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REVIEW - 9TH SPECIAL ISSUE ON GRAPEVINE TRUNK DISEASES

An annotated checklist of European basidiomycetes related to white rot of grapevine (*Vitis vinifera*)

Michael FISCHER[1] and Vicente GONZÁLEZ GARCÍA[2]

[1] Julius Kühn-Institut, Institut für Pflanzenschutz in Obst- und Weinbau, Geilweilerhof, D-76833 Siebeldingen, Germany
[2] Plant Pathology Lab, Dpto. de Investigación Aplicada y Extensión Agraria Instituto Madrileño de Investigación y Desarrollo Rural, Agrario y Alimentario (IMIDRA) 28800 Alcalá de Henares (Madrid), Spain

Summary. A considerable number of basidiomycetes are reported to live on *Vitis vinifera*. Detailed information about this relation dates back to the 19th and early 20th century. More recently, several basidiomycetes have been discussed as being associated with Grapevine Trunk Diseases, especially esca. On a European scale, we list 24 basidiomycetous taxa. Ten species are treated with respect to "life strategy and symptoms", "host plants", "geographic distribution", "transmission and vectors", "fruitbody characters" and "diagnosis". Fourteen additional species are listed with their main features only. References are given both to data provided in the literature and from our observations. *Fomitiporia mediterranea*, and, to a lesser degree, *Inonotus hispidus* are discussed as primary pathogens. The remaining taxa, including *Stereum hirsutum*, *Trametes hirsuta*, and *Schizophyllum commune*, are considered as subordinate only, mainly causing white rot on already dead parts of grapevine trunks. With the data at hand, the ecological significance of *Auricularia auricula-judae* remains uncertain.

Key words: esca disease, fruitbody formation, geographic distribution, host plants, pathogenic significance.

Introduction

Several thousands of basidiomycete species are known to live on wood as saprobionts and/or parasites (Gilbertson and Ryvarden, 1986-87). Basidiomycetes existing on hardwood hosts, such as species of *Vitis*, with few exceptions, cause white rot symptoms; brown rot is exceptional and is mainly limited to host members of the Fagaceae and Betulaceae (Nobles, 1958, 1965; Gilbertson, 1981). White rot fungi can degrade all components of cell walls, i.e. lignin, cellulose and hemicellulose.

White rot is often very prominent in older vines. In some areas of Germany, it is seen in 100% of vines older than 15 years (Fischer, 2000). Similar observations, although with lower incidence, have been made in other countries such as Italy (Mugnai *et al*., 1996; Cortesi *et al*., 2000), France (Larignon and Dubos, 1997), Spain (Armengol *et al*., 2001) or California (Chiarappa, 1959, 2000).

A considerable number of white rot basidiomycetes have been recorded on many grapevine cultivars, the ones mostly mentioned being *Phellinus igniarius*, *Stereum hirsutum*, and *Trametes hirsuta* (among others, see von Thümen, 1878; Ravaz, 1909; Bourdot and Galzin, 1927; Kreisel, 1961; Adaskaveg and Gilbertson, 1987; Ryvarden and Gilbertson, 1993-94; Larignon and Dubos, 1997; Rumbos and Rumbau, 2001; Fischer and Kassemeyer, 2003; Fischer, 2006; González *et al*., 2009; White *et al*., 2011; Cloete *et al*., 2014). A number of taxa assignable to accepted species and forming fruitbodies on grapevine in Europe are presented in the checklist presented in the present paper, together with available data on their life strategies, host range, geographic distribution, transmission and vectors, and diagnostic features. Clear relationships with grapevine trunk diseases (GTDs)

Corresponding author: M. Fischer
E-mail: michael.fischer@jki.bund.de

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are exceptional for most of them; where observed decay processes in living or dead wood of *Vitis* may be of different (or unknown) intensity, and the presence of such fungi is not clearly linked to typical GTD symptoms. To our knowledge, no basidiomycete species is restricted to *Vitis* as a plant host, and these fungi also exist on other hardwood (more rarely, conifer) host genera. In this way, occurrence on *Vitis* should be considered as marginal or secondary for most taxa.

In addition to the taxa presented here, several basidiomycetes of uncertain systematic affinity or lacking formal description have been recently detected on grapevine in non-European countries (e.g., Fischer *et al*., 2005; Fischer, 2006; White *et al*., 2011). These findings are often based on the existence of vegetative mycelia only; it is unknown to which degree such lesser or unknown species could also exist in Europe.

With the data at hand it is not possible to conclude if white rot fungi form an essential component of GTDs, or if injured wood should be simply seen as an important source of nutrients attracting a wide range of more or less adapted fungal decomposers capable of colonizing and decaying a broad range of hosts. Probably the great majority of basidiomycetes on grapevine do not have real pathogenic relevance (including host-specificity), or such relevance might be restricted to certain conditions in a certain area (well illustrated for *Inonotus hispidus*; González *et al*., 2009). For Europe, exceptions are the widespread *Fomitiporia mediterranea*, and, to some degree, the honey fungus, *Armillaria mellea*. The latter species, however, attacks host roots and is therefore treated as "minor" fungus in our study.

Among the economically important diseases of grapevine, only GTDs may be associated with basidiomycetes. In Petri disease, considered as a precursor of esca itself, it is recognized that wood deterioration, including symptoms such as brown-red wood, tracheomycosis and dark stripes, is caused by a number of anamorphic fungi, including taxa from genera such as *Phaeomoniella*, *Cadophora* and/or *Togninia* (*Phaeoacremonium*) . White rot however, contributing to esca proper, is always linked with the occurrence of basidiomycetes (for the definition of the concept of esca of grapevine, see Graniti *et al*., 2000; Surico, 2001, 2009). Studies on the geographical diversity of the basidiomycete component of late esca syndromes worldwide (Fischer *et al*., 2005; Fischer, 2006; Cloete *et al*., 2014) indicate a considerable diversity according to the country or continent surveyed.

The entries in the following checklist have been selected based on the specialized mycology and plant pathology literature, and, to a lesser extent, on other records compiled from taxonomic sources (including generic checklists, databases, herbaria and monographs). Our personal observations have been added to each entry. Species with some pathogenic significance, as discussed here and elsewhere, are covered in extended descriptions ("major taxa"). The included photographs provide an impression of *in situ* occurrence, rather than showing diagnostic details. In Table 1 we summarize 14 additional species with irregular and/or inconspicuous appearance ("minor taxa", with the root-rot fungus *Armillaria mellea* as an exception).

"Major taxa"

Detailed descriptions of ten selected basidiomycete species are presented in alphabetical order. Some of them have been frequently named as associated with GTDs, while others may play roles in decay processes of dead wood of grapevine.

Auricularia auricula-judae (Bull.) Quél. (Figure 1)

Synonym: *Hirneola auricula-judae* (Bull.) Berk.

Basionym: *Tremella auricula-judae* Bull.

Classification: Basidiomycota, Auriculariales, Auriculariaceae, *Auricularia*

Life strategy and symptoms: *Auricularia auricula-judae* colonizes old and decaying parts of woody plants, usually decorticated branches and trunks. It is considered both a saprobe and a parasite (Lowy, 1952; Kreisel, 1987). Findings on grapevine are on the uppermost part of living and dead trunks, often associated with cracks or old pruning wounds. No data are available about the intensity of the associated white rot. Spread of the fungus inside the host plant is unknown. No specific foliar symptoms are caused by *A. auricula-judae*.

Host plants: a wide variety of deciduous plants, most prominent on *Sambucus*, also often on species of *Acer*. Occurrence on *Vitis* is considered subordinate and might be influenced by the existence of main hosts in the vicinity of vineyards (Fischer and Kassemeyer, 2003; but see notes below).

Geographic distribution: in all temperate regions worldwide, although described only as holarc-

Figure 1. A dry-looking but still sporulating specimen of *Auricularia auricula-judae* on a dead grapevine; appearance of fruitbody was in late winter. Photograph: M. Fischer.

tic in older literature (Kreisel, 1961; for classification and systematic treatment of the Auriculariales, see Weiß and Oberwinkler, 2001). In maritime European countries it is considered as a "more southern species", i.e. it is well adjusted to areas with dry climatic conditions.

Transmission and possible vectors: basidiospores are spread by wind or water in relation to weather conditions. Spores are ejected from the undersides of fresh fruitbodies in large quantities (up to several hundred thousand per hour; easily reproduced under laboratory conditions); even under dry conditions, a small number of spores is still released (Ingold, 1985). Cultural practices may contribute to spread of the spores; old vines, bearing fruitbodies, are commonly uprooted (and transported through vineyards where they shed the spores) during main periods of fruiting, i.e. winter.

Fruitbodies in the field: species of *Auricularia* belong to the so-called "jelly fungi", i.e., fruitbodies shrivel up in dry weather, and rehydrate during cool and moist periods. Many of these fungi, including *Auricularia,* are able to rehydrate and then re-commence spore release. In this way, individual fruitbodies, active or not, may last for several months. As a result, *A. auricula-judae* is an all-year species. Fruitbodies are edible and are commonly used in Asian cuisine.

Main features of fruitbody and diagnosis: fruitbodies are ear-shaped, they appear both solitarily and gregariously; 3–8 cm wide; gelatinous when fresh, becoming hard and horny upon drying; pileus cover is tan-brown with minute greyish hairs, inner surface (fertile layer) is greyish-brown, smooth, often wrinkled ("ear-shaped"); spores are hyaline, allantoid, 16–23 × 6–8 μm.

ITS sequence based on primer pair ITS5-ITS4: GenBank accession KR867638.

No species-specific primers are known.

Notes: to our knowledge, *Auricularia auricula-judae* has been mentioned only once as a cause of wood rot in grapevine (Fischer and Kassemeyer, 2003). There is a possible entry in von Thümen (1878) under the designation of *Auricularia mesenterica* Pers., which is morphologically similar to *A. auricula-judae* (the description provided by von Thümen points to the latter species). In the same chapter von Thümen refers to P.A. Saccardo, who describes *A. mesenterica* as "very common on *Vitis*" in his "Mycotheca Veneta" (Saccardo, 1874-1879). We conclude that the reason for the rarity of records of *A. auricula-judae* in the literature is that the inconspicuous fruitbodies are easily overlooked during dry weather periods. With the data at hand, the significance of *A. auricula-judae* as a pathogen on grapevine is difficult to evaluate.

Flammulina velutipes (Curtis) Singer (Figure 2)

Basionym: *Agaricus velutipes* Curtis

Synonym: *Collybia velutipes* (Curtis) P. Kumm.

Classification: Basidiomycota, Agaricales, Physalacriaceae, *Flammulina*

Life strategy and symptoms: this species is both a saprobe and a parasite; fruitbodies are found on stumps, stems and branches both of dead and living host plants. *Flammulina velutipes* causes an intensive white rot, and may be harmful to host plants. On grapevine, it is usually associated with cracks in debarked wood or with older pruning wounds; no external symptoms are related to the fungus. All reports to date have been for occurrence on stem heads. Nothing is known about the possible vegetative spread of the fungus inside the host.

Host plants: on a wide variety of deciduous plants, most common on *Salix* or *Populus*, also on a variety of fruit trees; rarely also on gymnosperms such as *Picea* (Kreisel, 1961). *Flammulina velutipes* seems to be infrequent on *Vitis*; however, the species may be overlooked due to the development of fruitbodies mainly during wintertime (Fischer and Kassemeyer, 2003).

Figure 2. Often fruitbodies of *Flammulina velutipes* appear in clusters and develop out of cracks in the wood. Photograph: M. Fischer.

Geographic distribution: possibly widespread throughout the northern hemisphere, i.e. Europe, Asia, as well as North America. However, cryptic species might exist within the *F. velutipes* species complex and therefore geographic data are uncertain (see Methven *et al*., 2000). In Europe, it is more frequently reported north to the Alps. No extra-European records on grapevine exist.

Transmission and possible vectors: basidiospores are formed from fruitbodies and are spread by wind, water (rain) in the field. Vineyards are uprooted during main periods of fruiting, and in this way human impact may be significant for spreading the spores. However, few fruitbodies occur on *Vitis* in most areas.

Fruitbodies in the field: this species mostly appears during cool months (winter), although fruitbodies may be rarely found throughout the year on host plants other than *Vitis*. Fruitbodies are annual, and a period of cold weather is usually necessary for their development. They appear in small to large, fasciculate clusters, but are also rarely solitary; they are considered edible without the tough stipes even when collected in frozen condition. The fungus is cultivated on a semi-industrial scale and marketed under the name "enoki mushroom" with long, succulent stipes. Misidentification is possible with some species of genera *Pholiota* and *Kuehneromyces* or the poisonous *Galerina marginata*.

Main features of fruitbody and diagnosis: fruitbodies are gilled; they often appear in clusters; pilei are mostly small, up to 3-5 cm wide; golden-yellow to orange red-brown. Stipe is without an annulus, cream to pale when young but soon becoming yellow brown to dark brown, with the surface entirely velutinous. Spore print is white. Spores are elongate-ellipsoidal, 10–13 × 4–6 μm, hyaline to very slightly yellowish.

ITS sequence based on primer pair ITS5-ITS4: GenBank accession KR704649.

No species-specific primers are known.

Notes: *Flammulina velutipes* has been reported from *Vitis* as early as 1909 (Rübsaamen, 1909; then as *Collybia velutipes*). In our observations (Fischer, unpubl.) the species was regularly, but, infrequently, seen on grapevine in several viticultural areas of Germany. In one particular plot, fruitbodies appeared regularly over a period of 7 years, with irregular frequency and spatial distribution over the years. Obtained data indicate the fungus to be more common in some areas of Central Europe (also see Kreisel, 1961). It has not been recorded in viticultural zones of southern Europe.

Fomitiporia erecta (A. David, Dequatre & Fiasson) Fiasson (Figure 3)

Basionym: *Phellinus erectus* A. David, Dequatre & Fiasson

Classification: Basidiomycota, Hymenochaetales, Hymenochaetaceae, *Fomitiporia*

Life strategy and symptoms: *Fomitiporia erecta* produces white rot in living or dead hardwood (Ryvarden and Gilbertson, 1994; Polemis *et al*., 2013), typically decaying the basal part of host plants and producing fruitbodies in stumps, semi-buried logs or superficial roots.

Host plants: the species is typically associated with hardwood host species in both tree crops and natural forests (Ryvarden and Gilbertson, 1994); it occurs on the host genera *Quercus* (*Q. ilex*, *Q. coccifera*), *Rosmarinus*, *Prunus* (*P. dulcis*), *Ulex*, *Viburnum*, *Rosa* or *Vitis*.

Geographic distribution: *Fomitiporia erecta* is only known from Mediterranean countries.

Transmission and possible vectors: airborne basidiospores, which are produced in presumed an-

Figure 3. Fruitbody of *Fomitiporia erecta* on half-buried wood debris of a grapevine plant. Bar = 2 cm. Photograph: V. González-Garcia.

nual fruitbodies mainly from spring to autumn, are likely to be the main propagules.

Fruitbodies in the field: *Fomitiporia erecta* has been observed on grapevine plants (González, personal observations) and, like in other of its usual hosts, fruitbodies can be easily overlooked. The fruit bodies mostly grow on the base of trunks and stumps, or directly on buried wood remains or superficial roots (Figure 3).

Main features of fruitbody and diagnosis: fruitbodies are annual (possibly also perennial as indicated in Ryvarden and Gilbertson, 1994), up to 2–7 cm long and wide; emerging as tuberculate masses around host tissue, then more or less pileate or rounded; upper surface velvety, with golden-brown to foxy-brown tones; pores 5–7 per mm, ferrugineous-gray to rusty-brown; spores globose, smooth, hyaline and strongly dextrinoid in Melzer's reagent; setae especially abundant at the base of tube layers, 20–45 × 5–7 µm.

ITS sequence based on primer pairs ITS5-ITS4: GenBank accession KR704651.

No species-specific primers are known.

Notes: *Fomitiporia erecta* has Mediterranean distribution and is usually associated with plant species of thermophilous forests and shrub communities (David *et al*., 1982; Fiasson and Niemelä, 1984). Due to its erratic fruiting, the macromorphological aspect in plate culture (very similar to *F. mediterranea*), and the fact that there are scarce genomic sequences of this taxon in public databases, some of the numerous Mediterranean records of *F. mediterranea* in grapevine plants may, in fact, belong to *F. erecta*. Within and outside Europe, several species of *Fomitiporia* have been reported on grapevine (Fischer 2002; Cloete *et al*. 2014). All these species share the presence of large, globose and dextrinoid spores; *F. erecta*, is distinguished, however, by its abundant hymenial setae.

Fomitiporia mediterranea M. Fischer (Figure 4)

Classification: Basidiomycota, Hymenochaetales, Hymenochaetaceae, *Fomitiporia*

Life strategy and symptoms: primary parasite on trunks; also saprobic; uniform white rot of heartwood of living and dead hardwood hosts. Extensive wood decay is usually produced along the trunks and main branches of hosts, becoming increasingly evident on adult plants, which are 8–10 years or older. In *Vitis*, the decay often starts from large pruning wounds on the trunk extending into the woody tissue. Wood decay may or may not be accompanied by leaf and fruit symptoms.

Host plants: occurring on a wide variety of plants, both native and introduced in Europe (Fischer, 2002), including the hardwood genera *Vitis*, *Acer*, *Actinidia*, *Citrus*, *Corylus*, *Lagerstroemia*, *Laurus*, *Ligustrum*, *Olea*, *Quercus*, and *Robinia*.

Geographic distribution: Central Europe, the Mediterranean region; also in the Near East and

Figure 4. Typical appearance of *Fomitiporia mediterranea* fruitbody in the uppermost part of a *Vitis vinifera* trunk. Fruitbodies are perennial; cracks indicate dry weather conditions (i.e., winter in Central Europe). Photograph: M. Fischer.

in Iran. The distribution pattern covers vegetation zones of summergreen hardwood trees, Mediterranean evergreen forests, grasslands, and dry subtropical forests. The species is equally adapted to temperate and subtropical conditions. Geographic distribution of *F. mediterranea* suggests a close affinity with *V. vinifera*, and that the fungus is well adapted to a range of climatic conditions. With viticulture spreading into western and eastern countries, *F. mediterranea* made its way into an array of environments, with different climatic and vegetational conditions. Its distribution has largely been influenced by man.

Transmission and possible vectors: airborne basidiospores (Cortesi *et al*., 2000) transported by wind, water (rain etc.). Subject to the presumed dispersal by airborne spores, each fruitbody, within or outside of vineyards, may act as a potential source of inoculum.

Fruitbodies in the field: perennial; usually rare and/or inconspicuous; formed after some time of vegetative incubation inside host plants, mostly on the uppermost parts of the trunks, near pruning wounds.

Main features of fruitbody and diagnosis: fruitbodies are resupinate with yellowish brown to pale brown pore surfaces; pores are circular, 5–8 per mm; setae are usually absent, very rarely in the hymenium of some specimens, slightly ventricose, 14–17 × 4.5–7 μm; spores are broadly ellipsoidal to subglobose, hyaline, thick-walled, smooth, dextrinoid and cyanophilous, (5.5–) 6–7 (–7.5) × (4.5–) 5–6 (–6.5) μm.

ITS sequence based on primer pair ITS5-ITS4: GenBank accession KR867636

Specific primers: F. mediterranea1 – F. mediterranea2 (Fischer, 2006).

Notes: in Europe, *F. mediterranea* is by far the main fungus associated with wood decay symptoms in esca-affected grapevines; appearance is diagnostic for late stages of the disease. Fruiting structures of some other wood-decaying basidiomycetes (mostly *Stereum* and *Trametes*) also regularly appear during later stages of the disease, but these taxa act as saprobionts and play a subordinate role only. Interactions between *F. mediterranea* (and white rot fungi in general) and external symptoms are not fully understood, although several phytotoxic compounds have been demonstrated for this species (Tabacchi *et al*., 2000; Perrin-Cherioux *et al*., 2004). In the case of esca, wood decay caused by *F. mediterranea* may or may not be accompanied by leaf and fruit symptoms. For example, external symptoms may appear on young vines, showing no distinct signs of wood decay. Grapevines may also be affected with white rot without showing external symptoms. The incidence of white rot in the wood corresponds with a much lower incidence of external symptoms (ratio 10:1 or greater). *Fomitiporia mediterranea* is restricted to *V. vinifera* in Central Europe, while in the Mediterranean area it is observed on a wider range of host plants (Fischer, 2002, 2006; Elena *et al*., 2006; González *et al*., 2007; Roccotelli *et al*., 2014). Within a short period of time the species is able to colonize new host plants. As a valuable fruit, *Actinidia* was introduced to southern Europe some 60 years ago, and in the meantime is severely affected by white rot caused by *F. mediterranea* (Elena and Paplomatas, 2002; Di Marco *et al*., 2003, 2004).

Fomitiporia punctata (P. Karst.) Murrill (Figure 5)

Basionym: *Poria punctata* P. Karst.

Synonym: *Phellinus punctatus* (P. Karst.) Pilát

Classification: Basidiomycota, Hymenochaetales, Hymenochaetaceae, *Fomitiporia*

Life strategy and symptoms: *Fomitiporia punctata* may behave as a parasite or saprobe on living and dead trunks of hardwood and conifer hosts, where it causes uniform white rots. In grapevine it shows active decay of heartwood of living plants, associated to esca symptoms.

Host plants: on dead or living wood of many hardwood tree genera, also in numerous shrubs and

Figure 5. Resupinate fruitbodies of *Fomitiporia punctata* in a grapevine plant var. "Tempranillo". Bar = 2 cm. Photograph: V. González-Garcia.

a few conifer genera like *Taxus* or *Cephalotaxus* (Ryvarden and Gilbertson, 1994).

Geographic distribution: *Fomitiporia punctata* traditionally is considered a cosmopolitan species, widespread in forest regions of Europe, Asia, North and South America, Australasia or Africa. The species concept of *F. punctata* has been thoroughly discussed recently; in a strict sense the species is probably limited to Europe (Decock *et al*., 2007; see also Fischer and Binder, 2004).

Transmission and possible vectors: airborne basidiospores, produced during various times of the year, seem to be the most probable infective entities. It is possible that pruning debris, bark or uprooted plants remaining stacked for long periods in the vicinity of vineyards could act as additional sources of inoculum.

Fruitbodies in the field: there are no confirmed records of *F. punctata* fruitbodies in vineyards (but see "Notes" below). Under Mediterranean conditions, infective basidiospores could be released from fruitbodies developed in other adapted crops next to grapevine plants, such as *Prunus* (*P. dulcis, P. avium, P. cerasifera*, and others), *Olea* or *Citrus* spp. next to grapevine plants.

Main features of fruitbody and diagnosis: morphologically, the species is indistinguishable from *F. mediterranea* (Fischer, 2002). Fruitbodies are perennial, resupinate, and of woody consistence; pores are circular, pale yellowish brown to rust brown, 6–8 per mm; hymenial setae are very scarce or absent (for instance, see David *et al*., 1982); spores are broadly ovoid to subglobose, hyaline, smooth, strongly dextrinoid in Melzer's reagent, (5.5–) 6.5–8.5 × (5.2–) 5.5–7 μm.

ITS sequence based on primer pair ITS5-ITS4: GenBank accession KR867637.

No species-specific primers are known.

Notes: *Fomitiporia punctata* (as *Phellinus punctatus*) has been traditionally associated with esca symptoms in many vine-growing areas of Europe. For some time it was identified as the main basidiomycete taxon responsible of the intense wood decay processes that characterize the final stages of esca syndrome (Mugnai *et al*., 1999). Differentiation between fruitbodies of *F. punctata* and *F. mediterranea* (Decock *et al*., 2007) is difficult due to their common diagnostic features including the appearance of resupinate basidiocarps or the macromorphological aspect of plate cultures. *Fomitiporia pseudopunctata* is another closely related species, but is separated by the occurrence of abundant hymenial setae. There is some evidence of fruitbodies of *F. punctata* existing in certain vine-growing counties of the southeast of Spain (González, unpublished); these particular vineyards are surrounded by *Citrus* x *sinensis* crops heavily affected by white rot and related basidiomycetes such as *F. punctata*. A similar situation has been observed in the Moselle area of Germany, where *F. punctata* may have invaded a particular vineyard located next to a dense stand of *Corylus avellana* (one of the main hosts under boreal conditions). However, no diagnostic sequences have been generated for all these locations.

Inonotus hispidus (Bull.) P. Karst. (Figure 6)

Basionym: *Boletus hispidus* Bull.

Classification: Basidiomycota, Hymenochaetales, Hymenochaetaceae, *Inonotus*

Life strategy and symptoms: *Inonotus hispidus* is considered to be a primary parasite in most of its hosts, capable to causing death to entire plant stands. The species colonizes sapwood and cambium and soon penetrates through living heartwood. Decay processes in *V. vinifera* usually start from large pruning wounds and extend to inner woody tissues along the entire plants. Cross sections of these infected branches exhibit soft rotted, pale-yellowish rounded areas of spongy appearance, surrounded and limited

Figure 6. Fruitbody of *Inonotus hispidus* in one of the main wounds of a *Vitis vinifera* cv. "Moscatel Romano" plant stand. Photograph: V. González-Garcia.

by brown to blackish zones. Recent records of this fungus on *Vitis* (together with *Phaeomoniella chlamydospora* or *Phaeoacremonium aleophilum*) have reported the existence of esca symptoms on the leaves of decayed plants including "tiger-stripes" (González *et al*., 2009).

Host plants: *Inonotus hispidus* occurs on a wide range of plant species, decaying mainly living hardwoods, especially genera of the angiosperms *Fraxinus*, *Malus*, *Quercus*, *Robinia*, *Salix*, *Pistacia*, *Acer*, *Ficus*, *Fagus* or *Vitis*, but also conifers such as *Abies*.

Geographic distribution: the species is found circumboreal throughout the northern hemisphere; there are also reports of occurrence in North Africa and Asia (Ryvarden and Gilbertson, 1993-94).

Transmission and possible vectors: mostly by airborne basidiospores, transported by wind or rain. As with other basidiomycetes, pruning wounds may be the sites of infection. The presence of stacked branches nearby vineyards in rainy seasons (mainly autumn) could favour dispersal of the fungus.

Fruitbodies in the field: annual, mainly in the upper sections of host trunks just below the main wounds, appearing by the end of autumn (October to November) in vine-growing areas next to the coast in the east of Spain, remaining as woody dry basidiocarps in vineyards for up to 8–10 months after sporulation. In Central Europe, fruitbodies on grapevine have been observed as early as late May (Fischer, unpubl.).

Main features of fruitbody and diagnosis: large fruitbodies, projecting up to 15 cm from the substrate, are formed on trees such as *Fraxinus* or *Malus*; on grapevine, maximal size is approx. 5–6 cm. Fruitbodies are more or less applanate; upper surfaces are bright reddish orange when young, becoming coarsely ragged and dark reddish-brown to blackish over time; pores first yellowish-brown, turning dark brown at maturity; spores subglobose to ovoid, golden-brown and thick-walled, negative in Melzer's reagent, 8–11 × 6–8 μm; setae usually absent but abundant hooked setae, 20–24 × 6–8 μm, may be present in some specimens (Ryvarden and Gilbertson, 1993-1994).

ITS sequence based on primer pairs ITS1-ITS4: GenBank accession EU918122.1.

No species-specific primers are known.

Notes: species of *Inonotus* have been reported in some vine-growing areas of the world. Isolates associated with the so-called "hoja de malvón" in viticultural zones of Chile and Argentina (Gatica *et al*., 2000; Gottlieb *et al*., 2002; Lupo *et al*., 2006) have been assigned to *Inonotus jamaicensis* (= *Inocutis jamaicensis* (Murrill) A.M. Gottlieb, J.E. Wright & Moncalvo). In Europe, although *I. hispidus* has been reported living parasitically on *V. vinifera* in Germany (Fischer and Kassemeyer, 2003), there were no esca-associated records of this fungus until the contribution of González *et al.* (2009). These authors surveyed several vineyards of Mediterranean coastal areas in Spain (Alicante province) and found *I. hispidus* responsible for severe white rot decay and leaf chlorosis. Other esca-associated anamorphic fungi were also isolated in these plants. *Inonotus hispidus* grows on a broad range of hosts, often in the surroundings of affected vineyards. In Spain the fugus has been observed in adjacent traditional cultures such as *Prunus* spp. or *Olea europaea* (González, unpublished).

Pleurotus ostreatus (Jacq.) P. Kumm. (Figure 7)

Basionym: *Agaricus ostreatus* Jacq.

Classification: Basidiomycota, Agaricales, Pleurotaceae, *Pleurotus*

Life strategy and symptoms: the species is considered as mostly saprobic, but it may also be parasitic on living trunks. The associated white rot is intense, decomposing the hardwood of affected plants. Decayed wood has a typical vanilla or anise odour. The appearance of fruitbodies of *P. ostreatus* is not accompanied by external symptoms on grapevine

Figure 7. An old fruitbody of *Pleurotus ostreatus*, showing some drying on a living vine. Season is late winter. Photograph: M. Fischer.

leaves or berries. As a unique feature, *P. ostreatus* is one of the few known nematophagous fungi; soil-borne mycelium of the fungus may kill and digest nematodes by producing toxins on specialized hyphal stalks (Nordbring-Hertz *et al*., 2006).

Host plants: on a wide variety of deciduous plants, most common on *Fagus* and *Salix*; rarely also on gymnosperms. *Pleurotus ostreatus* rarely occurs on *Vitis*; however, it may be more prominent in certain years, probably under suitable weather conditions during winter. Extended monitoring of an experimental plot of 'Pinot noir' in southwestern Germany demonstrated the appearance of fruitbodies over three consecutive years on the same trunk (Fischer, unpublished).

Geographic distribution: the distinct variability of the species and the existence of several closely related taxa makes it difficult to assess the exact geographic distribution of *P. ostreatus* (Vilgalys and Sun, 1994). In general, the species is considered nearly cosmopolitan, with regular appearance in most European countries, especially in the boreal-temperate zones. Since it requires cool temperatures for initiation of fruiting (see below), it has been rarely recorded in viticulture areas of Southern Europe (González, unpubl.). No extra-European records exist of the fungus on grapevine.

Transmission and possible vectors: basidiospores are formed in large quantities during periods of sporulation and are spread by wind, water (rain etc.). Usually strains showing reduced sporulation are used for cultivation and culinary purposes to avoid allergies.

Fruitbodies in the field: annual and appearing under cool weather conditions only, i.e. winter and spring (winter mushroom). A period of cold weather is necessary prior to fruitbody formation (Bresinsky *et al*., 1987). In vineyards, fruitbodies occur both on living and dead vines. They may be formed on different parts of the trunks of vines, with some preference to the stem heads (Figure 7). However, occurrence on the trunks has also been observed.

Main features of fruitbody and diagnosis: fruitbodies developing isolated or in clusters of imbricate caps; spanning 5–15 cm; variable in colour: from cream to dark-brown or bluish; gills are decurrent; the stipe may be absent or present and then usually with a lateral attachment to the substrate. An anise or vanilla-like odour is often noted in affected wood, evident also in cultured mycelium. Spores are cylindrical, hyaline, smooth, 9–12 × 3–5 μm.

ITS sequence based on primer pair ITS5-ITS4: GenBank accession KR867641.

No species-specific primers known.

Notes: together with *Auricularia auricula-judae* and *Flammulina velutipes*, *P. ostreatus* represents one of the so-called "winter mushrooms" on grapevine. In this way the species is readily identified by its main appearance between October and March. *Pleurotus pulmonarius* (Fr.) Quél. is closely related and also has been reported from grapevine in Germany (Fischer and Kassemeyer, 2003). It differs from *P. ostreatus* by whitish fruitbodies developed during late summer and autumn; it causes distinct white rots in dead and living wood. Due to the infrequent occurrence on grapevine, *Pleurotus* species are not considered important pathogens on *Vitis*. No correlation exists between occurrence of this fungus and the complex of grapevine trunk diseases. The scattered findings of *Pleurotus* fruitbodies all originate from vines greater than 15 years old.

Schizophyllum commune Fr. (Figure 8)

Classification: Basidiomycota, Agaricales, Schizophyllaceae, *Schizophyllum*

Life strategy and symptoms: *Schizophyllum commune* is considered a saprobe on dead wood or occasionally as a parasite on living wood, decaying hardwood sticks and logs, and planks and boards of processed hardwood. Fruitbodies can be found during the whole year, surviving by shrivelling and being able to rehydrate and produce new spores

Figure 8. Multipileate basidiocarps of *Schizophyllum commune* growing on grapevine bark. Photograph: V. González-Garcia.

with moisture many times in a year. This fungus can cause serious damage especially in ornamental trees in parks and gardens.

Host plants and geographic distribution: *Schizophyllum commune* has been reported from all continents and from a wide range of hosts (more than 350 plant species), including hardwood trees and conifers (Farr and Rossman, 2006), also affecting grapevine (Zervakis *et al*., 1998).

Transmission and possible vectors: mostly by airborne basidiospores produced repeatedly from the same fruitbodies. *Schizophyllum commune* exhibits characteristic split gills that can open or close depending on the degree of hydration. This ecological strategy is adapted to climates with non-regular, sporadic rainy episodes, just as in the case in Mediterranean viticulture.

Fruitbodies in the field: on grapevine, *S. commune* is usually reported as growing saprobically on dead bark, more rarely on living wood. Groups of dried fruitbodies are commonly seen on the bark of grapevine plants that can be rehydrated and then are ready to release new basidiospores several times in a year.

Main features of fruitbody and diagnosis: fruitbodies are small (1–4 cm wide), fan-shaped to shell-shaped, usually with several imbricate caps attached to the substrate, whitish to grayish; upper surface is densely covered with hairs; stipe absent or rudimentary; gills are split in the middle, white to pinkish-gray; spores are cylindrical to ellipsoidal, smooth and white in mass, 5–5.7 × 1.5–2.5 μm. *Schizophyllum commune* can be easily identified by its characteristic shell-shaped, imbricate pilei with split gills.

ITS sequence based on primer pairs ITS1-ITS4: GenBank accession KR867639.

No species-specific primers are known.

Notes: *Schizophyllum commune* is a ubiquitous fungus that includes grapevine as one of its many hosts. It is observed and isolated from *V. vinifera* plants in many vine-growing areas of Europe, producing several waves of sporulation after wet weather periods. Despite producing vast amounts of spores, *S. commune* is considered to be an opportunistic fungus, appearing saprobically or as a weak pathogen only in advanced stages of GTD events. In addition, *S. commune* is one of the main experimental models for studying genetics of sexuality in fungi (Raper and Miles, 1958).

Stereum hirsutum (Willd.) Pers. (Figure 9)

Basionym: *Thelephora hirsuta* Willd.

Classification: Basidiomycota, Russulales, Stereaceae, *Stereum*

Life strategy and symptoms: this fungus is considered either a saprobe or more rarely a parasite, causing white rot in the heartwood of living and dead woody tissues of its hosts. In grapevine, *S. hirsutum* may act as a weak facultative parasite, affecting the external layers of the wood, and fruiting profusely. Only occasionally the species penetrates the heartwood of host plants, in this way producing very limited infections and decay of the inner tissues.

Host plants: *Stereum hirsutum* grows on bark and wood of trunks, twigs, or stumps of a wide range of dead or living deciduous trees, and, to a lesser extent, conifers (Eriksson *et al*., 1984).

Geographic distribution: Considered by many authors as a species complex, *S. hirsutum* exhibits a worldwide distribution, where its different variants have been cited from North America, Europe, Australasia or Africa. European forms associated with *V. vinifera* cultivars from old world viticulture regions have probably been introduced to viticulture areas of other continents.

Transmission and possible vectors: airborne basidiospores produced throughout the year are likely to be the main dispersal mechanism for *S. hirsutum*.

Fruitbodies in the field: annual, but persistent even in dry weather; usually appearing in groups

Figure 9. Fruitbodies of *Stereum hirsutum* on grapevine bark showing upper and hymenial surfaces; note appearance in groups and on uppermost part of trunk. Photograph: V. González-Garcia.

(Figure 9) they may be found both on dead and living vines, usually colonizing dead wood next to pruning wounds.

Main features of fruitbody and diagnosis: fruitbodies are thin, pileate to effused-reflexed, projecting 1–3 cm from the substrate; surface is reddish-brown to dark chestnut-brown, often zonate concentrically, with brownish or grayish matted hairs; flesh is thin and tenacious; hymenial surface is smooth to slightly cracked when dry; colour is from light yellow to dull orange-buff or even pinkish-buff, turning dark brown to chestnut-brown in older specimens; spores are smooth, ellipsoid to cylindrical, hyaline and amyloid, 5–8 × 2–3.5 μm.

ITS sequence based on primer pair ITS5-ITS4: GenBank accession KR704650.

No species-specific primers are known.

Notes: *Stereum hirsutum* is usually recognized by its white to woolly gray and hirsute pileus surface and the yellow to orange hymenium. It is commonly mentioned as a less important pathogen among the esca-associated fungi (Mugnai et al., 1999; Armengol et al., 2001), in spite of the fact that basidiocarps are frequently produced in great numbers on esca-diseased plants. The species has been recorded as the second most predominant (after *F. mediterranea*) isolated in several epidemiology studies from Mediterranean viticultural areas of Spain (Sánchez-Torres *et al*., 2008), suggesting that under dry Mediterranean climatic conditions, *S. hirsutum* is highly adapted to live on and colonize grapevine plants exhibiting late esca symptoms.

Trametes hirsuta (Wulfen) Lloyd (Figure 10)

Basionym: *Boletus hirsutus* Wulfen

Synonyms: *Polystictus hirsutus* (Wulfen) Fr., *Coriolus hirsutus* (Wulfen) Pat.

Classification: Basidiomycota, Polyporales, Polyporaceae, *Trametes*

Life strategy and symptoms: mostly saprobic, sometimes a wound parasite; strong white rot, often with demarcation lines indicating multiple infection events by different genets, on wounded or dead standing hardwood trees; also common on stumps and garden timber (Schmidt, 2006). It has been repeatedly reported as one of the primary colonizers on dead beech trees (Kreisel, 1961). Fruitbodies of *T. hirsuta* on *Vitis* are mostly found on older plants, next to pruning wounds or other injuries, in the uppermost part of host trunks. Wood decay is strong,

Figure 10. Hymenial and upper surfaces of fruitbodies of *Trametes hirsuta* on a living grapevine; note pileate appearance and different developmental stages. Photograph: V. González-Garcia.

but is related to wounds. The species is not considered a primary pathogen, but readily colonizes dead trunks. In grapevine, it is usually accompanied by other white rot fungi, such as *Fomitiporia mediterranea* or *Stereum hirsutum*.

Host plants: on a wide variety of deciduous plants, very rarely also on gymnosperms (Ryvarden and Gilbertson, 1993-1994). Most common on *Fagus* and *Salix*, appearance on *Vitis* is irregular. Hosts include indigenous and introduced plants.

Geographic distribution: throughout forest regions of Europe and circumpolar in the boreal-temperate zone (Ryvarden and Gilbertson, 1993-1994). Distribution of *T. hirsuta* is not associated with *V. vinifera*; it is prevalent in cooler climates, but well adaptable to different climatic regimes.

Transmission and possible vectors: airborne basidiospores are transported by wind or water (rain). Each fruitbody, within or outside of vineyards, may act as a potential source of inoculum. Different insects have been observed on fruitbodies of *T. hirsuta*; it is not known however, if and/or to which extent they contribute to the distribution of the fungus.

Fruitbodies in the field: annual, appearing throughout the year; fruitbodies of the previous year are often still attached to host plants; on *V. vinifera* infrequent in most areas; formed after some time of vegetative growth inside grapevines, mostly next to dead wood on the uppermost part of the trunks.

Main features of fruitbody and diagnosis: fruitbodies are effused-reflexed to rarely resupinate; 3–8 cm wide, with hairy ("*hirsutus*") upper surfaces; in older specimens, algae may cause a greenish discolouration on the otherwise gray pileus surfaces; pore surface white to tan, pores more or less angular, 2-4 per mm; spores are cylindrical, hyaline, 6–9 × 2–2.5 µm; no reaction in Melzer´s reagent.

ITS sequence based on primer pair ITS5-ITS4: GenBank accession KR867640.

No species-specific primers are known.

Notes: besides *Trametes hirsuta*, the closely related *Trametes versicolor* (L.) Lloyd also occurs on grapevine. The two species may be differentiated by their pileal surfaces, which is often with multicoloured and distinct concentric zones in *T. versicolor*, while it mostly is whitish to gray in *T. hirsuta*. Although *T. hirsuta* is more common on older trunks of *V. vinifera* in some areas, it has never been considered to be related to symptoms of GTDs, and is rarely mentioned in the literature (Reisenzein *et al*., 2000; Fischer and Kassemeyer, 2003). We consider both *T. hirsuta* and *T. versicolor* as ubiquitous wood-inhabiting fungi, which most likely only play subordinate roles as primary decomposer in grapevine. Pathogenic significance is therefore probably small, and the species are rarely isolated from inner parts of grapevine wood. Nevertheless, *T. versicolor* has been isolated as an endophyte in grapevine plants in southern Europe (González, unpublished). All reports of fruitbodies are derived from older vines, both dead and living, with minimum age of approx. 15 years.

"Minor taxa"

Table 1 lists 14 taxa which are inconspicuous and/or rare on grapevine. While *Armillaria mellea* is not considered as a true trunk pathogen, it has been included based on its confirmed pathogenic significance in some areas.

Discussion

We present 24 basidiomycete species known to occur on European *V. vinifera*. Besides our own observations, we have taken into account the better-known literature. The suggested selection is not considered to be complete for the following reasons: i) only a limited timespan was available for us to check for fruitbodies in the field, so some taxa that show inconsistent fruiting will have escaped observation; ii) our knowledge about the existence of vegetative structures inside grapevine tissues of basidiomycetes that possibly never form fruiting structures is limited; and iii) Europe is large, and several grape-growing areas have not been seriously monitored for basidiomycetes.

The selection of ten species presented in more extensive descriptions is based, firstly, on the putative pathogenic significance of the particular taxa on grapevine and/or other host plants, secondly, on the spread over a large(r) geographic area, with fruitbodies regularly developed in the field and likely to gain some attention from viticulturists; and thirdly, the species have been discussed as related to GTDs in the past.

In older vineyards (15 years or more), all of the vines may be affected by white rot (for Germany, see Fischer and Kassemeyer, 2003). This is favoured by the pruning procedures applied year by year. The resulting wounds – together with any other injuries of the wood (e.g. from mechanized grape harvesting or tilling practices) – are open to airborne fungal spores. As in other woody plants (see Erkillä and Niemelä, 1986), the chance of infection increases with the lifespan of the vines. Sparse development of fruitbodies in the field and, therefore, a few propagules, may be sufficient to infect a considerable number of suitable host plants (Edman and Gustafsson, 2003). In certain fungal grapevine diseases such as eutypa dieback, it has been shown that sexual propagules (ascospores) produced in scarce perithecia contribute heavily to infection processes in the field (Muruamendiaraz *et al*., 2009).

None of the ten species described is limited to grapevine as a host. Both intra- and extra-vineyard derived spores are likely to co-act in infection processes. With fruiting structures well above the ground, spores are likely to be transported over considerable distances through turbulent air (Ingold and Hudson, 1993). In most basidiomycete groups, spore discharge is an active, "ballistosporic", process (with basidia acting as "spore-guns"). Once having reached open air, the transport of spores is heavily influenced by factors such as wind or rain. The range of distribution by airborne spores is impressive. In *Schizophyllum commune*, genetical studies have demonstrated that identical strains have reached worldwide distribution (Raper *et al*., 1958).

Three of the taxa fully presented here belong to the otherwise small ecological group of so-called "winter mushrooms". *Auricularia auricula-judae*, *Pleurotus*

Table 1. Fourteen basidiomycete species (in alphabetical order) producing white rot on trunks of grapevine (*Vitis vinifera*). With the exception of *Armillaria mellea* (root rot) all these taxa are inconspicuous and/or rare, and their pathogenic relevance is considered low.

Taxon	Life strategy	Geographic distribution	Fruitbodies	Remarks
Armillaria mellea (Vahl.) P. Kumm.	Saprobiont, parasite; wood decay ("root rot" on hardwood and conifers)	Cosmopolitan	Annual, mainly from the end of summer until mid-winter; agaricoid; typically honey-colored ("Honey mushroom").	*Armillaria mellea* is an important pathogen on a variety of wooden plants, including grapevine. Its usual spread is by means of the roots, forming characteristic black rhizomorphs (von Thümen, 1878; Kreisel, 1961; Fischer and Kassemeyer, 2003; Prodorutti *et al.*, 2009).
Clitopilus hobsonii (Berk. & Broome) Orton	Saprobiont; wood decay on hardwood; also on dead grass or moss	Cosmopolitan?	Annual, from late spring to winter; circular, more or less pleurotoid, with stipe rudimentary or absent; cream-colored.	Fruitbodies of the species might be confused with small specimens of *Pleurotus*; it has been reported from bark of grapevine (Fischer and Kassemeyer, 2003).
Ganoderma applanatum (Pers.) Pat.	Saprobiont, parasite; white rot on hardwood (rarely conifers)	Cosmopolitan	Perennial; large fruitbodies, sessile, solitary to imbricate; sporulating throughout the year (however, see remarks).	*Ganoderma applanatum* so far has only been demonstrated as vegetative mycelium in old trunks of grapevine; no fruitbodies have ever been found (Fischer, unpubl.).
Lachnella alboviolascens (Alb. & Schwein.) Fr. ***Lachnella viticola*** Gonz. Frag. ***Lachnella macrochaeta*** Speg. ***Lachnella myceliosa*** W.B. Cooke	Saprobiont, weak parasite; wood decay on hardwood, also on rotten canes (Saccardo, 1874-1879; von Thümen, 1878).	Cosmopolitan	Annual, throughout the year; small and disc-shaped, often aggregated.	Although known for a long time, species of *Lachnella* are commonly overlooked in the vineyards due to their inconspicuous appearance (von Thümen, 1878; Unamuno, 1941; Batista and Ciferri, 1962; Farr, 1973; Boidin and Lanquetin, 1987). For the occurrence on wild grapevine see Schweinitz (1832).
Merismodes bresadolae (Grélet) Singer	Saprobiont, parasite; white rot on hardwood	Cosmopolitan	Annual, throughout the year; cyphelloid, pseudostipitate to pezizoid and densely aggregated; grayish to pale reddish.	*Merismodes bresadolae* is usually seen growing on both living and dead shoots, or on the bark of the grapevine plants (Farr, 1973; as *Cyphella monacha*).
Peniophora incarnata (Pers.) P. Karst. ***Peniophora albobadia*** (Schwein.) Boidin	Saprobiont; white rot on hardwood	Northern hemisphere	Annual, throughout the year; corticioid, resupinate; reddish (*P. incarnata*); purplish brown to dark brown with white margin (*P. albobadia*).	Both taxa form inconspicuous fruitbodies on stemheads and old branches of grapevine (Fischer and Kassemeyer, 2003; for North American vines, see Adaskaveg and Gilbertson, 1987).

Table 1. Continued.

Taxon	Life strategy	Geographic distribution	Fruitbodies	Remarks
Perenniporia tenuis (Schwein.) Ryvarden	Saprobiont, parasite; white rot on hardwood	Northern Hemisphere	Annual, throughout the year; crust-like, effuse; cream to yellowish.	*Perenniporia tenuis* is considered as a rare, but widespread taxon in temperate forests of Europe and North America (Kotlába, 1997); it is cited as parasitizing *Vitis vinifera* wood in Greece (Zervakis et al., 1998).
Scytinostroma alutum Lanq.	Saprobiont, parasite; wood decay on hardwood, rarely conifers (*Juniperus*)	Northern hemisphere (Europe)	Annual; resupinate, effused, with hard consistence; pale yellow to isabelline tones.	The species has a broad range of host plants, especially Mediterranean trees and shrubs; it is also cited from grapevine (Boidin and Lanquetin, 1987; Tellería, 1990; Farr and Rossman, 2006).
Thelephora atra Weinm.	Saprobiont; wood decay mainly on hardwood	Northern hemisphere	Annual, throughout the year; resupinate, crust-like with several concrescent and ascending pilei; blackish.	*Thelephora atra* has been reported from grapevine in Spain (Hernández, 2004). Besides, it is growing directly in the soil, probably in relation to the presence of dead wood remainings.
Tomentella bryophila (Pers.) M.J. Larsen	Saprobiont; wood decay on hardwood and conifers	Cosmopolitan	Annual, throughout the year; resupinate; ochraceous to reddish brown.	*Tomentella bryophila* is one of the most common taxa of the genus, showing a worldwide distribution and including *Vitis vinifera* as one of its hosts in Southern Europe (Hernández, 2004).

ostreatus and *Flammulina velutipes* preferentially form fruitbodies during periods of cold or at least cool weather. For *P. ostreatus* it has been demonstrated that fruiting under laboratory conditions is promoted by cool temperatures, e.g. 11°C (Bresinsky *et al*., 1987), and this is confirmed by our observations in the field. For grape growers this means that for the above species the periods of sporulation and pruning coincide, providing ample opportunity for the spores to colonize fresh wounds. Nevertheless, the respective fruitbodies seem to be less common (in most areas at least; see Saccardo´s observations in the Veneto region) when compared with *F. mediterranea*, *Schizophyllum commune* or species of *Trametes* and *Stereum*. This can be attributed to the longer-lasting fruitbodies of the latter species, which sporulate over extended periods. *Fomitiporia mediterranea* has a sporulation period of between approx. 190 and 250 d under Central European conditions; the amount of spore discharge was found to be correlated with daily average temperatures and, to a lesser degree, precipitation (Fischer, 2009).

Among the most common species in our survey are *Stereum hirsutum* and *Trametes hirsuta*, which are ubiquitous in the field. In view of the wide variety of host plants (for an overview see Ryvarden and Gilbertson, 1993-94), it is not surprising that they are readily detected in almost all older vineyards. A relation of these species to esca has repeatedly been discussed (Viala, 1926; Larignon and Dubos, 1997; Reisenzein *et al*., 2000; also see Mugnai *et al*., 1999). This connection is supported by the fact that toxic compounds, for instance sterehirsutinal, have been isolated from strains of *S. hirsutum* (Tabacchi *et al*., 2000). In our observations, however, *Trametes* and *Stereum* do not act as primary pathogens in grapevine, but are only involved in the decomposition of already dead wood (see also Jahn, 1963; Rayner and Boddy, 1988).

Since established as a distinct species (Fischer, 2002), *F. mediterranea* has been widely discussed as playing an essential role within the esca syndrome. Inner parts of old vines may be heavily infested by white rot, with *F. mediterranea* acting as the main causal agent in Europe and elsewhere. The frequency of fruitbody formation is comparatively well documented for *F. mediterranea*: in a 2 year survey of several vineyards in Tuscany between 0 and approx. 3% of sampled vines had fruitbodies (Cortesi *et al*., 2000); in an experimental plot of approx. 1,600 vines in southwestern Germany, 55 (3.4%) of the vines had developed fruitbodies, while 100% of 366 uprooted vines were infested with the fungus (Fischer, 2012). Besides reports from numerous tree species (Fischer, 2002, 2006; di Marco *et al*., 2003; Elena *et al*., 2006; Pilotti *et al*., 2009), *F. mediterranea*, at least in its vegetative state, is very common in European vineyards. There is some evidence, however, that under certain conditions favouring species with similar ecological niches, it might be partly or fully replaced by other more aggressive taxa such as *I. hispidus* (González *et al*., 2009) or *F. punctata* (this paper; Wiwiorra & Fischer, unpublished data). While white rot forms an essential part in defining esca, any basidiomycete species may fit this role: usually it is *F. mediterranea* in Europe and the Near East. In other continents, however, other, closely related, taxa take over (Fischer *et al*., 2005; Fischer, 2006; Cloete *et al*., 2014).

The existence of fungal organisms is very often restricted to the vegetative state, and fruitbodies are not at all or only rarely formed in the field (Rayner and Todd, 1979). There are new findings of the existence of other taxa decaying grapevine wood, different from the well-known *Fomitiporia* species and not previously described. These are being detected in viticultural areas of the continent including Spain (González, unpubl.), where severe wood decay processes related with GTD symptoms could be attributable to a novel *Phellinus* species whose fruitbodies have not yet been found.

Can basidiomycetes such as *F. mediterranea* be considered as primary pathogens on grapevine? From artificial inoculation studies Sparapano *et al*. (2000) concluded that *F. mediterranea* (then: *F. punctata*) behaved as a primary pathogen after observing white rot symptoms within 2 years. Field trials based on a range of Hymenochaetales species led to a similar assessment for South African conditions (Cloete *et al*., submitted). Pathogenicity tests conducted with *F. mediterranea* (and related taxa) have used mycelial plugs as inoculum, so do not represent natural conditions where basidiospores are the infection units. Therefore, conclusions drawn from such studies should be interpreted with caution. Under field conditions, white rot phenomena have not been observed in grapevines less than approx. 5 years old.

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