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REVIEW ARTICLE

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Cobweb, a serious pathology in mushroom crops: A review

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Abstract

Cobweb is a fungal disease of commercially cultivated mushrooms. Several members of the ascomycete genus *Cladobotryum* sp. have been reported as causal agents. White button mushroom is the most frequently cited host, but a wide range of cultivated edible mushrooms suffer cobweb. The pathology causes production losses and reduces the crop surface available. The parasite produces a great number of harmful conidia that can be released easily and distributed throughout the mushroom farm to generate secondary points of infection. To prevent initial outbreaks, hygiene is of primary importance within the facilities dedicated to mushroom cultivation, while additional measures must be implemented to control and reduce cobweb if there is an outbreak, including chemical and biological methods. This review summarizes and discusses the knowledge available on the historic occurrence of cobweb and its impact on commercial mushroom crops worldwide. Causal agents, disease ecology, including the primary source of infection and the dispersal of harmful conidia are also reviewed. Finally, control treatments to prevent the disease from breaking out are discussed.

Additional keywords: *Cladobotryum*; fungal disease; dispersal; production losses; edible mushroom; control.

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Introduction

Many fungal diseases can affect commercial mushroom crops (Fletcher & Gaze, 2008). Among them cobweb is considered one of the most serious diseases for white button mushroom [*Agaricus bisporus* (Lange) Imbach] cultures, the most widely cultivated species (Royse, 2014). Other edible cultivated mushrooms may also develop the harmful pathology (Gea *et al.*, 2011, 2017; Back *et al.*, 2012; Kim *et al.*, 2012). Its occurrence in commercial crops results in reductions in yield and quality, mainly due to cap spotting, a lesser surface area that can be used for cultivation and to the need for early crop termination when the disease becomes epidemic (Adie, 2000; Adie *et al.*, 2006).

Cobweb appears more often at the end of the crop cycle (although the earlier it appears, the more devastating it can be) during the autumn and winter cycles. First, small, white circular patches appear on the casing soil or basidiomes. These quickly spread by means of a fine grey-white mycelium that resembles a spider web (Carrasco *et al.,* 2016a). Eventually patches of mycelium start to sporulate, producing masses of dry spores that are easy to release when they are physically disturbed, mainly through watering or picking operations – even air currents from air-conditioning systems are sufficiently strong to mobilize the harmful spores (Adie *et al.*, 2006). Once released, conidia are spread throughout the mushrooms facilities by air currents to form secondary colonies on the casing layer or to simultaneously spot the basidiomes (Adie, 2000). As soon as a primary cobweb outbreak is located over the casing or carpophores, it must be treated before sporulation, covering the infected area with thick damp paper to avoid the release of conidia and disease dispersion (Pyck & Grogan, 2015).

Various species of filamentous fungi inhabiting soil, decaying wood and wild-mushrooms may cause cobweb: *Cladobotryum dendroides* (Bull.: Fr.) W. Gams & Hoozem (conidial state of *Hypomyces rosellus*) is the species historically associated with cobweb in *A. bisporus* crops, in recent years *Cladobotryum mycophilum* (Oudem.) W. Gams & Hoozem (conidial state of *Hypomyces odoratus*) has become the most commonly reported causal agent (Back *et al.*, 2012; Kim *et al.*, 2014; Chakwiya *et al.*, 2015; Carrasco *et al.*, 2016a; Zuo *et al.*, 2016). However, several other species have been reported as causing this pathology in commercial mushroom crops.

Control methods must be implemented through hygiene measures and by preventing the dissemination of spores, which are dry and easy to dislodge. When not properly treated, conidia will spread within crops, magnifying infection and increasing losses (Adie *et al.*, 2006; Pyck & Grogan, 2015). In this respect, public policies aimed at reducing the use of chemical pesticides through the use of sustainable agriculture practices (*e.g.* the French "Ecophyto 2018" plan) have led to the intensification of biological control efforts in agriculture. Although there have been attempts to identify biological control agents and environmentally-friendly biomolecules that are effective against fungal diseases in mushroom (Potočnik *et al.*, 2010; Kosanović *et al.*, 2013; Gea *et al.*, 2014; Geösel *et al.*, 2014), no efficient bio-treatment to control cobweb disease has been described. In view of this, control of the pathology still relies on the use of chemical fungicides. However, since the sensitivity of mycoparasites to approved pesticides is gradually diminishing and signals of resistance have been detected (McKay *et al.*, 1998; Gea *et al.*, 2005; Grogan, 2006), their use demands judicious management. In short, to optimize integrated disease control, the use of chemicals must be combined with good farming practices and with measures directed towards enhancing hygiene within growing facilities.

Cobweb disease: a recurrent visitor

Cultivated edible mushrooms are susceptible to diseases caused by bacteria, fungi and viruses. Among biotic agents, mycoparasites are responsible for the greatest mushroom crop losses, which have a significant economic impact on industry (Fletcher & Gaze, 2008).

Cobweb disease has been known as an edible mushroom crop pathology since the early days of mushroom cultivation (Carrasco, 2016). The pathology has been detected and reported in most edible mushroom-growing countries, including: Australia (Fletcher *et al.*, 2004), Belgium (Desrumeaux, 2005), China (Zuo *et al.*, 2016), Canada (Howard *et al.*, 1994), France (Largeteau & Savoie, 2010), Korea (Back *et al.*, 2010), India (Bhatt & Singh, 2002), Ireland (McKay *et al.*, 1999), Japan (Sawada *et al.*, 2005), New Zealand (De Hoog, 1978), Poland (Ślusarski *et al.*, 2012), Serbia (Potočnik *et al.*, 2008), South Africa (Eicker, 1984), Spain (Gea *et al.*, 2012), Taiwan (Kirschner *et al.*, 2007), Turkey (Bora & Özaktan, 2000); UK (Adie *et al.*, 2006) and the USA (Beyer & Kremser, 2004).

Historically treated as a minor disease, cobweb is currently considered one of the four most serious diseases of mushroom crops caused by parasitic fungi, together with dry bubble (*Lecanicillium fungicola*), green mould (*Trichoderma aggressivum*) and wet bubble (*Mycogone perniciosa*) (Fletcher & Gaze, 2008). In the mid-1990s, cobweb was reported to be the most serious disease affecting mushroom cultivation in UK and Ireland, where it reached epidemic proportions that involved production losses of up to 40% (Adie *et al.*, 2006).

The prevalence of cobweb disease in commercial mushroom crops has been reported to vary between 6.8 and 28% in Indian *A. bisporus* facilities (Seth & Dar, 1989; Bhatt & Singh, 2002), 33% in Turkey (Bora & Özaktan, 2000) and, up to 32% in Spanish commercial button mushroom crops (Carrasco *et al.*, 2016a). Its occurrence is associated with final flushes and is conditioned by the season (McKay *et al.,* 1999; Adie, 2000; Desrumeaux, 2005). The occurrence and severity of cobweb gradually increases from the first to the third flush. Although it may be established at any time during the year, it is of particular concern in autumn and winter (Carrasco *et al.*, 2016a).

Causal agent

Several species belonging to the genus *Cladobotryum* Nees *emend.* (syn. *Dactylium* Nees) can cause cobweb disease in edible mushroom crops (Table 1). They correspond to the conidial or asexual stage of species from the genus *Hypomyces* (Fries) L.R.Tulasne (Ascomycota, Hypocreales, Hypocreaceae).

As a rule of thumb, for its correct identification, *Cladobotryum* spp. must be evaluated by two independent methods: (1) morphology: screening for aurofusarin and camphor odour producers, registering conidia and phialide size as well as taxonomic characters (Carrasco *et al.*, 2016a); and (2) molecular and phylogenetic analysis. The best approach for complete molecular identification involves implementation of multigene phylogenetic analyses, including sequencing of the internal transcribed spacer (ITS) region of ribosomal DNA (rDNA), RNA polymerase subunit I

Table 1. *Cladobotryum* strains associated with cobweb disease in cultivated edible mushrooms.

Isolate [a]	Host	GenBank Accession [b]	Origin	Species	Reference
Africa					
TRS9, 11-14, 19, 29, 35-37	*A. bisporus*	KF981169-78	South Africa	*C. mycophilum*	Chakwiya *et al*. (2015)
Asia					
-	*G. tsugae*	DQ376084	Taiwan	*C. semicirculare*	Kirschner *et al*. (2007)
-	-	EU340835	India	*C. asterophorum*	Unpublished
NA	*P. eryngii*	JF693809	South Korea	*C. mycophilum*	Kim *et al*. (2012)
NA	*P. eryngii, A. bisporus*	AB527074	South Korea	*C. mycophilum*	Back *et al*. (2010, 2012)
NA	*H. marmoreus, F. velutipes*	AB591044	South Korea	*C. varium*	Back *et al*. (2012)
NA	*F. velutipes*	AB298708	Japan	*C. varium*	Unpublished
NA	*F. velutipes*	AB374290	Japan	*C. varium*	Unpublished
BAC01-07	*A. bisporus*	KJ808711-17	South Korea	*C. mycophilum*	Unpublished
NA	*A. bisporus*	EU340384	India	*C. mycophilum*	Unpublished
C-1	*C. comatus*	KU237239	China	*C. protrusum*	Wang *et al*. (2015)
LZ10	*G. lucidum*	KJ942816/KP137364/ KP137365/KP137366	China	*C. mycophilum*	Zuo *et al*. (2016)
Europe					
CM1-6	*A. bisporus*	JQ004732-36	Spain	*C. mycophilum*	Gea *et al*. (2012); Carrasco *et al*. (2016a)
CM7-23	*A. bisporus*	KP698960-73	Spain	*C. mycophilum*	Carrasco *et al*. (2016a)
PE32, 40, 53, 57, 68, 70, 71	*P. eryngii*	KP267824-30	Spain	*C. mycophilum*	Gea *et al*. (2017)
PE72	*P. eryngii*	JF505112	Spain	*C. mycophilum*	Gea *et al*. (2011, 2017)
MGB0003-05	*A. bisporus*	KC964103-104	Spain	*C. mycophilum*	Unpublished
IMI 267134	*A. bisporus*	Y17095/Y17101/HF911958/ HF911547/HF911744/ HF911637/ HF911854	UK	*C. dendroides*	McKay *et al*. (1999)
IMI 359310, 372795-96	*A. bisporus*	HF911959-61/HF911548-49/ HF911638-40/HF911855-57	UK	*C. dendroides*	Grogan &Gaze (2000); Tamm & Põldmaa (2013)
I.P. 15	*A. bisporus*	HF911962/HF911550/ HF911747/HF911641/ HF911858	Hungary	*C. mycophilum*	Tamm & Põldmaa (2013)
I.P. 21	*A. bisporus*	HF911963/HF911551/ HF911748/ HF911642/HF911859	Ireland	*C. mycophilum*	Tamm & Põldmaa (2013)
I.P. 17, 7	*A. bisporus*	HF911964-65/HF911552-53/ HF911749-50/HF911643-44/ HF911860-61	Serbia	*C. mycophilum*	Tamm & Põldmaa (2013)
I.P. 14-20	*A. bisporus*	HF911986-87/HF911570-71/ HF911774-75/HF911666-67/ HF911883-84	UK	*C. dendroides*	Grogan & Gaze (2000); Tamm & Põldmaa (2013)
MUCL-28202	*A. bisporus*	Y17092	Luxembourg	*C. dendroides*	McKay *et al*. (1999)

Table 1. Continued

Isolate [a]	Host	GenBank Accession [b]	Origin	Species	Reference
Z063015,Z15001, Z079004	*A. bisporus*	Y17094, 97, 103	Ireland	*C. mycophilum*	McKay *et al*. (1999)
CBS-111.92	*A. bisporus*	Y17098	Germany	*C. mycophilum*	McKay *et al*. (1999)
America					
PSU DC177	*A. bisporus*	HF911770/HF911662/ HF911879	USA	*C. dendroides*	Tamm & Põldmaa (2013)
CBS-148.46	*A. bisporus*	Y17100/HF911943/ HF911534/ HF911728/HF868622/ HF911838	Canada	*C. mycophilum*	McKay *et al*. (1999); Tamm & Põldmaa (2013)
PSU DC26-27	*A. bisporus*	Y17102/HF911947-48/ HF911537-38/HF911733-34/ FN868626/HF911843	USA	*C. dendroides*	McKay *et al*. (1999); Tamm & Põldmaa (2013)
PSU DC 294, 0,302,305,306,309,310,315	*A. bisporus*	HF911949-57/HF911539-46/ HF911950/HF911735-43/ HF911736/	USA	*C. dendroides*	Tamm & Põldmaa (2013)
Oceania					
Z385044	*A. bisporus*	Y17089	Australia	*C. astereophorum*	McKay *et al*. (1999)
Z385037	*A. bisporus*	Y17099	Australia	*C. mycophilum*	McKay *et al*. (1999)
CBS 472.71	*A. bisporus*	NR_121423/FN868786/ FN868659/ HF911724/FN868723/ HF911834	New Zealand	*C. multiseptatum*	De Hoog (1978); Põldmaa (2011)

[a]Collections listed (IMI: International Mycological Institute, Royal Botanic Garden, Kew, UK; MUCL: BCCM/MUCL - Belgian Co-ordinated Collections of Microorganisms, Belgium; CBS: CBS-KNAW - Westerdijk Fungal Biodiversity Institute, The Netherlands) and not listed by WFCC (World Federation for Culture Collections). NA: data not available. [b]GenBank Accession Numbers amplified respectively by ITS, RPB1, RPB2, TEF-1 or protein component of the 60S ribosomal subunit (FG1093) sequences.

(RPB1), DNA-dependent RNA polymerase subunit II (RPB2) and translation elongation factor (TEF) genes (Tamm & Põldmaa, 2013; Zuo *et al.*, 2016).

When plated on potato dextrose agar (PDA) these fungi develop a greyish-white mycelium with the reverse side of the plate turning yellow in few days. Usually 2-4 weeks later, the plates acquire a deep red colour (Fig. 1m,n,o). This pigment, most probably aurofusarin, is mainly secreted by the hyphae immersed in the growth media (Põldmaa, 2011). However, not every *Cladobotryum* species provoking cobweb generates the pigment (Potočnik *et al.*, 2008).

Cladobotryum spp. present verticillated hyphae at the end of which three or four conidiogenous cells, called phialides, are located. Most of the species show a conidial holoblastic ontogeny (in which the apex of the conidiogenous cells is incorporated as part of the generated conidium) through basipetal succession (Grogan & Gaze, 2000; Tamm & Põldmaa, 2013). Conidia, unicellular in origin, usually show from 1 to 3 septa (2 to 4 cells) (Desrumeaux, 2005; Adie *et al.*, 2006). They are hyaline, globose to subglobose, bacilliform, cylindrical and often lightly tapered, slightly curved in some cases, with a conspicuous basal hilum in the base. The apex shape and dimensions of the subulate phialides (narrowing towards the apex) vary among species (Fig. 1a-f).

In vitro, the fungi produce dark, thin walled microsclerotia. Multicellular, globose structures (chlamydospores) have been also reported associated to these microsclerotia (Fig. 1g-l) (Carrasco *et al.,* 2016a). Both are generally associated with the life cycle stage of the fungus that survives under unfavourable conditions (Rogerson & Samuels, 1993).

Cladobotryum dendroides (Bull.: Fr.) W. Gams & Hoozem. (syn. *Dactylium dendroides*) has been the species historically associated with cobweb disease (teleomorph: *Hypomyces rosellus* (Alb. & Schwein.:Fr.) Tul.). *In vitro*, it secretes the above described pigment when the strain ages (Põldmaa, 2011). It is the only species in the genus characterised by a thin-walled sympodial conidiogenous rachis at the phialide tip that apparently is formed after

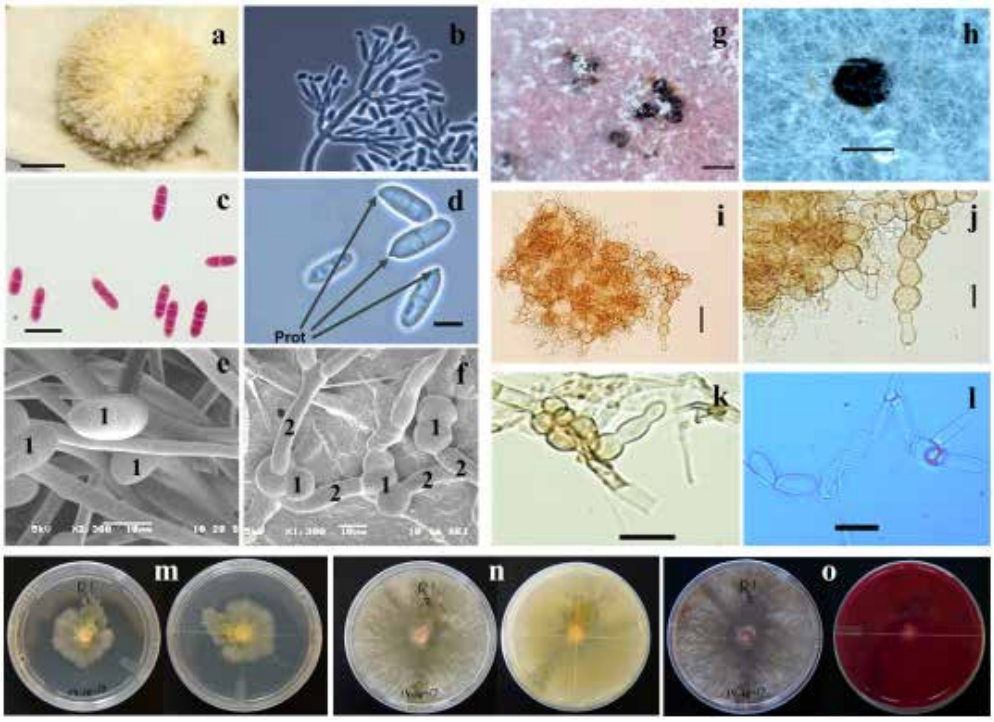

Figure 1. Morphology of *C. mycophilum*, most cited causal agent of cobweb disease. (a) Conidia clouds engulfing the infected carpophore. (b) Mycelium. (c, d) Conidia (Prot: scar of union to the phialide, hilum basal). (e) Conidia in the my cosphere of *A bisporus* (1: conidia). (f) Germinating conidia in the mycosphere of *A. bisporus*. (1: conidia; 2: germinative tubes). (g, h, i) Microsclerotia. (j, k, l) Chlamydospores. (m, n, o) Front and back side of PDA medium plated with the mycoparasite. Evolution of the colony (2, 4 and 21 days of incubation at 22ºC in darkness). Scale: a=1 cm; b,c,k,l=20 µm; d,e,f,j=10 µm; g=500 µm; h=127 µm; i=30 µm.

successive conidia are released (Tamm & Põldmaa, 2013). The conidia mostly present 2-3 septa.

Cladobotryum mycophilum (Oudem.) W. Gams & Hoozem. (syn. *Dactylium mycophilum* Oudem.), the anamorph of *Hypomyces odoratus* G.R.W. Arnold, is currently the most cited causal agent of cobweb. It has recently been described as parasitizing different edible crops in Africa, Asia and Europe, including *Agaricus bisporus, Pleurotus eryngii* and *Ganoderma lucidum* (Back *et al.*, 2010; Chakwiya *et al.*, 2015; Carrasco *et al.*, 2016a; Zuo *et al.*, 2016; Gea *et al.*, 2017). *C. mycophilum* is also a red pigment producer *in vitro* (Carrasco *et al.*, 2016a). Colonies generate a camphor odour, whose intensity varies with the age of the strain and the growth medium, and which is perceptible when lifting the lid of the Petri plate (Põldmaa, 2011). Phialide tips are simple and regular, without any evident rachis, and conidia are mostly uniseptate (Carrasco *et al.*, 2016a). *C. mycophilum* spores start to germinate 2 h after isolation on PDA at room temperature. Spores first undergo constriction of the septum ("septa constricta"), and then grow, acquiring a globose shape from which several germinative tubes are generated. The estimated growth rate of germinative tubes is 11.6 µm/h (Carrasco, 2016).

Cladobotyum mycophilum Type II was described in the mid-1990s as a highly resistant variety to bencimidazole fungicides (McKay *et al.*, 1999; Grogan & Gaze, 2000). The colonies, which showed higher and earlier sporulation, lost the characteristic camphor odour, and conidia usually presented 1, 2 or 3 septa (Adie, 2000; Grogan & Gaze, 2000).

C. varium Nees ex Steud. does not secrete aurofusarin. The species has been described as a causal agent of cobweb disease in Korean edible mushroom crops (*F. velutipes, H. marmoreus, P. eryngii*) (Back *et al.*, 2012; Kim *et al.*, 2012). *C. varium* was also reported as pathogenic to *A. bisporus* in cross pathogenicity tests (Back *et al.*, 2012).

Two GenBank sequences of the aurofusarin-producing *C. asterophorum* have been related to cobweb disease in mushroom crops (McKay *et al.*, 1999; Tamm & Põldmaa, 2013). *C. asterophorum* has also recently been identified on beech mushrooms in Korea. This species was pathogenic against *H. marmoreus, F. velutipes* and *P. eryngii* (Back *et al.*, 2012).

C. multiseptatum (de Hoog), also a producer of aurofusarin, was isolated by A. W. Smith as causal agent of cobweb disease in *Agaricus brunnescens* Peck (an *A.*

bisporus variant), in New Zealand. The strain presented 2-4 cell conidia (1-3 septa) (De Hoog, 1978; Tamm & Põldmaa, 2013).

C. protrusum was isolated from infected tissue of *Coprinus comatus* in commercial mushroom farms of China. Colonies of the pathogen on PDA plates turned ocherous or pinkish. Conidiophores were cylindrical, long clavate, or fusiform and conidia presented 1 to 2 septa (Wang *et al.*, 2015).

C. semicirculare, an aurofusarin producer characterized by the presence of curved conidia with 0-3 septa, was isolated from commercial *Ganoderma tsugae* crops in Taiwan (Kirschner *et al.*, 2007).

Disease ecology

In the wild

Certain species of *Cladobotryum* parasite members of the basidiomycetes group, mostly belonging to the orders Aphyllophorales and Agaricales (Gams & Hoozeman, 1970). In addition, some species are found on different substrates, such as bark, decaying wood or leaf litter.

Some of the *Cladobotryum* spp. known to cause cobweb disease in edible mushroom crops have also been reported as parasitizing polyporus and agaricales in the wild (Gams & Hoozemans, 1970; Rogerson & Samuels, 1993, 1994; Kirschner *et al.*, 2007; Põldmaa, 2011).

Figure 2. a) Fluffy mycelium growing over the casing layer and *A. bisporus* basidiomes. b) Mass of conidia engulfing carpophores. c) Regular grey-yellow spots or decoloration. d) Brown spots with an ill-defined edge. e, f) Mycelium and mass of conidia colonizing *P. eryngii* basidiomes and casing layer.

In commercial edible mushroom crops

Cladobotryum spp. has been reported as infecting different species of cultivated edible mushroom, among them: *Agaricus bisporus* (Gea *et al.*, 2012; Carrasco *et al.*, 2016a), *Agaricus bitorquis* (Potočnik *et al*., 2008), *Agaricus blazei* (Geösel, 2011), *Auricularia mesenterica* (Eicker *et al.,* 1990), *Coprinus comatus* (Wang *et al.*, 2015), *Flammulina velutipes* (Kim *et al.,* 1999), *Ganoderma tsugae* (Kirschner *et al.*, 2007), *Ganoderma lucidum* (Zuo *et al*., 2016), *Hypsizygus marmoreus* (Back *et al.*, 2012), *Pleurotus eryngii* (Gea *et al.*, 2011, 2017), *Pleurotus ostreatus* and *Pleurotus pulmonarius* (Mignucci *et al*., 2000).

Infection

Primary source of infection

According to literature, casing contamination is frequently considered a source of primary infection (Fletcher & Gaze, 2008). Casing materials artificially inoculated with the pathogen reproduced cobweb disease in *A. bisporus* and *P. eryngii* (Carrasco *et al.*, 2016a; Gea *et al.*, 2017). The presence of the host in the casing layer seems necessary to desensitize the dormant spores and to stimulate their germination and the development of *Cladobotryum* mycelium. In pilot trials, we noted that raw casing material remains healthy after inoculation with a suspension of *C. mycophilum* conidia, while the same casing colonized by *A. bisporus* expressed the disease in every replicate (our unpublished data). Likewise, *L. fungicola* is inhibited by the microflora of the casing layer due to a phenomenon called fungistasis; however, the presence of the host removes the fungistasis to facilitate disease development (Berendsen *et al.*, 2010).

Tamm & Poldmaa (2013) concluded that the endemic species determines the causal agent of cobweb in commercial crops. This seems to indicate that a primary source of infection may be wild specimens infected near the farm. Under unfavorable conditions, particularly when the relative humidity (RH) is low, most *C. dendroides* spores do not survive for long periods. However, the fungus produces microsclerotia, resistant structures that can germinate even when they are stored at 0% RH (Lane *et al.*, 1991). High humidity conditions outside the cropping rooms will facilitate survival of the pathogenic conidia and their dispersal through the production area (Carrasco, 2016; Carrasco *et al.*, 2016a).

Conversely, compost is not usually considered to be a primary source of infection. During phase II, compost undergoes a high-temperature pasteurisation process to eliminate pathogens (Fletcher & Gaze, 2008). Likewise, spawn or host mycelium is not a source of infection due to high-standard hygiene conditions while the spawn grain is prepared (Desrumeaux, 2005; Fletcher & Gaze, 2008).

Finally, alternative sources of primary infection are contaminated packages and containers, external visits, vehicles, etc. Contaminated water could be also a source of infection since some mycopathogens, such as *Lecanicillium* and *Mycogone* spores, are known to survive in water for many months.

Symptoms

Cobweb disease induces both qualitative and quantitative losses in commercial mushroom crops, where it compromises mushroom quality and provokes a significant drop in profitability within the crop cycle (Carrasco *et al.,* 2016a).

Primary outbreaks are characterised by the occurrence of a white, fluffy mycelium over the mushroom beds and infected carpophores. Infected mushrooms usually present discoloration and eventually rot. If not properly controlled, localized outbreaks tend to grow radially outwards over the casing layer, colonizing a larger crop surface and therefore reducing it (Fig. 2). The light, invasive mycelium quickly evolves towards a dense white mass with a mealy texture due to massive sporulation (Adie, 2000). When they age, colonies usually acquire pink-red hues (Tamm & Poldmaa, 2013).

One of the main causes of harvest depreciation is mushroom discoloration through the action of fungal and bacterial diseases. The secretion of hydrolytic enzymes (combined with mechanical pressure and the formation of penetration structures) and toxic compounds have been related to the interaction between mycoparasites and hosts (Calonje *et al.*, 2000; Abubaker *et al.*, 2013). Certain secondary metabolites produced by fungal parasites are known for being antagonistic towards *A. bisporus* (Krupke *et al.*, 2003). Mycoparasitic *Cladobotryum* species produce a wide variety of secondary metabolites with marked activity, including antibacterial, antifungal and repressive effects on cancer cells (Sakemi *et al.*, 2002; Feng *et al.*, 2003; Mitova *et al.,* 2006).

In particular, *Cladobotryum* spp. causes two types of cap spotting on infected mushrooms, dark-brownish spotting with an ill-defined edge and grey-yellowish spotting (Grogan & Gaze, 2000; Grogan, 2006) (Fig. 2c,d). The spotting can even appear post-harvest, and therefore the sale of the product must be conditioned (Adie, 2000; Fletcher & Gaze, 2008).

Brown spots are generated when a single spore lands on the mushroom surface and germinates. These spots usually provoke depression of the cap tissue. From the localized spots a parasitic mycelium emerges that eventually engulfs the whole basidiome. The grey-yellowish spotting is due to the interaction between parasitic mycelium and the host basidiomes; spots progressively discolour the mushroom tissue, which succumbs to wet rot (Adie, 2000) (Fig. 2c).

Dispersal

The key factor that conditions the incidence and severity of the disease in commercial mushroom crops is the spread of harmful conidia within culture facilities (Adie *et al.*, 2006; Fletcher & Gaze, 2008).

Pathogenic spores are numerous, dry and easily dislodged by physical contact. Once released, these conidia quickly spread through the air-conditioning systems.

Previous reports suggest that the major causes of conidia release are splashing and runoff while watering, and the application of salt through incorrect procedures (Adie & Grogan, 2000). The main measures to prevent conidia dispersal are: avoiding irrigation over or near cobweb patches; covering the patches with thick, damp paper instead of salting; switching off the fans while removing the spent mushroom compost; hermetically closing the doors of growing rooms and, finally using 5 µm ø pore size air filters (HEPA) (Fletcher & Gaze, carra; Pyck & Grogan, 2015; Carrasco *et al.*, 2016a).

Prevention and disease control

Hygiene

Prevention is crucial to precluding the emergence of cobweb and to limiting its impact once installed. Control methods should prevent dispersion of conidia (as previously described), which is the main way of infection (Adie, 2000; Adie & Grogan, 2000; Fletcher & Gaze, 2008).

The end of the crop cycle is a crucial time for removal of any residual disease. Wet conidia of *Cladobotryum* spp. are killed by treatment at 45 ºC for 30 min, but they resist higher temperatures when dry, even up to 100 ºC (Desrumeaux, 2005). Similarly, the pathogenic mycelium, which is susceptible to a 15 min, 40 ºC treatment when wet, requires temperatures of 70 ºC for 15 min when dry (Fletcher & Gaze, 2008). Consequently, *in situ* thermal disinfection

at the end of the crop cycle through "cooking-out" (65-70 ºC for 9-12 hours) is the best way to ensure correct disinfection (Fletcher & Gaze, 2008). When not possible, it is advisable to clean the empty facility with water and suitable disinfectants.

It is also possible to prevent disease outbreaks by controlling the humidity and the temperature within mushroom facilities, since few spores of *C. dendroides* can germinate with a RH lower than 85% , while at low temperatures (17 ºC) development and spread of the disease are unlikely (Desrumeaux, 2005).

Chemical control

Control of cobweb disease is still highly dependent on routine application of fungicides from several chemical groups: prochloraz-Mn (DMI-fungicide, FRAC code: 3) is the fungicide currently recommended by the European Union to treat cobweb (Carrasco, 2016; FRAC, 2016). Chlorothalonil (chloronitrile, FRAC code: M5) is also approved for use in France, Poland and Spain. Two DMI fungicides, imazalil (to control green mould disease) and prochloraz-Mn (for cobweb), are licensed for use in Australian mushroom crops. In South Africa, prochloraz-Mn and thiabendazole are the fungicides approved for use in mushroom (Chakwiya *et al.*, 2015). Thiabendazole (MBC-fungicide, FRAC code: 1) can be used in USA mushroom crops, as well as chlorothalonil formulates. Recently, metrafenone (benzophenone, FRAC code: U8) has been authorized for use in France to fight cobweb disease (FRAC, 2016). Recently, too, metrafenone obtained a temporary approval for use on mushroom crops in Spain. When compared with prochloraz-Mn and chlorothalonil, metrafenone showed higher selectivity towards *C. mycophilum in vitro* and was the most effective treatment to control cobweb in crop, which suggests that it could be an efficient alternative to prochloraz-Mn (Carrasco *et al.*, 2016b, 2017).

The sensitivity of mycoparasites to approved pesticides is gradually diminishing (Gea *et al.*, 2005), and symptoms of cobweb resistance have been detected (McKay *et al.*, 1998; Grogan, 2006; Carrasco, 2016). The continuous usage of a given fungicide frequently contributes to pathogen resistance and, consequently, to undermining the value of the active substances available for cobweb control (Chakwiya *et al.*, 2015).

In this context, improved hygiene in growing facilities before the disease develops, as well as a better understanding of the pathogen's behaviour, will lengthen the half-life of available fungicides by streamlining doses to prevent the occurrence of resistant outbreaks (Schwinn & Morton, 1990).

Alternative control methods

Due to consumer demand and environmental concerns, there is a strong pressure to reduce the use of chemical pesticides (French plan EcoPhyto 2018), which has led to the intensification of biological control in agriculture.

The antagonistic effect of *Pseudomonas* for the biocontrol of *Cladobotryum dendroides* was evaluated in Turkey, where application of *P. fluorescens* and *P. putida* (Bora & Özaktan, 2000) increased yields. However, *Bacillus subtilis* QST 713 (Serenade®) failed to control cobweb disease (*C. dendroides*) in artificially inoculated experiments (Ślusarski *et al.*, 2012).

Compost tea from spent mushroom compost and essential oils from aromatic plants have been tested as alternative, environmentally-friendly biomolecules with different degrees of success to cope with fungal diseases (Potocnic *et al.*, 2010; Kosanović *et al.*, 2013; Gea *et al.*, 2014; Geösel *et al.*, 2014). Timorex 66 EC (66% "tea tree oil) showed higher activity than Sonata® (*Bacillus pumilus*) against *C. dendroides*, although the efficacy of Timorex was far lower than that of prochloraz-Mn (Potočnik *et al.*, 2010). The application of aerated compost tea from spent mushroom compost was efficient to control dry bubble (Gea *et al.*, 2014), although the results were disappointing when used for cobweb control (unpublished data).

Finally, Savić *et al.* (2012) tested the antifungal activity of organic selenium against *C. dendroides.* The addition of 70-100 µg/g selenium to the substrate inhibited growth of the mycopathogen and resulted in the enrichment of basidiomes with this trace element.

Conclusion and perspectives

Certain species from the genus *Cladobotryum* may generate cobweb disease in a wide range of edible mushroom crops worldwide. Control of this pathology currently relies on prevention and hygiene measures in mushroom farms, together with chemical fungicide treatments. However, the range of available substances approved for mushroom crops is limited by the fungal nature of the host as well as by restrictive legislation. Understanding the mechanisms involved in the interaction between parasite and host is a powerful tool in the design of novel control strategies, including the production of resistant host varieties. However, many questions involving mycoparasites remain unanswered, including the pathway for infection followed by harmful species

to detect and colonize the host, the molecular basis for the observed symptoms, the molecules implied in the attack on the host tissues, or the mechanisms used to overcome host defences. On the other hand, fungicide alternatives to fight cobweb disease in the form of environmentally-friendly biomolecules are being actively investigated, accompanied by a search for efficient biocontrol agents to cope with *Cladobotryum* infection. Successful biological control of the fungal diseases would satisfy the mushroom industry's continuous efforts to minimize the use of chemicals. However, to date, no biocontrol agent has been found to be as effective as approved fungicides.

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