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MINI-REVIEW

Colletotrichum: species complexes, lifestyle, and peculiarities of some sources of genetic variability

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Abstract

The genus *Colletotrichum* comprises species with different lifestyles but is mainly known for phytopathogenic species that infect crops of agronomic relevance causing considerable losses. The fungi of the genus *Colletotrichum* are distributed in species complexes and within each complex some species have particularities regarding their lifestyle. The most commonly found and described lifestyles in *Colletotrichum* are endophytic and hemibiotrophic phytopathogenic. Several of these phytopathogenic species show wide genetic variability, which makes long-term maintenance of resistance in plants difficult. Different mechanisms may play an important role in the emergence of genetic variants but are not yet fully understood in this genus. These mechanisms include heterokaryosis, a parasexual cycle, sexual cycle, transposable element activity, and repeat-induced point mutations. This review provides an overview of the genus *Colletotrichum*, the species complexes described so far and the most common lifestyles in the genus, with a special emphasis on the mechanisms that may be responsible, at least in part, for the emergence of new genotypes under field conditions.

Keywords Phytopathogens · *Colletotrichum* species complexes · sexual cycle · parasexual cycle · Repeat Induced Point Mutation · transposable elements

Introduction

Colletotrichum is a genus of phytopathogenic fungi that deserves special attention, not only because of its importance for agribusiness but also because of the unsolved questions about some mechanisms responsible for genetic variability in this genus. Anthracnose is a disease caused by *Colletotrichum* spp., which leads to yield reduction in a large number of crops worldwide. Disease management is hampered, in some cases, by the occurrence of several *Colletotrichum* species associated with a single host, as well as by the occurrence of a single *Colletotrichum* species infecting multiple hosts (Da Silva and Michereff 2013; Lima et al. 2013; Schena et al. 2014; Talhinhas et al. 2015). These problems make anthracnose an important disease at both preharvest and postharvest stages, especially in tropical and subtropical regions (Cai et al. 2011), and place the genus *Colletotrichum* among the top 10 genera of fungi of economic and scientific importance (Dean et al. 2012).

In addition to their importance as phytopathogens, there are reports of *Colletotrichum* spp. as causative agents of diseases in humans (Cano et al. 2004; Shivaprakash et al. 2011). There are also saprophytic isolates and endophytes of various plant species in the genus *Colletotrichum* (Araújo et al. 2018; Fernandes et al. 2015; Gautam 2014; Gonzaga et al. 2015; Leite et al. 2013; Promputtha et al. 2007), as well as producers of important secondary metabolites (for review, see Moraga et al. 2019).

Many species of this genus, representing different physiological races, show a wide genetic variability (Ali and Warren 1987; Chakraborty et al. 1999; Davide and Souza 2009; Kelly et al. 1994). However, some mechanisms responsible for the genetic variability found in the genus *Colletotrichum* are not yet fully understood and require in-depth studies. Therefore, we present in this review a summary of different characteristics of the genus *Colletotrichum*, drawing attention to species complexes, lifestyle, and some mechanisms that generate

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genetic variability, to discuss the importance of such mechanisms and the aspects that still need to be explored. Our goal is not to explore all sources of genetic variability in fungi. We have tried to exploit those mechanisms that we consider peculiar in *Colletotrichum* spp., considering that there are important mechanisms that generate genetic variability in fungi that were not included in this review. For a review of other mechanisms of genetic variability in fungi, we recommend Taylor et al. (2017).

Species complexes in *Colletotrichum* and their characteristics

The identification of *Colletotrichum* species has been a major challenge over the years because of the lack of reliable morphological characteristics. *Colletotrichum* fungi have few and variable morphological characteristics, and boundaries between species are confusing and ambiguous (Cai et al. 2009; Crouch, 2014; Hyde et al. 2009; Liu et al. 2014, 2016; Weir et al. 2012). Several genetic markers have been used following the species delimitation concept proposed by Taylor et al. (2000), known as the genealogical concordance phylogenetic species recognition (GCPSR), to delimit the boundaries between species (Cannon et al. 2012; Damm et al. 2012a, b; Weir et al. 2012). Species identification is now performed using a polyphasic approach, which can combine analysis of various markers or barcodes with morphological and physiological description, pathogenicity testing, analysis of metabolite production, and ecological studies (Liu et al. 2016). The internal transcribed spacer is used as a barcode for genus identification and for complex positioning (Jayawardena et al. 2016a).

The vast majority of *Colletotrichum* species are classified into complexes. Initially, nine complexes of *Colletotrichum* were established, along with a series of small groups and monophyletic species (Cannon et al. 2012). Subsequent studies used phylogenetic analysis of concatenated sequences, following the GCPSR concept, using different markers, such as actin (*act*), chitin synthetase (*chs1*), β-tubulin (*Tub2*), calmodulin (*cal*), glyceraldehyde 3-phosphate dehydrogenase (*gapdh*), histamine (*his3*), glutamine synthetase (gs), DNA lyase (*apn2*), and an intergenic region of the *apn2* and MAT1-2-1 (*ApMat*) genes (Cannon et al. 2012; Damm et al. 2012a, b; Doyle et al. 2013; Lijuan et al. 2012; Sharma et al. 2013; Weir et al. 2012). Currently, 11 complexes (*caudatum*, *graminicola*, *spaethianum*, *destructivum*, *acutatum*, *dematium*, *gigasporum*, *gloeosporioides*, *boninense*, *truncatum*, and *orbiculare*) are recognized (Marin-Felix et al. 2017), and recently, three more complexes (*dracaenophilum*, *magnum*, and *orchidearum*) have been proposed (Damm et al. 2019).

There are large phenotypic and genetic differences between different species complexes. For example, the *caudatum* complex can be distinguished by the presence of a filiform appendix at the apex of conidia (Crouch 2014), while conidia of the *dematium* complex are typically angular (Damm et al. 2009), and the *gigasporum* complex, as the name implies, is characterized by the formation of oversized conidia (Liu et al. 2014). In addition, there are differences, e.g., in morphological characteristics, between and within species that make up each complex (Cannon et al. 2012; Weir et al. 2012). As with other fungi, characteristics such as conidial morphology, the growth rate, colony coloration, pigment production, the presence of setae, and the sexual cycle have been used for species differentiation (Freeman et al. 1998). Some of these characteristics, such as conidial morphology and the presence of setae, are shared among several species of the same complex; however, characteristics such as the growth rate and the presence of a sexual cycle may vary among isolates of the same species (Cannon et al. 2012; Hyde et al. 2009; Weir et al. 2012). In addition, characteristics such as the colony coloration may vary between monosporic cultures of the same isolate, as reported for *C. kahawae* subsp. *ciggaro* (Weir et al. 2012).

Similarly, there are variations in the host ranges between species within the same complex. Although determination of the host range is biased because most of ecological studies have been performed with diseased plants of agronomic interest, in all complexes, there are species with a specific host and also species with multiple hosts (Table 1). Only some complexes, such as *acutatum*, *boninense*, *destructivum*, *gloeosporioides*, *orchidearum, spaethianum*, and *truncatum*, contain species with a wide range of hosts, and in most cases, the representative species are the ones after which the complexes were named (Table 1). However, these same complexes include species with specific hosts, which are, in some cases, used for biological weed control. Some examples are *C. aeschynomenes*, the exclusive pathogen of *Aeschynomene virginica*, which has been used as a biological control agent under the name of Collego® (Ditmore et al. 2008), and *C. hanaui*, from the *graminicola* complex, with its range of hosts limited to species of the genus *Digitaria* (Zhao et al. 2012). Some characteristics of *Colletotrichum* species point to these fungi as interesting for biological weed control agents (Jayawardena et al. 2016b).

The particularities of the complexes are also evidenced in different lifestyles of their species. Although the genus *Colletotrichum* is recognized as comprising important phytopathogens, some species have been described as endophytes, saprophytes, entomopathogens, and human pathogens, and several species are even characterized by more than one lifestyle (Table 1). Phytopathogenic species have been described in all complexes, but endophytic species have only been described in 12 out of the 14 complexes (Table 1). The *orbiculare* complex only includes species described as phytopathogenic, while the *truncatum* complex, in addition to phytopathogenic species, includes saprophytic ones, such as

Table 1 Comparison between species complexes in lifestyles and host range*

Species complex	Pathogen (P)				Endophyte (E)				Saprobe (S)				P-E				P-S				S-E				P-Human Pathogen				P-E-S				P-E-EM			
	S	LS	NS	W	S	LS	NS	W	S	LS	NS	W	S	LS	NS	W	S	LS	NS	W	S	LS	NS	W	S	LS	NS	W	S	LS	NS	W	S	LS	NS	W
Acutatum																																				
Boninense																																				
Caudatum																																				
Dematium																																				
Destructivum																																				
Dracaenophilum																																				
Gigasporum																																				
Gloeosporioide																																				
Graminicola																																				
Magnum																																				
Orbiculare																																				
Orchidearum																																				
Spaethianum																																				
Truncatu																																				
Singleton																																				

*Elaborated from the accepted species and the data published by Damm et al. (2019) and Jayawardena et al. (2016). Reported to be associated to only one plant species (specific [S]), plants of the same genus or family (less-specific [LS]), plants of two or three different families (no-specific [NS], plants of more than three different families (wide [W]). Shaded squares indicate the presence of *Colletotrichum* species with the correspondent lifestyles and host range

C. fusiforme, isolated from a decaying leaf in Thailand (Ariyawansa et al. 2015). Meanwhile, *C. truncatum*, which is an important phytopathogen, is also known to be pathogenic to human beings (Damm et al. 2009; Squissato et al. 2015). Other species reported to cause infections in humans are *C. graminicola* from the *graminicola* complex (Ritterband et al. 1997) and *C. gigasporum* from the *gigasporum* complex (Liu et al. 2014). In particular, the species *C. fioriniae* from the *acutatum* complex, besides being reported as phytopathogenic, has been described as an endophyte of *Mangifera indica* in Australia and as an entomopathogen of *Fiorinia externa* in the USA (Marcelino et al. 2008). On the other hand, there are species that have exclusively been reported as saprophytic, e.g., *C. citricola* (Huang et al. 2013), and endophytic, e.g., *C. parsonsiae* isolated from *Bletilla ochracea* in China (Tao et al. 2013), both from the *boninense* complex.

Lifestyles of *Colletotrichum*

Endophytic lifestyle

In the phylum *Ascomycota*, endophytism has been shown to be an evolutionarily labile state, characterized by frequent transitions between endophytism and pathogenicity (Higgins et al. 2007). Thus, endophytic interactions may continuously evolve from mutualism to parasitism (Kogel et al. 2006). In addition, pathogenic fungi may reside as asymptomatic endophytes in plant tissues (Kuldau and Yates 2000; Suryanarayanan and Murali 2006; Vettraino et al. 2005).

Colletotrichum has been reported as one of the most widely distributed endophytic fungal genera, and its members are known as producers of a large number of secondary metabolites (for review, see Moraga et al. 2019). Some endophytic fungi of the genus *Colletotrichum*, such as *C. karstii* and *C. boninense*, have a wide range of hosts and colonize several taxonomically distinct plant species (Jayawardena et al. 2016a). Some others are specific to a host, such as *C. parsonsiae*, isolated from *B. ochracea* in China (Tao et al. 2013), and *C. colombiense*, isolated from *Passiflora edulis* in Colombia (Damm et al. 2012b). However, the most significant endophytic species is *C. tofieldiae*, which has been shown to provide beneficial effects to its host (Hiruma et al. 2016). *Colletotrichum tofieldiae* colonizes the roots of *Arabidopsis thaliana*, improving its phosphorus uptake and growth, which consequently increases the plant ability to grow under phosphate-deficient conditions (Hiruma et al. 2016).

On the other hand, the genus *Colletotrichum* provides clear examples of endophytism as an evolutionarily labile state. Thus, Freeman and Rodriguez (1993) were able to genetically convert *C. magna* phytopathogenic to a non-pathogenic endophytic fungus by deleting a single gene. Abang et al. (2009) showed that an asymptomatic endophytic isolate of *C. gloeosporioides* was unable to produce a toxic metabolite, which is produced by pathogenic strains and induces symptoms of disease in the host plant. However, it is unclear whether various defense reactions, induced after fungal penetration into the host, such as programmed cell death, phytoalexin induction, and production of pathogenesis-related proteins, which are observed in pathogen–host interactions (De Lorenzo and Ferrari 2002), also occur in endophyte–host interactions (Sieber 2007).

Phytopathogenic lifestyle

Most fungi of the genus *Colletotrichum* show a hemibiotrophic lifestyle (Münch et al. 2008; Perfect and Green 2001). In the biotrophic phase, the pathogen acquires nutrients necessary for its survival from living plant cells, without disturbing the host cell. Symptoms of the disease are not observed at this stage of infection. After initial host colonization by primary hyphae, the

pathogen shifts to a necrotrophic state and then begin colonizing other plant cells (Wharton and Julian 1996). In this destructive phase, the pathogen secretes toxins and an enzymatic arsenal responsible for degrading plant tissue, causing cell disorganization and destruction (Anand et al. 2008). As the fungal growth progresses in plant tissue, the most characteristic symptom of the disease, necrosis of infected tissues, appears. The duration of the transition period between the biotrophic and necrotrophic phases varies among species of *Colletotrichum* and depends on the host and environmental conditions (Latunde-Dada et al. 1997; O'Connell et al. 1985, 1993; Wharton and Julian 1996).The pathogen may also initially colonize the host and remain in a latent or quiescent state for a longer period, until it begins to macerate plant tissue (Ranathunge et al. 2012).

To complete its cycle of infection, the pathogen produces an acervulus, which is a typical asexual reproduction structure, formed intracuticularly in plant tissue (Khan and Hsiang 2003). With the growth of a stroma, formed by the fungal mycelium between the plant epidermis and cuticle, the tension on the cuticle increases, until the mature acervulus breaks the cuticle and is exposed to the environment. Then, from the stroma present in the acervulus, conidiophores are initiated, in which unicellular conidia of the pathogen are produced (Curry et al. 2002). The conidia produced are wrapped in a water-soluble mucilaginous matrix, composed of glycoproteins and germination inhibitors, which protect conidia against dissection and toxic molecules produced by the host (Leite and Nicholson 1992).

Upon contact with water from raindrops or irrigation and with the wind, conidia produced in acervuli are spread to new locations on the same host plant or to new hosts, which may lead to a new cycle of infection (Ntahimpera et al. 1997). Eventually, if conditions are favorable for the pathogen, perithecium formation may be induced, as well as the formation and production of ascospores, which, when released, may be able to infect plant tissues in which they are deposited (Sutton and Shane 1983).

Some sources of genetic variation in *Colletotrichum* genus

Hyphal anastomosis and parasexual cycle

Genetic variants of *Colletotrichum* spp. can be produced via different mechanisms, which in some cases, may be closely related. Heterokaryosis has been induced in *Colletotrichum* spp. mainly through the use of Nit mutants, associated with nitrogen metabolism. Spontaneous Nit mutants are easily isolated, without the need for mutagenic treatment (Cove 1976), and have been used for the analysis of vegetative compatibility groups (VCGs) as a tool for detecting variability within different *Colletotrichum* species, such as *C. gloeosporioides* (Chacko et al. 1994), *C. graminicola* (Vaillancourt and Hanau 1994), *C. lindemuthianum* (Carvalho and Mendes-Costa 2011), *C. acutatum* (Franco et al. 2011), and *C. kahawae* (Varzeaa et al. 2002), among others.

Although heterokaryons can be obtained and isolates can easily be classified into VCGs in the laboratory, the importance of heterokaryosis for the emergence of field variants, which can lead to resistance breakdowns, has not been well documented. Heterokaryosis is the first step in the parasexual cycle, which is preceded by a nuclear fusion in the hyphal compartments and haploidization through mitotic nondisjunction, with a possible occurrence of mitotic crossover (Pontecorvo et al. 1953). In the genus *Colletotrichum*, the parasexual cycle has been confirmed in some species but has never been documented in others. In *C. gloeosporioides*, heterokaryons were obtained between Nit mutants, but no diploid or recombinant strain was isolated, and heterokaryosis was restricted to limited portions of the colony (Chacko et al. 1994). *Colletotrichum gloeosporioides*, infecting *Stylosanthes* spp. in Australia, has two biotypes (A and B), which form different VCGs (Irwin and Cameron 1978; Masel et al. 1996). Although the biotypes are incompatible, a transfer of a 2-Mb chromosome from biotype A to biotype B was detected in a field isolate and demonstrated experimentally; however, the mechanism responsible for this transfer was not determined (He et al. 1998; Manners and He, 2011; Masel et al. 1996). A parasexual cycle was not detected, and the chromosome transfer did not appear to involve the complete genomes of the isolates belonging to biotypes A and B. In *C. graminicola*, no evidence of the occurrence of a parasexual cycle was found either (Vaillancourt and Hanau 1994).

The occurrence of a typical parasexual cycle, with the detection of a heterokaryon, diploids, and recombinants, has been demonstrated in *C. lindemuthianum* (Rosada et al. 2010). Hyphal anastomosis between compatible isolates, carrying complementary mutations, allowed the isolation of heterokaryons that generated diploid strains, which in turn produced recombinant haploid sectors (Castro-Prado et al. 2007; Rosada et al. 2010). In *C. sublineolum*, a causative agent of anthracnose in sorghum, heterokaryons were produced between auxotrophic and benomyl-resistant mutant colonies, and aneuploid and recombinant strains were directly obtained from these heterokaryons, without the detection of a diploid strain (Souza-Paccola et al. 2003), indicating the occurrence of an atypical parasexual cycle. Isolation of recombinant strains directly from heterokaryons has been previously demonstrated in *Aspergillus niger* (Bonatelli Jr et al. 1983), *Metarhizium anisopliae* (Bagagli et al. 1991), and *Beauveria bassiana* (Paccola-Meirelles and Azevedo 1991).

Because the occurrence of conidial anastomosis tubes (CATs) has been confirmed in *Colletotrichum* spp. (Roca et al. 2003, 2004), it should be taken into consideration that the parasexual cycle (heterokaryosis) can be initiated in the genus *Colletotrichum* via both hyphal anastomosis and CATs.

CATs are formed between conidia of the same or different species of the genus *Colletotrichum*, and fusion may also occur between isolates of *C. lindemuthianum* that show vegetative incompatibility (Ishikawa et al. 2012; Roca et al. 2003, 2004). In this species, conidial germination and CAT formation depend on the age of conidia, the culture medium, and the strain used, and germ tube formation is reduced with an increase in CAT formation (Ishikawa et al. 2010). Gonçalves et al. (2016) analyzed the occurrence of CATs in *Colletotrichum* spp., which cause two diseases in apples (bitter rot and *Glomerella* leaf spot). It was observed that not all isolates of the same species were capable of producing CATs under the conditions tested and that appressorium melanization and the development of CATs were antagonistic processes. The signals that trigger the formation of CATs in *Colletotrichum* spp. are still unclear, although this mechanism has been extensively studied in *Neurospora crassa*, and several genes involved in this process are already known (for review, see Herzog et al. 2015). However, the formation of CATs in *C. lindemuthianum* takes longer than that in *N. crassa* and is inhibited by nutrients (Ishikawa et al. 2010).

Given what we know about the parasexual cycle in *Colletotrichum* spp., there are still many questions to be answered, such as: Is the parasexual cycle responsible for the wide variability found in many phytopathogenic *Colletotrichum* species or at least in some species? Is the isolation of recombinant strains directly from heterokaryons a result of rapid haploidization of the diploid nucleus, which does not allow the isolation of a stable diploid, or is it a result of the nucleus and chromosome fragmentation or simply a transfer of DNA fragments? What proteins are involved in the induction, recognition, and nuclear transfer in CATs? Is there an inductive signal? Is there a recognition mechanism?

Sexual cycle

Sexual compatibility is controlled in ascomycetes by DNA-binding regulatory proteins, encoded by genes grouped in the mating-type locus, which has two idiomorphs, *Mat1-1* and *Mat1-2*, following the nomenclature proposed by Turgeon and Yoder (2000). The *Mat1-1* locus may have more than one gene but will always carry at least the *Mat1-1-1* gene, which encodes a transcription factor with an alpha-1 domain. The *Mat1-2* locus will have at least the *Mat1-2-1* gene, which encodes a protein with a high-mobility group DNA-binding domain. Fungi can be homothallic, when they are self-fertilized, or heterothallic, when they are cross-fertilized. Homothallic ascomycetes have the *Mat1-1* and *Mat1-2* idiomorphs linked or separated in the same nucleus, while heterothallic ascomycetes have either *Mat1-1* or *Mat1-2* idiomorph.

Species of the genus *Colletotrichum* apparently do not follow the traditional organization of mating-type genes, described in other ascomycetes. Both homothallic and heterothallic forms have already been isolated, but although the *Mat1-2-1* gene of the *Mat1-2* idiomorph has been found in several *Colletotrichum* species and is used as a molecular marker in phylogenetic analyses of the genus (Baroncelli et al. 2015; Chen et al. 2002; Crouch et al. 2009; Du et al. 2005; Garcia-Serrano et al. 2008), gene sequences that characterize the *Mat1-1* idiomorph have not yet been detected and isolated. Vaillancourt et al. (2000) observed multiple mating groups in *C. graminicola*, presenting many alleles. These results showed that mating in *C. graminicola* was genetically complex and led the authors to hypothesize that unbalanced heterothallism could be involved, at least in part. Unbalanced heterothallism was proposed in *C. gloeosporioides* by Wheeler (1954), based on a previous work by Edgerton (1914). *Colletotrichum lindemuthianum* also represents an unusual mating system. Using crosses among 19 Mexican isolates of *C. lindemuthianum*, Rodriguez-Guerra et al. (2005) demonstrated that the isolates had a heterothallic crossing system. Nevertheless, both parental isolates that produced a mature perithecium showed sequence homology with the *Mat1-2-1* gene. It has been suggested that the mating type in this case is not determined by the *Mat1-1* locus.

Although the sexual cycle has already been described in different *Colletotrichum* species, such as *C. lindemuthianum* (Rodriguez-Guerra et al. 2005), *C. truncatum* (Armstrong-Cho and Banniza 2006; Menat et al. 2012), *C. tanaceti* (Barimani et al. 2013), *C. graminicola* (Politis 1975; Vaillancourt and Hanau 1991), there is as yet no proof of its real importance under field conditions. Some species of *Colletotrichum* of agricultural importance, such as *C. lentis*, perform the sexual cycle under laboratory conditions, but its occurrence has never been found under field conditions (Menat et al. 2016). Thus, the genetic basis that controls sexual reproduction in the genus *Colletotrichum* still needs to be unraveled. *Colletotrichum* spp. do not certainly involve the mechanism found in other ascomycetes, and genes responsible for the control of this process are not yet completely known.

Some questions remain open, such as: Is there a predominance of *Colletotrichum* species with balanced heterothallism? What protein in *Colletotrichum* spp. fulfills the role played by the *Mat1-1-1* gene product in other ascomycetes? Is the sexual cycle important in generating genetic variants in the field?

Transposable elements and repeat-induced point mutations

With advances in sequencing technologies and reduction in cost, genomes of many phytopathogenic fungi, including *Colletotrichum* spp., have been sequenced. The first fungi of this genus to have their genomes sequenced were *C. graminicola*, *C. higginsianum*, *C. fructicola*, and

C. orbiculare, belonging to different species complexes (Gan et al. 2013; O'Connell et al. 2012). To date, 29 *Colletotrichum* genomes have been sequenced (Table 2), and most of them analyzed. However, this number is still small, considering the number of species in this genus and their great importance for agriculture.

A portion of the fungal genome consists of transposable elements (TEs). These elements may be autonomous, encoding proteins necessary for their transposition; non-autonomous, which do not encode transposition-involved proteins but have sequences necessary for transposition, which can be recognized by proteins encoded by other elements; and inactive, which have accumulated mutations and/or rearrangements and are unable to transpose, some of which may have been "domesticated," playing an important role in the host organisms. According to the transposition mechanism, TEs are divided into classes (I and II), orders, superfamilies, and families (Wicker et al. 2007). Class I elements undergo replicative transposition using an RNA as an intermediate, and class II elements may undergo conservative transposition (cut-and-paste) or replicative transposition (copy-and-paste), without the presence of an intermediate RNA (Wicker et al. 2007). The most common TEs in the genomes of filamentous fungi are class I LTR (long terminal repeats) elements, mainly from the *Gypsy* and *Copia* superfamilies (Foulongne-Oriol et al. 2013; Grandaubert et al. 2015; Horns et al. 2017; Santana et al. 2012).

TEs are responsible for gene expression modifications, rearrangements, and mutations. The importance of TEs has already been demonstrated in different fungi. The *Penicillium digitatum* transposon *PdMLE1* confers resistance to sterol synthesis inhibitors. *PdMLEI1* is a non-autonomous MITE (miniature inverted repeat transposable element)-like element of 199 base pairs (bp), with strong promoter characteristics; when inserted into the promoter of the *P. digitatum PdCYP51B* gene, *PdMLEI1* enables the overexpression of this gene, which makes the fungus resistant to sterol 14-α-

Table 2 Colletotrichum species with sequenced genome.

Species	Genbank access number	Reference
Colletotrichum acutatum	LUXP00000000.1	(Han et al. 2016)
Colletotrichum chlorophyti	MPGH00000000.1	(Gan et al. 2017)
Colletotrichum coccodes	LECQ00000000.1	Unpublished
Colletotrichum falcatum	LPVI00000000.1	(Viswanathan et al. 2016)
Colletotrichum fioriniae	JARH00000000.1	(Baroncelli et al. 2014b)
Colletotrichum fructicola	ANPB00000000.1	(Gan et al. 2013)
Colletotrichum gloeosporioides	AMYD00000000.1	(Alkan et al. 2013)
Colletotrichum godetiae	LZRM00000000.1	Unpublished
Colletotrichum graminicola	ACOD00000000.1	(O'Connell et al. 2012)
Colletotrichum higginsinum	LTAN00000000.1	(O'Connell et al. 2012)
Colletotrichum incanum	LFIW00000000.1	(Gan et al. 2016)
Colletotrichum lentis	NWBT00000000.1	(Bhadauria et al. 2019)
Colletotrichum lindemuthianum	MASP00000000.2	(de Queiroz et al. 2017)
Colletotrichum musae	NWMS00000000.1	(Silva Junior et al. 2018)
Colletotrichum nymphaeae	JEMN00000000.1	(Baroncelli et al. 2016)
Colletotrichum orbiculare	AMCV00000000.1	(Gan et al. 2013)
Colletotrichum orchidophilum	MJBS00000000.1	(Baroncelli et al. 2018)
Colletotrichum salicis	JFFI00000000.1	(Baroncelli et al. 2016)
Colletotrichum sansevieriae	NJHP00000000.1	(Nakamura et al. 2018)
Colletotrichum shisoi	PUHP00000000.1	(Gan et al. 2019b)
Colletotrichum siamense	RJJI00000000.1	(Meng et al. 2019)
Colletotrichum sidae	QAPF00000000.1	(Gan et al. 2019a)
Colletotrichum simmondsii	JFBX00000000.1	(Baroncelli et al. 2016)
Colletotrichum spinosum	QAPG00000000.1	(Gan et al. 2019a)
Colletotrichum sublineola	JMSE00000000.1	(Baroncelli et al. 2014a)
Colletotrichum tanaceti	PJEX00000000	(Lelwala et al. 2019)
Colletotrichum tofieldiae	LFHR00000000.1	(Hacquard et al. 2016)
Colletotrichum trifolii	RYZW00000000.1	(Gan et al. 2019a)
Colletotrichum truncatum	NBAU00000000.2	(Rao and Nandineni 2017)

demethylation inhibitor fungicides (Sun et al. 2013). Insertion of the *Hormin* (*Hornet1* in miniature) transposon into the *AVR1* gene was responsible for new biotypes in races 2 and 3 of *Fusarium oxysporum* f. sp. *lycopersici* (Inami et al. 2012; Kashiwa et al. 2016). *Hormin* is a 759 bp non-autonomous transposon, which belongs to the hAT family of class II elements. TEs are also involved in the regulation of melanin-related genes in *Zymoseptoria tritici* (Krishnan et al. 2018).

Initially, before sequencing and annotation of complete genomes, few TEs were identified in *Colletotrichum* spp. (Crouch et al. 2008a, b; He et al. 1996; Santos et al. 2012; Zhu and Oudemans 2000). However, as genomes are sequenced and TEs are annotated, it has become obvious that TEs may represent an important portion of the *Colletotrichum* genomes, and a possible role of these elements in genetic variability in the genus *Colletotrichum* has been suggested. *Cgt1* is the first transposon identified in *Colletotrichum* spp. It is a non-LTR class I transposon of the order LINE (long interspersed nuclear elements), which is approximately 5.7 kb (kilobase) in length and is present in *C. gloeosporioides*, which causes anthracnose in *Stylosanthes* spp. in Australia. *Cgt1* is present in biotype B but absent in biotype A (He et al. 1996). The *Cgret* element is also a class I transposon, but it belongs to the order LTR and was isolated from *C. gloeosporioides* that infects cranberry. *Cgret* was found in all isolates from NJ and MA and was absent in isolates from WI or Chile (Zhu and Oudemans 2000). Five different transposons were detected in *C. cereale* by Crouch et al. (2008a, b). Recently, the content of TEs in the genomes of seven *Colletotrichum* species was analyzed (Rao et al. 2018), and the following percentages were found: 4.89% in *C. truncatum*; 6.01% in *C. higginsianum*; 14.79% in *C. graminicola*; 44.88% in *C. orbiculare*; 4.31% in *C. scovillei*; 9.54% in *C. chlorophyti*; and 5.41% in *C. orchidophilum*. Class I TEs from the *Gypsy* superfamily were found at the highest numbers in all genomes analyzed, except for *C. orbiculare*, in which *Copia* superfamily elements were the most abundant (12.08%). The highest percentage of TEs was found in *C. orbiculare*, which has one of the largest genomes among the *Colletotrichum* species so far (Gan et al. 2013). Interestingly, 26.41% of *C. orbiculare* TEs are unknown (Rao et al. 2018), demonstrating that much remains to be discovered about these TEs.

The association of TEs with genes encoding effector proteins and with genes of secondary metabolism has been reported in *C. higginsianum*, in which two minichromosomes (chromosomes 11 and 12) were found to be enriched in TEs. In addition, 30% of TEs in *C. higginsianum* are probably active transposons, as they are transcribed in at least one stage of the fungal development (Dallery et al. 2017). A loss of one of the minichromosomes (chromosome 11) led to changes in the virulence, without affecting the vegetative growth of *C. higginsianum* (Plaumann et al. 2018), demonstrating that the minichromosomes are important for pathogenicity. Comparison of the genomes of two *C. higginsianum* strains revealed differences in the occurrence of large rearrangements, in the presence of strain-specific regions, and in effector candidate genes. Apparently, these variations are associated with TEs (Tsushima et al. 2019). The proximity of TEs to genes important for pathogenicity was also observed in *C. truncatum* (Rao et al. 2018). These examples suggest that TEs may play an important role in the polymorphism found in the *Colletotrichum* spp. genomes and in the regulation of pathogenicity-related gene expression.

TEs are known to be important for variability and adaptability of different species. However, their activity may lead to decreased genome stability, and therefore, many transposons are silenced. Different types of silencing mechanisms have been documented in fungi. The main ones are methylation induced premeiotically (Goyon and Faugeron 1989), meiotic silencing by unpaired DNA (Shiu et al. 2001), quelling (Romano and Macino 1992), and repeat-induced point (RIP) mutations (Selker and Stevens 1987; Selker 1990), among others. In particular, RIP mutations are a gene-silencing mechanism, first observed in *N. crassa* (Selker and Stevens 1987; Selker 1990). Preliminary results on *N. crassa* suggested that RIP mutations occurred during a sexual cycle, between fertilization and nuclear fusion, inducing GpC to ApT mutations in both strands of duplicate homologous sequences, with more than 80% identity and a minimum size of 0.4 kb (Cambareri et al. 1998; Selker and Stevens 1987; Selker 1990). However, a recent study has further elucidated the process characteristics, resulting in the reduction of the minimum repetitive sequence size for a RIP mutation to occur to 155 bp, with a higher frequency of mutations in fragments between 220 and 550 bp (Gladyshev and Kleckner 2016). Importantly, although the presence of perfect homology was advantageous, it did not seem to be necessary in some cases, as DNA segments with global sequence identity of only 35–36% could still be recognized. In addition, short islands of homology of only 3 bp could be recognized, provided that many of these islands were grouped at an interval of 11 or 12 bp across a pair of DNA molecules (Gladyshev and Kleckner 2017a). In *N. crassa*, where this mechanism is best documented, RIP mutations are mediated by cytosine C-5 methylation, followed by deamination, and so far, two genes related to C-5 DNA methyltransferase have been identified, *rid1* (RIP-deficient 1) (Freitag et al. 2002) and *dim-2* (decrease in DNA methylation-2) (Kouzminova and Selker 2001). RID preferentially acts in duplicate regions during the sexual cycle, while DIM-2 targets not only repetitive regions but also non-repetitive ones during the *N. crassa* vegetative cycle. RID was originally proposed to be essential for RIP mutations (Freitag et al. 2002), but new evidence indicates that DIM-2 can also mediate RIP mutations, with the involvement of DIM-5 (histone H3 lysine methyltransferase), HP1 (heterochromatin 1 protein), and

other known heterochromatin factors (Gladyshev and Kleckner 2017b). Thus, the current model for the mechanism of mutations predicts repeat-induced methylation of C5-cytosine by DIM-2 or RID, which can be converted to mutations by a DNA deaminase that is specifically activated in the premeiotic phase (Gladyshev and Kleckner 2017b). However, further elucidation of the complete molecular process is still needed, including the fact that the dependence of RID on the regulation of sexual development in some fungi is not always related to the levels or severity of RIP mutations or C-5 cytosine methylation (Li et al. 2018).

To demonstrate the RIP mutation activity in fungal genomes, it is necessary to perform sexual crosses and genetic transformation. As it is difficult to obtain a sexual cycle in the laboratory for most agronomically important fungi, analysis of RIP-like sequences in repetitive DNA sequences is mainly used to find evidence of RIP mutations. The RIPCAL software is the most widely used tool for detecting RIP-like events in complete or partial genomes (Hane and Oliver 2008). The program usually calculates the frequency of RIP products and correlates it with false positives, with TpA/ApT and (CpA + TpG)/(ApC + GpT) being the two most frequently used indices (Hane and Oliver 2008). Thus, by using bioinformatics, RIP mutations have been described in a wide range of fungi, both Ascomycota (Clutterbuck 2011) and Basidiomycota (Hane et al. 2014; Horns et al. 2012).

The main expected consequence of RIP mutations is the silencing of TEs, mainly retrotransposons, which are usually present in multiple copies, owing to their transposition mechanism. However, RIP mutations have also been reported in sequences near repetitive RIPed regions (Fudal et al. 2009), and from the point of view of phytopathogenic organisms, this is of great evolutionary importance, as many virulence-related genes are located near genomic regions rich in repetitive elements. This can accelerate the rate of evolution of virulence-related genes, leading to their silencing or diversification (Howlett et al. 2015). On the other hand, in genomes with severe RIP mutations, such as those of *Paecilomyces variotii* and *N. crassa*, the impediment or lack of gene duplications has been associated with RIP mutations, leading to a reduction in the number of genes within gene families (Urquhart et al. 2018).

In the genus *Colletotrichum*, evidence of RIP mutations has been exclusively based on bioinformatics analysis. The analyses support the presence of this mechanism in all strains studied, with the CpA dinucleotide preferentially mutated (Braga et al. 2014; Rao et al. 2018). However, the mechanism does not appear to be conserved within the genus, being classified as severe in *C. graminicola* (Braga et al. 2014) and *C. tanaceti* and poorly expressed in *C. higginsianum* (Dallery et al. 2017), *C. cereale* (Crouch et al. 2008a), and *C. truncatum* (Rao et al. 2018). This divergence seems to be related to the mechanism and the proteins involved. Thus, there are different patterns of mutation severity and the presence or absence of the RID and DIM-2 proteins in the genus. In *C. graminicola*, where RIP mutations have silenced all *Tc-1 Mariner* elements analyzed (Braga et al. 2014), RID-like methyltransferase sequences were identified, suggesting the possible involvement of this protein in the RIP mutation process. Because the sex cycle is rarely observed in *C. graminicola* in nature, the authors speculated that the results might indicate that RIP mutations are a rare event in this species or that there are mechanisms similar to RIP mutations but involving other proteins. Evidence of RIP mutations has also been found in asexual *C. cereale*, suggesting that RIP mutations may have occurred at an ancestral state of sexual reproduction or that meiosis cryptically occurs in nature (Crouch et al. 2008a). In *C. truncatum*, although there is evidence of RIP mutations, no RID-related sequences have been found, and no sexual stage has been identified yet. However, domains related to DIM-2 have been identified in sequences present in the genome (Rao et al. 2018). Finally, *C. higginsianum* has sequences homologous to RID and DIM-2, but no evidence of a sexual cycle has been obtained (Dallery et al. 2017). In contrast, in the sexual fungus *C. tanaceti* (Barimani et al. 2013), RIP mutations have been considered severe, and homologous sequences have been identified for both RID and DIM-2 (Lelwala et al. 2019). Regarding the evolutionary impact of the presence of RIP mutations on *Colletotrichum* genomes, besides transposon silencing, the phenomenon has been related to the rapid evolution of virulence genes, as they are closely related to repetitive sequences. In fact, Queiroz et al. (2019) have identified RIP-like signatures in effector genes predicted for *C. lindemuthianum*, although the mechanism has not yet been investigated in this species. In the *C. tanaceti* genome, strong signs of RIP-like mutations in the genes of pathogenicity may indicate an accelerated evolutionary rate of this region relative to the rest of the genome (Lelwala et al. 2019). This phenomenon has been called a "two-speed" genome. Different evolutionary rates within the same genome have also been suggested for *C. orbiculare* and *C. graminicola* (Gan et al. 2013; Rao et al. 2018). Thus, RIP mutations may play a key role in generating a high evolutionary potential in genes of pathogenicity in *Colletotrichum* (Lelwala et al. 2019).

We still need answers to several questions about the role of TEs in genetic variability of *Colletotrichum* spp., such as: Are TEs the great architects of genomic rearrangements found in *Colletotrichum* spp.? How are these elements activated and what controls are exercised over them? How can RIP mutations be responsible for the production of new pathogenic variants, if in several *Colletotrichum* species of agronomic importance, the sexual cycle is rarely or never observed in

the field? Is there a mechanism similar to RIP mutations but operating during vegetative growth?

As shown above, the mechanisms leading to genetic variability in *Colletotrichum* spp. still need to be thoroughly studied. There are also some questions that need to be answered regarding *Colletotrichum* clades and lifestyle. Why do clado orbiculare representatives have the largest genomes? Many endophytic isolates belong to species that are known as important phytopathogens. Does this endophytic lifestyle depend on the physiological state of the plant? Under stress conditions, could these fungi behave like phytopathogens or do they have mutations that ensure permanence as endophytes? Do the abundance of endophytic isolates identified as *Colletotrichum* prove their widespread distribution or is it due to the endophytic isolation techniques employed that favor fast growing fungi? Much remains to be explained in this important genus of phytopathogenic fungi.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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