develop lesions). One main quantitative trait locus was identified with highly significant and large effects on all three traits after inoculation with *C. gloeosporioides* and on true lesion diameter after inoculation with *C. capsici*. Three other quantitative trait locus with smaller effects were found for overall lesion diameter and true lesion diameter after inoculation with *C. gloeosporioides*, two of which also had an effect on infection frequency. The resistant parent carried a susceptible allele for a quantitative trait locus for all three traits that was closely linked to the main quantitative trait locus. Although the main quantitative trait locus was shown to have an effect on true lesion diameter after inoculation with *C. capsici*, no significant quantitative trait locus were identified for overall lesion diameter or infection frequency.

**Table 2** List of species of *Colletotrichum* treated as currently used following Hyde et al. (2009), and location of type specimens and their sequenced genes (new additions in bold).

| Species | Type strain | ITS | Calmodulin | Actin | GAPDH | Tub2 | GS | Mat1 | Tub1 | CHS-1 | HIS3 | 5'- *tef1* | 3'- *tef1* | *apn2* | *rpb1* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C. acutatum* | IMI 117617 | AF411700 | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. agaves* | **x** | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. anthrisci* | CBS 125334 | GU227845 | x | GU227943 | GU228237 | GU228139 | x | x | x | GU228335 | GU22804 | **x** | **x** | **x** | **x** |
| *C. asianum* | MFU090233 | FJ 972612 | FJ 917506 | FJ 907424 | FJ972576 | FJ 907439 | FJ 972595 | x | x | x | x | **x** | **x** | **x** | **x** |
| *C. axonopodi* | IMI 279189 | x | x | x | x | x | x | FJ377907 | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. boninense* | MAFF 305972 | AB051400 | x | x | GQ221769 | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. capsici* | CBS 120709 | EF683603 | x | x | x | EF683602 | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. caudatum* | MAFF 057001 | EU5541101 | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. cereale* | KS 20BIG | DQ12617 | x | x | x | x | x | DQ131946 | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. chlorophyti* | IMI 103806 | GU227894 | x | GU227992 | GU228286 | GU228188 | x | **x** | **x** | GU228384 | GU228090 | **x** | **x** | **x** | **x** |
| *C. circinans* | CBS 221.81 | GU227855 | x | GU227953 | GU228247 | GU228149 | x | **x** | **x** | GU228345 | GU228051 | **x** | **x** | **x** | **x** |
| *C. cliviae* | CBS 125375 | GQ485607 | GQ849464 | GQ856777 | GQ856756 | GQ849440 | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| ***C. cordylinicola*** | **BCC38864** | **HM470247** | **HM470238** | **FJ 907425** | **HM470241** | **HM470250** | **HM470244** | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. crassipes* | **x** | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. curcumae* | IMI 288937 | GU227893 | x | GU227991 | GU228285 | GU228187 | x | **x** | **x** | GU228383 | GU228089 | **x** | **x** | **x** | **x** |
| *C. dematium* | CBS 125.25 | GU227819 | x | GU227917 | GU228211 | GU228113 | x | **x** | **x** | GU228309 | GU228015 | **x** | **x** | **x** | **x** |
| *C. echinochloae* | MAFF 511473 | AB439811 | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| ***C. falcatum*** | **CGMGC 3.14187** | **HM171677** | **x** | **x** | **x** | **x** | **x** | **HM569769** | **x** | **x** | **x** | **x** | **x** | **HM569770** | **x** |
| *C. fiorinae* | EHS 58 | EF464594 | x | x | x | EF593325 | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. fragariae* | CBS 142.31 | GU174546 | x | x | GU174564 | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. fructi* | CBS 346.37 = CCT 4806 | GU227844 | x | GU227942 | GU228236 | GU228138 | x | **x** | **x** | GU228334 | GU228040 | **x** | **x** | **x** | **x** |
| *C. fructicola* | MFU 090228 | FJ972603 | FJ917508 | FJ907426 | FJ972578 | FJ907441 | FJ972593 | | | | | **x** | **x** | **x** | **x** |
| *C. fuscum* | **x** | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. gloeosporioides* | IMI 356878 =CBS 953.97 | EU371022, AY376532, FJ976209 | FJ917512 | FJ907430 | FJ972582 | FJ907445 | FJ972589 | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. gossypii* | **x** | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. graminicola* | M 1.001 | DQ003110 | x | x | x | x | x | FJ377994 | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. hanaui* | MAFF 305404 | EU554101 | x | x | x | x | x | FJ377922 | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. higginsianum* | **x** | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. hippeastri* | CBS 125376 | GQ485599 | GQ849469 | GQ856788 | GQ856764 | GQ849446 | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. horii* | ICMP 10492 | GQ329690 | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. hymenocallidis* | CBS 125378 | GQ485600 | GQ849463 | GQ856775 | GQ856757 | GQ849438 | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. jacksonii* | MAFF 305460 | EU554108 | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| ***C.ignotum*** | **CBS125390** | **GU944376** | **x** | **x** | **x** | **GU94469** | **x** | **GU94440** | **x** | **x** | **x** | **GU94279** | **GU94498** | **GU94411** | **GU94527** |
| ***C. jasminigenum*** | **LLTX-01** | **HM131513** | **HM131494** | **HM131508** | **H131499** | **HM153770** | **HM131504** | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |

**Table 2(Continued)** List of species of *Colletotrichum* treated as currently used following Hyde et al. (2009), and location of type specimens and their sequenced genes (new additions in bold).

| Species | Type strain | ITS | Calmodulin | Actin | GAPDH | Tub2 | GS | Mat1 | Tub1 | CHS-1 | HIS3 | 5'- *tef1* | 3'- *tef1* | *apn2* | *rpb1* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***C. jasmini-sambac*** | **LLTA-01** | **HM131513** | **HM131494** | **HM131507** | **HM131499** | **HM153768** | **HM131504** | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. kahawae* | IMI 319418 | GU174550 | x | x | GQ329681 | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. lilii* | **x** | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. lindemuthianum* | **x** | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. lineola* | | GU227829 | x | GU227927 | GU228221 | GU228123 | x | **x** | **x** | GU228319 | GU228025 | **x** | **x** | **x** | **x** |
| *C. linicola* | **x** | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. liriopes* | CBS 119444 | GU227804 | x | GU227902 | GU228196 | GU228098 | x | **x** | **x** | GU228294 | GU228000 | **x** | **x** | **x** | **x** |
| *C. lupini* | BBA 70884 | x | x | x | x | x | x | DQ174704 | AJ301948 | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. lupini* var. *setosum* | BBA 70352 | x | **x** | **x** | **x** | **x** | x | DQ174702 | AJ301923 | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. malvarum* | **x** | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. miscanthi* | MAFF 510857 | EU554121 | x | x | x | x | x | EU365028 | x | x | x | **x** | **x** | **x** | **x** |
| *C. musae* | **x** | **x** | **x** | **x** | x | x | x | **x** | x | x | x | **x** | **x** | **x** | **x** |
| *C. navitas* | CBS 125086 | GQ919067 | **x** | **x** | x | x | x | GQ919071 | x | x | x | **x** | **x** | **x** | **x** |
| *C. nicholsonii* | MAFF 511115 | EU554126 | **x** | **x** | x | x | x | FJ377946 | x | x | x | **x** | **x** | **x** | **x** |
| *C. nymphaeae* | **x** | **x** | x | x | x | x | x | | x | x | x | **x** | **x** | **x** | **x** |
| *C. orbiculare* | **x** | **x** | x | x | x | x | x | | x | x | x | **x** | **x** | **x** | **x** |
| *C. paspali* | MAFF 305403 | EU554100 | x | x | | x | x | FJ377921 | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. phaseolorum* | **x** | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. phormii* | **x** | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. phyllachoroides* | **x** | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. rusci* | CBS 119206 | GU227818 | x | GU227916 | GU228210 | GU228112 | x | **x** | **x** | GU228308 | GU228014 | **x** | **x** | **x** | **x** |
| *C. sansevieriae* | MAFF 239721 | AB212991 | **x** | x | x | x | x | x | x | x | x | **x** | **x** | **x** | **x** |
| *C. siamense* | MFU 090230 | FJ972631 | FJ917505 | FJ907423 | FJ972575 | FJ907438 | FJ972596 | x | x | x | x | **x** | **x** | **x** | **x** |
| *C. simmondsii* | BRIP 28519 | FJ972601 | FJ917510 | FJ907428 | FJ972580 | FJ907443 | FJ97259 | x | x | x | x | **x** | **x** | **x** | **x** |
| *C. spaethianum* | CBS 167.49 = BBA 4804 | GU227807 | | GU227905 | GU228199 | GU22810 | x | x | x | GU228297 | GU228003 | **x** | **x** | **x** | **x** |
| *C. spinaciae* | **x** | x | x | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. sublineola* | S 3.001 | DQ003114 | x | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. tofieldiae* | **x** | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. trichellum* | **x** | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. trifolii* | **x** | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** | **x** | **x** |
| ***C. tropicale*** | **CBS124949** | **GU944336** | **x** | **x** | **x** | **GU944452** | **x** | **GU94423** | **x** | **x** | **x** | **GU94261** | **GU94481** | **GU94394** | **GU94510** |
| *C. truncatum* | CBS 151.35 | GU227862 | x | GU227960 | GU228254 | GU228156 | x | **x** | **x** | GU228352 | GU228058 | **x** | **x** | **x** | **x** |
| *C. verruculosum* | IMI 45525 | GU227806 | x | GU227904 | GU228198 | GU228100 | x | x | x | GU228296 | GU228002 | **x** | **x** | **x** | **x** |
| *C. xanthorrhoeae* | BRIP 45094 | GU048667 | x | x | GU174563 | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** |
| *C. yunnanense* | AS 3.9167 | EF369490 | x | x | x | x | x | x | x | **x** | **x** | **x** | **x** | **x** | **x** |

The main quantitative trait locus is the most important genetic factor in all the resistant-related traits studied (Voorrips et al. 2004). A substantial part of the different resistance-related traits was controlled by one quantitative trait locus with mostly additive effects. Therefore, the different resistant-related traits were inherited in an intermediary or partly dominant manner. The results of the quantitative trait locus study deviated from those in earlier studies, which were based on intraspecific *C. annuum* crosses and did not use a quantitative trait locus approach. All the information on linkages and estimates of specific quantitative trait locus effects offers a new opportunity for resistance breeding against anthracnose fruit rot.

**Identification of *Colletotrichum* species**

Traditionally, *Colletotrichum* species were identified and delimited based on morphological characters (Cai et al. 2008). Several identifying features have been utilized by taxonomists, including the size and shape of conidia and appressoria, the presence or absence of setae and sclerotia, acervuli form and teleomorph characters (Bailey 1992, Sutton et al. 1992, Abang et al. 2009). Cultural characters such as colony colour, growth rate and texture have also been utilized (Simmonds 1965, Sutton 1992, Photita et al. 2004, Than et al. 2008a,b,c, Cai et al. 2009, Hyde et al. 2009, Prihastuti et al. 2009, Yang et al. 2009). These criteria alone are not always adequate for reliable differentiation among *Colletotrichum* species due to variation in morphology and phenotype among species under environmental influences and the fact the many similar species were actually part of a species complex.

To overcome the inadequacies of these traditional schemes, molecular techniques have been used to characterize and identify taxa within *Colletotrichum* (Cai et al. 2009, Hyde et al. 2009a, Prihastuti et al. 2009, Yang et al. 2009, Phoulivong et al. 2010). Cannon et al. (2000) stated that nucleic acid analyses should provide the most reliable framework to classify *Colletotrichum*, as DNA characters are not directly influenced by envi-ronmental factors.

A combined technique of molecular diagnostic tools along with traditional morphological techniques is at present an appropriate and reliable approach for studying *Colletotrichum* species complexes (Cannon et al. 2000, Cai et al. 2009a). Photita et al. (2004) separated 34 isolates of *Colletotrichum* from banana, *Draceana sanderian*, *Eupatorium thymifolia*, ginger, longan, mango and soybean. from Thailand into four morpho-groups viz: *C. musae*, *C. gloeosporioides* group 1, *C. gloeosporioides* group 2, *C. gloeosporioides* group 3 and *C. truncatum*. Whitelaw-Weckert et al. (2007) proposed a new *C. acutatum* group based on cultural, morphological, RAPD-PCR and sequencing of parts of the 5.8S-ITS regions and the β-tubulin 2 gene. Than et al. (2008a) differentiated the isolates of chili anthracnose from Thailand into three species viz: *C. acutatum*, *C. capsici* and *C. gloeosporioides* based on morphological characterization, sequencing based on rDNA-ITS region and beta tubulin gene and pathogenicity testing, however these have since been shown to represent other species (Prihastuti et al. 2009, Yang et al. 2009, Cai et al. 2009a, Phoulivong et al. 2010, Noireung et al. 2011).

**Using *Colletotrichum* in weed biocontrol**

Numerous plant pathogens have been considered as potential biocontrol agents but in reality there has been little commercial success (Zidack & Quimby 1999). However, with the move towards organic vegetables and restricted use of pesticides there is a need to develop more effective biocontrol bioherbicides. Biotrophs are usually host-specific but do not often cause serious disease and are thus not good herbicides (Goodwin 2001). Necrotrophs on the other hand, are often severe pathogens but are generally not host-specific and thus also not suitable bioherbicides. As discussed earlier, *Colletotrichum* species are hemibiotrophs having an initial biotrophic phase with high host specificity followed by a necrotrophic phase with extensive tissue death; thus species have relatively high specificity and virulence (i.e., degree of pathogenicity). *Colletotrichum* species are therefore prime targets for use in weed control and there are presently several products on the market and several under investigation (Templeton 1992).

There has been much research on using *Colletotrichum* species in weed control. *Colletotrichum gloeosporioides* f. sp. *malvae* (Penz.)

Penz. & Sacc. has been developed as a mycoherbicide to control round-leaved mallow (*Malva pusilla*) weed in Canada (Goodwin, 2001). *Sesbania exaltata* (hemp sesbania) is a weed of soybean. Microsclerotia of a putative strain of *C. truncatum*, formulated in wheat gluten-kaolin granules called 'Pesta' resulted in highly significant weed control (Boyette et al. 2007). Microsclerotia formulated in 'Pesta' granules had an excellent shelf-life, retaining high viability after storage for 10 years at 4°C. These results suggest that microsclerotia of *C. truncatum* formulated in 'Pesta' granules offer an effective method for controlling this important weed and preserving the activity of this bioherbicide. Another example of a *Colletotrichum* species with potential for use as a bioherbicide is *C. gloeosporioides* f. sp. *Aeschynomene*, which is highly virulent against the leguminous weed *Aeschynomene virginica* also know as northern jointvetch (Boyette et al. 2009).There have also been several patents using *Colletotrichum* species as biological herbicides (Table 1). What is most interesting concerning the bioherbicides is that the names often used in publications or registered in patents have been outdated by recent developments in the taxonomy of species based on molecular data. This must throw doubt on the use of names and the validity of patents themselves. The taxa used in bioherbicides therefore should be reevaluated using a polyphasic approach and renamed where necessary.

**Should we use *Colletotrichum* or *Glomerella***

The dual nomenclature system adopted for naming of fungi has long been problematic as the same biological species can have two names (Shenoy et al. 2007). With molecular sequence data it is now often possible to link the anamorph with the teleomorph or to establish the relationship of the anamorphic genus within the teleomorph taxonomic framework (Hyde et al. 2011) and this system should be changed to using just one name.

There are at least three ways in which anamorphic genera and species names should be dealt (Hyde et al. 2011). In *Colletotrichum* this includes using only one name *Glomerella*, which follows the sexual state, or the earliest introduced name *Colletotrichum*, or keeping the status quo of using two names. In *Colletotrichum* the second approach has already been adopted by some researches who have introduced new species under the oldest *Colletotrichum* name and within the description describing the teleomorph state. If the oldest name in *Colletotrichum is* adopted, then the name of species that are generally know as important in disease causing agents will be maintained. The teleomorph state is *Glomerella* and very few species in this genus are known for their ability to cause serious disease. Therefore one name *Colletotrichum*, should be adopted for all species in *Glomerella* and *Colletotrichum* and all *Glomerella* species should be considered to be synonyms of *Colletotrichum*.

**Names in current use updated**

Hyde et al. (2009a) published a list of *Colletotrichum* names that they considered were in current use and provided a Table of the ex-type cultures and GenBank sequence data from ex-type cultures. At this time 66 taxa are recognized based on name usage since 1980. Five new species of *Colletotrichum* have been described since the publication of Hyde et al (2009a) and *C. theobromicola* Delacr. from cocao has been characterized with morphology and sequence data and the currently excepted species are updated in Table 2 with the location of ex-type cultures and ex-type related gene sequences. The species are *C. cordylinicola* Phoulivong, L Cai & KD Hyde isolated from leaf spots of *Cordyline fruiticosa* (Phoulivong et al. 2010), *C. ignotum* Rojas, Rehner & Samuels isolated from *Therbroma cacao* and *C. tropicale* Rojas, Rehner & Samuels from *Tetragastris panamensis* (Rojas et al. 2010) and *C. jasminigenum* Wikee, KD Hyde, L Cai & McKenzie isolated and *C. jasminisambac* Wikee, KD Hyde, L Cai & McKenzie isolated from *Jasminum sambac* (Wikee et al. 2011).

**Future challenges**

Future studies need to establish the host range of *Colletotrichum* species and establish whether any pathogenic species are host specific. This is important in terms of disease control, quarantine and plant breeding.

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