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REVIEW

O. Comandini · M. Contu · A. C. Rinaldi

An overview of *Cistus* ectomycorrhizal fungi

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Abstract The genus *Cistus* comprises a group of about 20 shrub species found in wide areas throughout the whole Mediterranean region to the Caucasus. Being one of the main constituents of the Mediterranean-type maquis, this plant genus is peculiar in that it has developed a range of specific adaptations to resist summer drought and frequent disturbance events, such as fire and grazing. In addition, it can form both ectomycorrhizas and arbuscular mycorrhizas. In this paper, we review the information available on the ectomycorrhizal fungi of *Cistus* across its entire geographic range, as gathered and critically sifted from both published literature sources and personal observations. Although the resulting data matrix was based primarily on accounts of sporocarp inventories in the field, existing knowledge on the features of *Cistus* natural and synthesized ectomycorrhizas was also included and discussed. In total, more than 200 fungal species belonging to 40 genera have been reported so far to be associated with *Cistus*. An analysis of the pattern of ectomycorrhizal diversity and host specificity revealed that members of the *Cortinariaceae* and *Russulaceae* make the most of both *Cistus*-aspecific and *Cistus*-specific mycobionts. Further studies are needed to expand our preliminary knowledge of the mycorrhizal ecology and biology of *Cistus* and its fungal associates, focusing on topics such as mycobiont diversity, host specificity, fungal succession, mycorrhizal influence on stress tolerance, and impact of disturbances, while comparing the findings with those from other ecosystems.

O. Comandini (✉)
Dipartimento di Scienze e Tecnologie Biomediche,
Sezione di Chimica Biologica e Biotecnologie Biochimiche,
Università di Cagliari,
I-09042 Monserrato (CA), Italy
e-mail: ornella_comandini@yahoo.it
Tel.: +39-070-6754521
Fax: +39-070-6754527

M. Contu · A. C. Rinaldi
via Traversa via Roma snc,
I-07026 Olbia (SS), Italy

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Introduction

Although Europe and adjacent areas are relatively well known from the mycological point of view, some ecosystems have received comparatively little attention, especially concerning the role played by mycorrhizal symbiosis. In particular, given the ecological importance of host specificity for plant ectotrophic communities and the associated mycota, studies describing the specificity patterns occurring in selected ecosystems are of premium significance, as they can contribute to a better definition of the environmental biotic and abiotic factors that affect specificity phenomena, and how the specialization of ectomycorrhizal fungi and plant hosts originated and evolved (Molina et al. 1992; Erland and Taylor 2002; Van der Heijden and Sanders 2002). A significant example of these "neglected mycorrhizal niches" is the *Cistus*-dominated maquis. *Cistus* harbors a group of about 20 woody, evergreen or semi-deciduous shrub species found in wide semi-arid areas from Madeira and the Canary Islands throughout the whole Mediterranean region to the Caucasus (Arrington and Kubitzki 2003). Some species, such as *C. carthaginensis* in Spain (Boscaiu and Guemes 2001), have a very limited or even punctiform range and are severely threatened of extinction. *Cistus* species have evolved specific adaptations to resist severe summer drought stress and to regenerate rapidly after fire, a key ecological factor influencing the evolution and dynamics of the Mediterranean vegetation. Thanks to their ability as early colonizers after disturbance, *Cistus* species often form pure stands in vast areas heavily subjected to fire and/or grazing (for an extensive bibliography on various aspects of *Cistus* ecology and biology, see (http://www.cistuspage.org.uk).

Cistus may form both ectomycorrhizas and vesicular arbuscular mycorrhizas, the other widespread type of mycorrhizal association (Smith and Read 1997). Although

most plant species form only one type of association, the dual mycorrhizal status is not unique of *Cistus*, but is also present in *Populus*, *Salix*, *Alnus*, and *Eucalyptus* (Smith and Read 1997), and also in some tropical tree genera such as the myrtaceous *Ixora*, *Syzygium*, and *Tristania* (Reddell et al. 1996; Moyerson et al. 2001). In these hosts, ectomycorrhizas and arbuscular mycorrhizas can either co-occur at a comparable level in the root system or one type can be predominant, but it is not yet clear which factors favour dominance by each functional association. In the case of *Cistus* and *Eucalyptus*, both genera inhabiting fire-susceptible ecosystems, it has been suggested that mycorrhizal plasticity may represent an important adaptive trait to the cyclical pattern of accumulation and loss of organic resources due to fire (Smith and Read 1997). At variance with the cistaceous host genus *Helianthemum* (Yu et al. 2001), no reports of ectendomycorrhizas formation by *Cistus* species are known to date.

To expand current knowledge of mycorrhizal biology of *Cistus*, a new research program at our institution is focusing on the isolation and full characterization of the ectomycorrhizas formed by the fungal symbionts exclusively or prevalently associated with *Cistus* spp. (Nuytinck et al. 2004; Rinaldi and Comandini, unpublished observations). While screening published data on *Cistus* mycorrhizas to select suitable candidates for ectomycorrhizal characterization, we were struck by the fact that information on *Cistus*-associated mycota is generally widely dispersed in the mycological literature, and no recent comprehensive accounts exist on the topic. In the present review paper, we attempt to fill this gap by providing an updated checklist of fungal species reported to establish ectomycorrhizas on *Cistus* spp. on the basis of field observations. The cases where the association has been confirmed experimentally, either through direct observation of naturally occurring or synthesized mycorrhizas, and by molecular approaches, have been highlighted. We also attempt to discuss the ecological significance of *Cistus* mycorrhizas in relation to what is known on the role played by ectomycorrhizal diversity in other better-studied ecosystems. Finally, we indicate those we believe are the main research needs to fully disclose *Cistus* mycorrhizal ecology.

Collecting the data

Data on the association between *Cistus* spp. and ectomycorrhiza-forming fungi presented in this paper are overwhelmingly based on reports of field observations of sporocarp associations with potential hosts. The data set contains both information collated from a variety of published sources, including taxonomic monographs of specific groups of ectomycorrhizal fungal genera and the few previous surveys of fungi associated with *Cistus*, and personal collections and observations. Fungal taxa belonging to genera for which the mycorrhizal status is currently uncertain were not listed. Only records clearly mentioning (potential) *Cistus* hosts were included in the data matrix. When more than one host genus was mentioned in the original reference, for example "under *Quercus* and *Cistus*", or "in *Quercus* stands with *Cistus* understory", the relevant fungal species was generally not considered as a *Cistus* symbiont, unless this particular association was confirmed by other sources. When more than one *Cistus* species was present, the relevant mycobiont(s) was assigned to all potential hosts. Evidence from studies on the morpho-anatomical and molecular characterization of ectomycorrhizas formed by taxonomically diverse fungal species on *Cistus* spp. were also inserted in the data set, as they support hypotheses from field observations. In addition to studies concerning naturally-occurring, field-collected mycorrhizas, data coming from synthesized mycorrhizas were also considered.

Despite all efforts to cover as large a number of bibliographic sources as possible, our literature survey was clearly partial and incomplete, and a number of valuable records may have been missed. However, we are confident that the assembled data matrix includes the majority of the ecologically relevant information available on *Cistus*-associated fungal species, especially when *Cistus*-specific mycobionts are concerned. As the vast majority of the data set consists of field observations of sporocarps rather than associations confirmed by direct inspection of ectomycorrhizas, the limitations inherent to data sources must be emphasized. Indeed, the reports of putative mycorrhizal relationships based solely on sporocarp associations are obviously subject to an unquantifiable degree of error. Trappe (1962) has explained the criteria that should lead to the exclusion or inclusion of literature reports when compiling lists of mycorrhizal associations based on sporocarp observations. In compiling the data set for this study, we strictly observed these guidelines and, also on the basis of our personal experience, discarded or labeled all spurious and/or dubious records. As regards synthesized ectomycorrhizas, it should be stressed that associations induced in laboratory experiments may not occur under field conditions (Harley and Smith 1983; Molina et al. 1992). Finally, the identification of some fungi in the references we have considered may not be correct.

Diversity and host specificity of *Cistus* ectomycorrhizal fungi

Current knowledge about *Cistus* ectomycorrhizal fungal diversity is based mostly on above-ground observations of fungal fruitbodies (Table 1). About 230 fungal species belonging to 40 genera are listed, belonging to both Ascomycota and Basidiomycota, a number of *Cistus* associates considerably larger than previous accounts (Malloch and Thorn 1985; Lavorato 1991; Ballero et al. 1992; Vila and Llimona 1999, 2002). Early studies reviewing ectomycorrhizal fungi and relevant plant hosts overlooked *Cistus* and its mycoflora (e.g., Trappe 1962), partly due to a focus on forests rather than shrublands. On the plant side, nine different *Cistus* species [*albidus*, *clusii*,

crispus, *incanus*, *ladanifer* (often mentioned under the synonym *ladaniferus*), *laurifolius*, *monspeliensis*, *populifolius*, *salvifolius*] are explicitly reported in the literature to form specific associations. Most fungal records are referred to common host species occurring over large geographic areas (*C. incanus*, *C. monspeliensis*, *C. salvifolius*), and few records are available for rare or uncommon species such as *C. clusii*, *C. crispus*, and *C. populifolius*.

In most cases, the potential host species was not indicated in the original reference, probably due to the rather homogeneous morphology of the species within the genus *Cistus*, with subsequent identification problems for non-specialists, and to the common occurrence of several *Cistus* species growing tightly together in a stand, which made it difficult, if not impossible, to specify the plant partner in a number of instances. Geographically, the largest number of records were originally collected in Spain, followed by peninsular and insular Italy and southern France, and a few in Morocco. Virtually no information is available for other extended regions in North Africa (e.g., Tunisia and Algeria) and for the eastern side of the *Cistus* range, i.e., the Balkans, the Aegean Archipelago, the coasts of Anatolia, the Caucasus, Syria, Lebanon. In Israel, studies on the mycorrhizal status of naturally occurring *C. incanus* and *C. villosus* have been conducted (Litav 1965; Berliner et al. 1986), although the involved fungal taxa were not identified.

In general, all the larger and ecologically key ectomycorrhizal fungal genera harbor a significant number of species that are associated with *Cistus*. *Cortinarius* (29 species) and *Russula* (28) are the best represented in the list, followed by *Inocybe* (23), *Amanita* (22), *Hygrophorus* (13), *Lactarius* (12, excluding the probable spurious report of *L. deliciosus*, see below), *Hebeloma* (12), *Boletus* (10), *Tuber* (10, excluding *T. californicum*), *Tricholoma* (10). At the family level, *Cortinariaceae* (for a comment on the concept of families in the Agaricales, see notes in Table 1) and *Russulaceae*, clearly form the prevalent groups. The association of *Cistus* with numerous hypogeous ascomycetes (Table 1) seems to be a common feature of the Cistaceae as a whole, as other genera, such as *Helianthemum*, also show similar mycorrhizal preferences (e.g., Malloch and Thorn 1985).

"Broad host range" fungi, which can form mycorrhizas with host plants from diverse plant families, orders, and even classes (Molina et al. 1992), occur frequently in the list, and include *Amanita vaginata*, *Hebeloma crustuliniforme*, *Paxillus involutus*, *Telephora terrestris*, and *Tricholoma sulphureum*. Many other listed fungal species are more frequently associated with *Quercus* spp., and their association with *Cistus*, when reliably identified, is probably sporadic and/or occasional. These include, for example, several of the *Lactarius* species reported here, such as *L. atlanticus*, *L. chrysorrheus*, *L. ilicis*, *L. mairei*, and *L. zonarius* (Basso 1999). However, these records are important because they provide valuable information concerning the mycorrhizal ecology of selected fungal species, revealing their tendency to switch hosts when these share the same environment—a feature that has certainly played a major role in the evolution of host specificity among ectomycorrhizal fungi—and broaden our perspective of *Cistus*-compatible fungi.

The analysis of the assemblage of the fungal taxa more closely linked to *Cistus* also reveals an interesting pattern. Two different groups of mycorrhizal fungi can be discerned here. The first comprises "narrow host range" fungi, i.e., fungal species forming mycorrhizas only in association with a single plant genus (Molina et al. 1992), *Cistus* in this case. About 35 *Cistus*-specific fungi are identifiable to date, all of them being epigeous basidiomycetes. These include *Leccinum corsicum*, *Amanita cistetorum*, *Hebeloma album*, *H. cavipes*, *H. cistophilum*, *H. erumpens*, *Inocybe cistobulbipes*, *I. rocabrunae*, *Hygrophorus pseudodiscoideus* var. *cistophilus*, *Lactarius cistophilus*, *L. cyanopus*, *L. tesquorum*, *Russula cistoadelpha*, *R. monspeliensis*, *R. tyrrhenica*, and a number of *Cortinarius* species. Again, a few genera within the Cortinariaceae and, on a minor scale, Russulaceae, seem to comprise almost all the fungal species highly specialized to *Cistus*. A second group has those fungal species which although not associated exclusively with *Cistus*, commonly establish functional symbiosis with this host, and are often a component of the macromycetous fungal flora in *Cistus*-dominated plant communities. *Tuber melanosporum*, *Amanita muscaria*, *Hebeloma hiemale*, *Laccaria laccata* fo. *pseudobicolor*, and *L. proxima* belong to this group.

Among the macromycetes putatively linked to *Cistus* spp., it is apparent that some of the claimed associations are very unlikely. This is the case, for example, of the related *Suillus collinitus* and *Rhizopogon* spp., both genera being currently accepted as specific to conifers (almost exclusively Pinaceae) (Kretzer et al. 1996; Molina et al. 1999). Also *Amphinema byssoides* has been reported as being restricted to coniferous tree species (Erland and Taylor 1999). Another clear example of a most likely spurious report is that of the common *Pinus*-associated *Lactarius deliciosus* from Greece (Zervakis et al. 1998) and Spain (Ortega and Esteve-Raventós 1999). It is, thus, possible that some fungi in the list are in reality not compatible with *Cistus*, but rather with other hosts present in the same community, most frequently *Quercus* spp. (see above) and *Pinus* spp. The absence of *Cenococcum* in Table 1 is also noticeable, as this symbiont is almost ubiquitous on the roots of most ectomycorrhizal hosts in a range of ecological situations (LoBuglio 1999). Given the little attention devoted so far to the observation of *Cistus* ectomycorrhizal morphotypes (see below), however, it cannot be excluded that *Cenococcum* forms mycorrhizas with *Cistus*.

In spite of the fairly large number of ectomycorrhizal macromycetes linked to *Cistus* spp. in Mediterranean-type ecosystems, information on the features of relevant mycorrhizas is remarkably limited. To date, only very few accounts of *Cistus* ectomycorrhizal types exist in the literature. Most studies focused on the ectomycorrhizas formed by hypogeous ascomycetes, such as *Tuber* and *Terfezia* with *Cistus* spp., both under natural and cultured conditions. These investigations resulted in the full

Table 1 Ectomycorrhizal fungi reported or confirmed to be associated with *Cistus* spp.[§]

Species	Host	Reference
Ascomycota		
Elaphomyces trappei Galán and Moreno	*C. ladanifer* L.	Maia et al. 1996; Moreno-Arroyo et al. 2000
Balsamia vulgaris Vitt.	*C. albidus* L.	Maia et al. 1996; Moreno-Arroyo et al. 2000
Picoa juniperi Vitt.	*C. albidus*	Moreno-Arroyo et al. 2000
Delastria rosea Tul. and C. Tul.	*C. albidus*/*C. ladanifer*/*C. salvifolius* L.	Moreno-Arroyo et al. 2000; Anonymous 2001
Terfezia arenaria (Moris) Trappe (=*T. leonis* Tul.)	*C. ladanifer*/*C. monspeliensis* L./*C. salvifolius*	Maia et al. 1996
Terfezia claveryi Chat.	*C. salvifolius*	Trappe 1969
Terfezia leptoderma Tul. and C. Tul. (=*T. olbiensis* (Tul. and C. Tul.) Tul. and C. Tul.)	*C. albidus*/*C. ladanifer*/*C. populifolius* L./*C. salvifolius*/*Cistus* sp.	Leduc et al. 1986 (ECM); Calonge et al. 1994; Moreno-Arroyo et al. 2000; Díez et al. 2002
Terfezia sp.	*Cistus* sp.	Maia et al. 1996
Tirmania spp.	*Cistus* sp.	Maia et al. 1996
Genea verrucosa Vitt.	*C. albidus* (?)	Maia et al. 1996
Genabea cerebriformis (Harkn.) Trappe	*C. albidus*	Moreno-Arroyo et al. 2000
Hydnocystis clausa (Tul.) Ceruti	*C. ladanifer*	Moreno-Arroyo et al. 2000
Hydnocystis sp.	*Cistus* sp.	Maia et al. 1996
Choiromyces gangliformis Vitt.	*C. ladanifer*	Moreno-Arroyo et al. 2000
Choiromyces magnusii (Mattir.) Paol.	*C. ladanifer*	Maia et al. 1996; Calonge and Vidal 2000
Choiromyces venosus (Fr.) Th. Fr. (=*C. meandriformis* Vitt.)	*C. ladanifer*	Maia et al. 1996
Tuber aestivum Vitt.	*C. incanus* L./*C. salvifolius*	Chevalier et al. 1975 (ECM); Giovannetti and Fontana 1982 (ECM)
Tuber asa Tul. and C. Tul.	*C. albidus*/*C. ladanifer*/*C. salvifolius*	Maia et al. 1996; Moreno-Arroyo et al. 2000
Tuber borchii Vitt. (=*T. albidum* Pico ex Ceruti)	*C. incanus*	Giovannetti and Fontana 1982 (ECM)
Tuber brumale Vitt.	*C. incanus*/*C. salvifolius*	Chevalier et al. 1975 (ECM); Giovannetti and Fontana 1982 (ECM)
Tuber californicum Harkn.	*C. incanus* (?)	Maia et al. 1996
Tuber macrosporum Vitt.	*C. incanus*	Giovannetti and Fontana 1982 (ECM)
**Tuber melanosporum* Vitt.	*C. incanus*	Fontana and Giovannetti 1979 (ECM); Fusconi 1983 (ECM); Giovannetti et al. 1994; Wenkart et al. 2001 (ECM); Roth-Bejerano et al. 2003 (ECM)
	C. albidus	Giovannetti et al. 1994
	C. albidus/*C. crispus* L./*C. laurifolius* L./*C. monspeliensis*	Giovannetti and Fontana 1982 (ECM)
	C. salvifolius	Chevalier et al. 1975 (ECM); Giovannetti and Fontana 1982 (ECM)
Tuber mesentericum Vitt.	*C. incanus*	Giovannetti and Fontana 1982 (ECM)
Tuber oligospermum Tul. and C. Tul. (Trappe)	*C. ladanifer*	Moreno-Arroyo et al. 2000
Tuber puberulum Berk. and Br.	*Cistus* sp.	Calonge et al. 1996
Tuber rufum Pico (=*T. ferrugineum* Vitt.)	*C. incanus*	Giovannetti and Fontana 1982 (ECM)
Basidiomycota		
Amanita argentea Huijsm	*Cistus* sp.	Lavorato 1991
Amanita aspera (Fr.) Hooker (=*A. franchetii* (Boud.) Fayod,=*A. queletii* Bon and Dennis)	*Cistus* sp.	Lavorato 1991
**Amanita cistetorum* Contu and Pacioni[a]	*C. albidus*/*C. monspeliensis*/*C. salvifolius*	Contu and Pacioni 1998; Contu 1999a; Vila and Llimona 1999, 2002 (as *A. vaginata* var. *cistetorum* Vila et Llimona)
Amanita codinae (Maire) Sing.	*Cistus sp.*	Lavorato 1991
Amanita crocea (Quél.) Sing.	*Cistus sp.*	Lavorato 1991
Amanita curtipes Gilb.	*Cistus sp.*	Lavorato 1991

Table 1 (continued)

Species	Host	Reference
Amanita excelsa (Fr.: Fr.) Bertill.	*Cistus* sp.	Lavorato 1991
Amanita gilbertii Beaus. fo. *subverna* Bert. and Parr. (invalid name)	*Cistus* sp.	Lavorato 1991
Amanita gioiosa Curreli	*Cistus* sp.	Lavorato 1991
Amanita junquillea Quél.	*Cistus* sp.	Lavorato 1991
Amanita magnivolvata Aalto	*Cistus* sp.	Lavorato 1991
Amanita mairei Foley (=? *A. bertauldii* Contu)	*Cistus* spp.	Contu 1989a; Lavorato 1991
**Amanita muscaria* (L.: Fr.) Pers.	*C. albidus*/*C. monspeliensis*/ *C. salvifolius*/*Cistus* spp.	Contu 1989a; Quadraccia and Lunghini 1990; Lavorato 1991; Vila and Llimona 1998, 2002, Rinaldi unpub. observ.
Amanita oblongospora Contu ex Tulloss and Contu (=*A. malleata* ss. Piane pp.)	*Cistus* sp.	Lavorato 1991
Amanita pachyvolvata (Bon) Krieglst	*Cistus* sp.	Lavorato 1991
Amanita pantherina (D.C.: Fr.) Krombh	*C. albidus*/*C. monspeliensis*/ *Cistus* sp.	Lavorato 1991; Vila and Llimona 1998
Amanita phalloides Fr.	*Cistus* sp.	Lavorato 1991
Amanita ponderosa Malç., Romagn. and Heim	*Cistus* sp.	Lavorato 1991
Amanita rubescens Pers.	*Cistus* sp.	Lavorato 1991
Amanita solitaria (Bull.: Fr.) Meràt.	*Cistus* sp.	Lavorato 1991
Amanita vaginata (Bull.: Fr.) Lamarck	*Cistus* sp.	Lavorato 1991
Amanita valens (Gilb.) Bert.	*C. ladanifer*	Pérez de Gregorio 1996
Torrendia pulchella Bres.[b]	*C. monspeliensis*/ *C. salvifolius*	Malloch and Thorn 1985; Anonymous 2001
**Cortinarius assiduus* Mahiques, Ortega and Bidaud	*C. albidus*/*C. laurifolius*	Mahiques et al. 2001; Vila and Llimona 2002
**Cortinarius aureocistophilus* Vila and Llimona ad. Int.	*C. albidus*/*C. monspeliensis*	Vila and Llimona 2002
**Cortinarius ayanamii* Ortega, Vila, Bidaud and Llimona	*C. monspeliensis*	Ortega et al. 2000; Vila and Llimona 2002
**Cortinarius bulbosovolvatus* Henry and Contu	*C. monspeliensis*	Henry and Contu 1985
Cortinarius bulliardii (Pers.: Fr.) Fr.	*Cistus* sp.	Lavorato 1991
**Cortinarius castaneus* (Bull. ex Fr.) Fr. var. *monspeliensis* Bidaud and Fillion	*Cistus* spp.	Bidaud 1995; Contu 2000
**Cortinarius cistoadelphus* Moreno and Esteve-Raventós (=*Dermocybe cistoadelpha* Moreno, Pöder, Kirchmair, Esteve-Raventós and Heykoop)	*C. ladanifer*	Bidaud 1995; Moreno et al. 1997; Moreno and Esteve-Raventós 1997
**Cortinarius cistohelvelloides* Bon	*C. laurifolius*/*C. monspeliensis*/ *C. salvifolius*	Bon 1992; Vila and Llimona 2002
**Cortinarius cistohelvelloides* var. *phyllophlebophorus* Vila and Llimona	*C. monspeliensis*	Vila and Llimona 2002
**Cortinarius cistophilus* Henry and Contu	*C. monspeliensis*	Henry and Contu 1989
**Cortinarius coeruleopallescens* Contu (=*C. croceocoeruleus* (Pers.: Fr.) Fr. var. *meridionalis* Bidaud, Ortega and Mahiques)	*C. albidus*/*C. monspeliensis*/ *C. salvifolius*	Contu 1999b; Vila and Llimona 2002
**Cortinarius conico-obtusarum* Ortega and Chevassut	*C. monspeliensis*/ *C. salvifolius*	Ortega and Chevassut 1999
**Cortinarius contui* Henry	*C. monspeliensis*/ *C. salvifolius*	Henry and Contu 1987; Contu 1991; Vila and Llimona 2002
Cortinarius cristallinus Fr.	*C. albidus*/*C. monspeliensis*	Vila and Llimona 2002
Cortinarius dionysae Henry	*Cistus* sp.	Vila and Llimona 2002
Cortinarius glaucescens (J. Schff. ap. Mos.) Mos. var. *maritimus* (Bruchet) Bon	*Cistus* sp.	Lavorato 1991
Cortinarius fulmineus Fr. var. *sulphureus* Kauffman	*C. laurifolius*	Vila and Llimona 2002
Cortinarius illibatus Fr.	*C. ladanifer*	Malençon and Bertault 1970

Table 1 (continued)

Species	Host	Reference
**Cortinarius llimonae* Vila	*C. monspeliensis*	Vila and Llimona 2002
**Cortinarius longisporus* Beller (=*C. belleri* Moser)	*C. monspeliensis*/*C. salvifolius*	Lavorato 1991; Contu and Lavorato 1986 (as *C. belleri*)
**Cortinarius parvostriatus* Henry and Contu	*C. monspeliensis*	Henry and Contu 1985
Cortinarius pesudoprivignus Henry	*C. ladanifer*	Malençon and Bertault 1970
**Cortinarius sabulicola* Henry and Contu	*C. monspeliensis*	Henry and Contu 1987; Contu 1991
**Cortinarius scobinaceus* Malç. and Bert.	*C. crispus*/*C. ladanifer*/ *C. salvifolius*	Ortega and Mahiques 1995
	C. albidus/*C. monspeliensis*/ *C. salvifolius*	Vila and Llimona 1998; 1999
**Cortinarius subcaninus* Maire (=*C. xerophilus* Henry and Contu)	*C. albidus*/*C. monspeliensis*/ *Cistus* spp.	Henry and Contu 1986; Contu 1991; Vila and Llimona 1999; 2002
Cortinarius variiformis Malençon	*C. albidus*/*C. monspeliensis*	Vila and Llimona 2002
Cortinarius variiformis var. *crustulinicolor* Bon and Gaugué.	*Cistus* sp.	Lavorato 1991
Cortinarius venetus Fr.	*C. albidus*/*C. monspeliensis*	Vila and Llimona 1999
Cortinarius sp. 1	*C. albidus*/*C. monspeliensis*	Vila and Llimona 1999
Cortinarius sp. 2	*C. albidus*/*C. monspeliensis*/ *C. salvifolius*	Vila and Llimona 1999
Cortinarius sp. 3	*C. monspeliensis*	Vila and Llimona 1999
**Hebeloma album* Peck	*C. albidus*/*C. laurifolius*/ *C. monspeliensis*/*Cistus* spp.	Bruchet 1970; Hacskaylo and Bruchet 1972; Contu 1989b; Lavorato 1991; Vila and Llimona 1999
**Hebeloma cavipes* Huijsman	*C. salvifolius*/*Cistus* sp.	Bruchet 1970; Quadraccia and Lunghini 1990; Lavorato 1991
**Hebeloma cistophilum* Maire	*C. albidus*/*C. laurifolius*/ *C. monspeliensis*/ *C. salvifolius*/*Cistus* sp.	Bruchet 1970; Malençon and Bertault 1970; Ortega and Buendía 1986; Contu 1989b; Quadraccia and Lunghini 1990; Lavorato 1991; Heykoop and Esteve-Raventós 1997; Vila and Llimona 1999; 2002
Hebeloma crustuliniforme (Bull.: Fr.) Quélet	*Cistus* sp.	Marmeisse et al. 1999
Hebeloma cylindrosporum Romagnesi	*Cistus* sp.	Marmeisse et al. 1999
**Hebeloma erumpens* Contu (=*H. truncatum* (Schaeff.) Kumm. var. *pruinosum* Moser)[c]	*C. albidus*/*C. ladanifer*/ *C. laurifolius*/ *C. monspeliensis*/*Cistus* spp.	Contu 1989b; Ortega and Esteve-Raventós 1999 (as *H. truncatum*); Vila and Llimona 2002 (as *H. truncatum*)
**Hebeloma hiemale* Bresadola	*C. albidus*/*C. laurifolius*/ *C. monspeliensis*/ *C. salvifolius*	Bruchet 1970; Hacskaylo and Bruchet 1972; Contu 1989b; Lavorato 1991; Vila and Llimona 1999
Hebeloma pyrophilum Moreno and Moser (=*H. versipelle* (Fr.) Bull. pp.)	*Cistus* sp.	Lavorato 1991
Hebeloma sacchariolens Quél.	*C. salvifolius*/*Cistus* sp.	Rosell 1981 (ECM); Lavorato 1991
Hebeloma subcaespitosum Bon	*Cistus* sp.	Lavorato 1991
Hebeloma xerophilum Rudn.-Jez.	*C. salvifolius*	Quadraccia and Lunghini 1990
Hebeloma sp.	*C. salvifolius*	Quadraccia and Lunghini 1990
Hymenogaster lycoperdineus Vitt.[d]	*C. albidus* (?)	Moreno-Arroyo et al. 2000
Hymenogaster populetorum Tul.	*C. albidus*	Moreno-Arroyo et al. 2000
Inocybe aurantiifolia Beller (=*I. croceifolia* Beller)[e]	*C. monspeliensis*	Esteve-Raventós et al. 2002
**Inocybe cistobulbipes* Esteve-Raventós and Vila	*C. monspeliensis*	Esteve-Raventós et al. 2002
Inocybe cryptocystis Stuntz (=*I. mystica* Stangl. and Glow.)	*Cistus* sp.	Lavorato 1991
Inocybe curvipes P. Karst. (=*I. decipientoides* Peck)	*Cistus* sp.	Malençon and Bertault 1970; Lavorato 1991
Inocybe decipiens Bresad.	*Cistus* sp.	Lavorato 1991
Inocybe dulcamara (Alb. and Schw.) Kumm.	*Cistus* sp.	Lavorato 1991
Inocybe flocculosa (Berk.) Sacc.	*C. monspeliensis*	Esteve-Raventós et al. 2002

Table 1 (continued)

Species	Host	Reference
Inocybe fuscidula Vel. (=*I. virgatula* Kühn.)	*Cistus* sp.	Lavorato 1991
Inocybe geophylla (Fr.: Fr.) Kumm.	*C. albidus*/*C. ladanifer*/*C. monspeliensis*/*C. salvifolius*/*Cistus* sp.	Lavorato 1991; Jiménez Antonio 1994; Vila and Llimona 1999; Esteve-Raventós et al. 2002
Inocybe glabripes Ricken (=*I. microspora* J.E. Lange)	*C. albidus*/*C. monspeliensis*	Esteve-Raventós et al. 2002
Inocybe grammopodia Malençon	*C. monspeliensis*	Esteve-Raventós et al. 2002
Inocybe aff. *leiocephala* Stunz.	*C. salvifolius*	Quadraccia and Lunghini 1990
Inocybe mixtilis (Britzelm.) Sacc.	*C. ladanifer*/*C. monspeliensis*/*C. salvifolius*/*Cistus* sp.	Lavorato 1991; Heykoop and Esteve-Raventós 1994; Esteve-Raventós et al. 2002
Inocybe muricellata Bresad.	*C. laurifolius*	Heykoop and Esteve-Raventós 1994
Inocybe personata Kühn.	*Cistus* sp.	Lavorato 1991
Inocybe pruinosa Heim (=*I. halophila* Heim)	*C. salvifolius* (?)	Quadraccia and Lunghini 1990
Inocybe pusio P. Karst.	*C. monspeliensis*	Villarreal and Heykoop 1997
Inocybe queletii Maire and Konr.	*Cistus* sp.	Malençon and Bertault 1970; Lavorato 1991
Inocybe rimosa (Bull.: Fr.) Kumm.	*C. monspeliensis*	Esteve-Raventós et al. 2002
**Inocybe rocabrunae* Esteve-Raventós and Vila	*C. albidus*/*C. ladanifer*/*C. monspeliensis*	Esteve-Raventós et al. 2002
Inocybe suporospora Kuyp.	*C. monspeliensis*	Siquier and Lillo 1994
Inocybe tenuicystidiata Horak and Stangl.	*C. albidus*/*C. monspeliensis*/*Cistus* sp.	Lavorato 1991; Vila and Llimona 1999; Esteve-Raventós et al. 2002
Inocybe vulpinella Bruyl.	*C. incanus* (?)/*C. salvifolius* (?)	Quadraccia and Lunghini 1990
Hygrophorus acutoconicus (Clem.) Smith	*Cistus* sp.	Malençon and Bertault 1975
Hygrophorus arbustivus Fr.	*Cistus* sp.	Lavorato 1991
Hygrophorus carneogriseus Malençon	*Cistus* sp.	Malençon and Bertault 1975; Lavorato 1991
Hygrophorus chrysodon (Batsch: Fr.) Fr.	*C. albidus*/*C. ladanifer*/*C. monspeliensis*/*Cistus* sp.	Lavorato 1991; Bañares Baudet and Beltrán Tejera 1993; Jiménez Antonio 1994; Vila and Llimona 1999
Hygrophorus cossus (Sow.) Fr.	*Cistus* sp.	Lavorato 1991
Hygrophorus eburneus (Bull.: Fr.) Fr.	*Cistus* sp.	Lavorato 1991
Hygrophorus nitratus (Pers.) Fr.	*Cistus* sp.	Malençon and Bertault 1975
Hygrophorus niveus (Scop.) Fr.	*Cistus* sp.	Malençon and Bertault 1975
Hygrophorus obrusseus (Fr.) Fr.	*Cistus* sp.	Malençon and Bertault 1975
Hygrophorus penarius Fr. var. *barbatulus* (Becker) Bon	*Cistus* sp.	Lavorato 1991
Hygrophorus persoonii Arnolds var. *fuscovinosus* Bon	*Cistus* sp.	Lavorato 1991
Hygrophorus pseudodiscoideus (Maire) Malç. and Bert.	*Cistus* spp.	Malençon and Bertault 1975; Contu 1989c; Lavorato 1991
**Hygrophorus pseudodiscoideus* var. *cistophilus* Bon and Riousset (=*H. pseudodiscoideus* fo. *subpersicolor* Contu)	*C. albidus*/*C. monspeliensis*/*Cistus* spp.	Lavorato 1991; Candusso 1997; Vila and Llimona 1998; 1999
Hygrophorus roseophyllus Cetto (invalid name)	*Cistus* sp. (?)	Lavorato 1991
Laccaria affinis (Singer) Bon[f]	*C. monspeliensis*	Vila and Llimona 1999
Laccaria bicolor (Maire) Orton	*Cistus* sp.	Malençon and Bertault 1975; Lavorato 1991
Laccaria laccata (Scop.: Fr.) Cooke	*C. albidus*/*C. ladanifer*/*C. monspeliensis*/*Cistus* sp.	Lavorato 1991; Bañares Baudet and Beltrán Tejera 1993; Torres et al. 1995 (ECM); Vila and Llimona 1999
**Laccaria laccata* fo. *pseudobicolor* Bon	*Cistus* spp.	Lavorato 1991; Contu 1996
Laccaria macrocystidiata (Migl. and Lav.) Pàzmàny (=*L. affinis* var. *sardoa* Bon and Contu)	*Cistus* sp.	Lavorato 1991 (as *L. affinis* (Sing.) Bon fo. *macrocystidiata*)
**Laccaria proxima* (Boudier) Pat.	*C. ladanifer*/*Cistus* sp.	Lavorato 1991; Contu 1996; Villarreal and Heykoop 1997
Laccaria purpureobadia Reid	*C. ladanifer*	Romero de la Osa 2002
Laccaria tetraspora Singer	*Cistus* sp.	Lavorato 1991

Table 1 (continued)

Species	Host	Reference
Tricholoma caligatum (Viviani) Ricken	*Cistus* sp.	Lavorato 1991
Tricholoma focale (Fr.) Ricken	*Cistus* sp.	Lavorato 1991
Tricholoma psammopus (Kalchbr.) Quél.	*C. albidus/C. monspeliensis/ Cistus* sp.	Lavorato 1991; Vila and Llimona 1999
Tricholoma saponaceum (Fr.: Fr.) Kummer	*C. monspeliensis/Cistus* sp.	Lavorato 1991; Vila and Llimona 2002
Tricholoma scalpturatum (Fr.) Quél.	*Cistus* sp.	Lavorato 1991
Tricholoma squarrulosum Bresad.	*C. monspeliensis/Cistus* sp.	Lavorato 1991; Vila and Llimona 2002
Tricholoma sulphureum (Bull.: Fr.) Ricken	*Cistus* sp.	Lavorato 1991
Tricholoma terreum (Schaeff.: Fr.) Kummer	*C. albidus/C. monspeliensis/ Cistus* sp.	Lavorato 1991; Mateo-Álvarez 2002; Vila and Llimona 2002
Tricholoma ustale (Fr.: Fr.) Kummer	*Cistus* sp.	Lavorato 1991
Tricholoma ustaloides Romagn.	*Cistus* sp.	Lavorato 1991
Boletus aemilii Barbier (=*B. spretus* Bertéa, *B. speciosus* ss. March.)	*Cistus* sp.	Lavorato 1991; Andrés et al. 1994
Boletus aereus Bull.: Fr.	*C. albidus/C. monspeliensis/ Cistus* sp.	Alessio 1981; Lavorato 1991; Vila and Llimona 2002
Boletus aestivalis (Bonord.) Demoulin	*Cistus* sp.	Vila and Llimona 2002
Boletus appendiculatus Schaeff.: Fr.	*Cistus* sp.	Alessio 1981
Boletus edulis Bull.: Fr.	*Cistus* sp.	Lavorato 1991
Boletus impolitus Fr.	*Cistus* sp.	Lavorato 1991
Boletus permagnificus Pöder (=*B. siculus* Inzenga ss. Alessio,=? *B. inchnusanus* Alessio, Galli and Littini)	*Cistus* sp.	Lavorato 1991
Boletus queletii Schulzer var. *zugazae* Moreno	*C. ladanifer*	Moreno 1977
Boletus regius Krombh.	*Cistus* sp.	Zervakis et al. 1998
Boletus rhodoxanthus Kallenb.	*C.* cfr. *ladanifer*	Hahn 2001 (ECM)
Chalciporus piperatus (Bull.: Fr.) Bat.[g]	*C. albidus* (?)/*C. monspeliensis* (?)/*C. salvifolius* (?)/*Cistus* sp. (?)	Lavorato 1991; Vila and Llimona 1999; 2002
**Leccinum corsicum* (Rolland) Sing. (=*L. crocipodium* var. *corsicum* (Roll.) Bert., *Boletus sardous* Belli and Sacc., *L. hispanicum* Moreno)	*C. albidus/C. ladanifer/ C. monspeliensis/ C. salvifolius/Cistus sp.*	Moreno 1977; Alessio 1981; Quadraccia and Lunghini 1990; Lavorato 1991; Lannoy and Estades 1995; Vila and Llimona 1998
Leccinum sp. (cfr. *L. arenarium* Redhead and Watling)[h]	*C. salvifolius*	Contu 1990
Suillus collinitus (Fr.) Kuntze (=*S. fluryi* Huijsman)	*Cistus* sp. (?)	Lavorato 1991
Xerocomus subtomentosus (L.: Fr.) Quél.	*Cistus* sp.	Lavorato 1991
Xerocomus cfr. *leonis* (D.A. Reid) Bon	*C. albidus/C. monspeliensis*	Vila and Llimona 1999
Melanogaster broomeianus Berk. ex Tul.	*C. ladanifer*	Romero de la Osa 1996
Melanogaster variegatus (Vitt.) Tul.	*C. albidus*/*C. clusii* Dun./ *C. ladanifer*/*C. laurifolius*/ *C. monspeliensis*	Calonge et al. 1994; Moreno-Arroyo et al. 2000; Vila and Llimona 2002
Paxillus ammoniavirescens Dessi and Contu	*C. laurifolius* (?)/ *C. monspeliensis*	Dessi and Contu 1998; Vila and Llimona 2002
Paxillus involutus (Batsch: Fr.) Fr.	*Cistus* sp.	Ortega and Esteve-Raventós 1999
Rhizopogon luteolus Fr.	*C. ladanifer* (?)	Castro et al. 1994
Rhizopogon roseolus (Corda) Th. M. Fr.	*C. crispus* (?)	Moreno-Arroyo et al. 2000
Rhizopogon vulgaris (Vitt.) M. Lange	*C. monspeliensis*	Malloch and Thorn 1985
Astraeus hygrometricus (Pers.) Morgan	*C. albidus/C. monspeliensis*	Malloch and Thorn 1985; Vila and Llimona 1998
Pisolithus tinctorius (Pers.) Coker and Couch (=*P. arrhizus* (Scop.: Pers.) Rauschert)	*C. ladanifer/C. monspeliensis*	Calonge and Demoulin 1975; Pérez de Gregorio 1996; Díez et al. 2001 (as *P.* cfr. *tinctorius*)
Scleroderma cepa Pers.	C. *monspeliensis*	Malloch and Thorn 1985
Scleroderma meridionale Dem. and Mal.	*C. salvifolius*	Quadraccia and Lunghini 1990

Table 1 (continued)

Species	Host	Reference
Wakefieldia macrospora (Hawker) Hawker	*C. albidus* (?)	Moreno-Arroyo et al. 2000
Gymnomyces dominguezii Moreno-Arroyo, Gómez and Calonge[i]	*C. crispus* (?)	Moreno-Arroyo et al. 1999; 2000
Gymnomyces xanthosporus (Hawker) A.H. Smith	*C. crispus* (?)/*C. ladanifer* (?)	Moreno-Arroyo et al. 2000
Lactarius atlanticus Bon	*Cistus* sp.	Lavorato 1991
Lactarius chrysorrheus (Fr.) Fr.	*Cistus* sp./*C. ladanifer*	Lavorato 1991; Jiménez Antonio 1994
**Lactarius cistophilus* Bon and Trimbach	*C. albidus*/*C. monspeliensis*/ *Cistus* spp.	Vila and Llimona 1998; Basso 1999; Vila and Llimona 2002, Comandini and Rinaldi unpub. observ. (ECM)
**Lactarius cyanopus* Basso	*C. albidus*	Basso 1999
Lactarius deliciosus (L.: Fr.) S.F. Gray	*Cistus* sp. (?)	Zervakis et al. 1998; Díez Rodríguez (in Ortega and Esteve-Raventós 1999)
Lactarius ilicis Sarnari	*C. monspeliensis*/*Cistus* sp.	Vila and Llimona 1998; Llistosella 2000
Lactarius mairei Malençon	*Cistus* sp.	Lavorato 1991
Lactarius pallidus (Pers.: Fr.) Fr.	*Cistus* sp. (?)	Lavorato 1991
Lactarius pyrogalus (Bull.: Fr.) Fr.	*Cistus* sp. (?)	Lavorato 1991
Lactarius rugatus Kühn. and Romagn.	*C. incanus*/*C. salvifolius*/ *Cistus* sp.	Quadraccia and Lunghini 1990; Lavorato 1991; Brotzu 1998; Comandini and Rinaldi unpub. observ.
**Lactarius tesquorum* Malençon	*C. albidus*/*C. monspeliensis*/ *Cistus* spp.	Malençon 1979; Contu 1984; Contu 1986; Vila and Llimona 1998; Basso 1999; Vila and Llimona 1999; Zotti and Orsino 2001; Nuytinck et al. 2004 (ECM)
Lactarius violascens (Otto: Fr.) Fr.	*Cistus* sp.	Lavorato 1991
Lactarius zonarius (Bull.) Fr.	*Cistus* sp.	Contu unpub. observ.
Russula amoena Quél.	*C. monspeliensis*	Vila and Llimona 2002
Russula amoenolens Romagn.	*C. monspeliensis*/*Cistus* sp.	Sarnari 1998; Vila and Llimona 2002
Russula chloroides (Krombh.) Bres.	*Cistus* sp.	Martínez Macarro 1996
**Russula cistoadelpha* Moser and Trimbach	*C. albidus*/*C. monspeliensis*/ *C. salvifolius*	Moser and Trimbach 1981; Contu 1984; Bon 1988; Quadraccia and Lunghini 1990; Vila and Llimona 1999; 2002
Russula delica Fr.	*Cistus* sp.	Lavorato 1991
Russula foetens Pers.: Fr.	*Cistus* sp.	Lavorato 1991
Russula fragilis (Pers.: Fr.) Fr.	*Cistus* sp.	Lavorato 1991
Russula fragrantissima Romagnesi	*C. ladanifer*	Calonge and Pérez-de-Gregorio 2002
Russula grata Britzelm. (=*R. laurocerasi* Melzer)	*Cistus* sp.	Martínez Macarro 1996
Russula graveolens Romell.	*Cistus* sp.	Lavorato 1991; Sarnari 1998
Russula insignis Quél.	*Cistus* sp.	Lavorato 1991; Sarnari 1998
Russula livescens (Batsch) Quélet	*Cistus* spp.	Contu 1984
Russula krombholzii Schaffer (=*R. atroporpurea* (Krmbh.) Britz.)	*Cistus* sp.	Lavorato 1991
**Russula monspeliensis* Sarnari	*C. monspeliensis*[j]	Sarnari 1987; Bon 1988; Lavorato 1991; Brotzu 1998; Sarnari 1998; Vila and Llimona 1998; 1999; 2002
**Russula monspeliensis* var. *sejuncta* Sarnari (=*R. anatina* Romagn. var. *sejuncta* Sarnari)	*C. monspeliensis*/ *C. salvifolius*	Sarnari 1993; 1998
Russula odorata Romagn.	*Cistus* sp.	Sarnari 1998
Russula odorata var. *rutilans* Sarnari	*Cistus* sp.	Lavorato 1991
Russula parazurea J. Schaeffer	*C. monspeliensis*	Vila and Llimona 2002
Russula parazurea J. Schaeffer var. *dibapha* Romagn.	*Cistus* sp.	Lavorato 1991
Russula praetervisa Sarnari	*Cistus* sp.	Sarnari 1998
Russula pseudoaeruginea (Romagn.) Kuyper & Vuure fo. *galochroa* sarnari	*Cistus* sp.	Lavorato 1991
Russula pseudoimpolita Sarnari	*Cistus* sp.	Lavorato 1991; Sarnari 1998

Table 1 (continued)

Species	Host	Reference
Russula rhodomarginata Sarnari	*Cistus* sp.	Lavorato 1991; Sarnari 1998
Russula sanguinea (Bull.) Fr.	*Cistus* sp.	Lavorato 1991
Russula seperina Dupain	*Cistus* spp.	Contu 1984; Lavorato 1991
Russula sororia Fr.	*Cistus* spp.	Contu 1984
Russula subazurea Bon	*Cistus* sp.	Lavorato 1991; Sarnari 1998
**Russula tyrrhenica* Sarnari	*Cistus* sp.	Lavorato 1991; Sarnari 1998
Russula vesca Fr.	*Cistus* sp.	Lavorato 1991
Russula werneri Maire	*Cistus* spp.[k]	Contu 1984; Lavorato 1991; Hermosilla and Sánchez 2000
Russula sp.	*C. albidus*/*C. monspeliensis*	Vila and Llimona 1999
Hysterangium clathroides Vitt. var. *clathroides* Vitt. Vidal	*C. ladanifer*	Moreno-Arroyo et al. 2000
Hysterangium clathroides Vitt. var. *cistophilum* Tul. and C. Tul. (=*H. cistophilum* (Tul. and C. Tul.) Zeller and Dodge)	*C. ladanifer*/*C. laurifolius*/ *C. monspeliensis*/ *C. populifolius*	Calonge et al. 1994; Moreno-Arroyo et al. 2000; Vila and Llimona 2002
Amphinema byssoides (Pes.: Fr.) J. Erikss.	*Cistus* sp. (?)	Tellería et al. 1997
Thelephora caryophyllea (Schaeff.) Pers.	*C. albidus*/*C. monspeliensis*	Vila and Llimona 1998; Mateo-Álvarez 2002
Thelephora terrestris Pers.: Fr.	*C. albidus*/*C. monspeliensis*	Vila and Llimona 2002
Unidentified sebacinoid mycobiont	*Cistus sp.*	Rinaldi and Comandini unpub. observ. (ECM)
Cantharellus cibarius (Fr.: Fr.) Fr.	*C. albidus*/*C. monspeliensis*/ *Cistus* spp.	Vila and Llimona 1998; Rinaldi unpub. observ

For some species, e.g., *Amanita vaginata* and *A. junquillea*, the several varieties and formae reported to be associated with *Cistus* are not listed

Several species belonging to fungal genera, whose mycorrhizal status is either highly improbable, uncertain, or not fully confirmed, have been explicitly reported by some authors as establishing ectomycorrhizal symbiosis with *Cistus* spp. For the sake of clarity, these species were not included in the present checklist. Relevant examples include the following: *Bovista aestivalis* (Bon.) Demoulin, *Geastrum minimum* Schw., *Calvatia excipuliformis* (Scop.: Pers.) Perdeck, *Vascellum pratense* (Pers.: Pers.) Kreisel (all in Malloch and Thorn 1985, who interpreted some data collected by Demoulin 1983), *Entoloma cistophilum*, *E. sordidulum*, *Entoloma sp.*, *Limacella grisea*, *Lyophyllum ovisporum*, *L. transforme* (all in Vila and Llimona 1999)

ECM Description or report of naturally occurring or synthesized ectomycorrhiza

[§]The higher classification system used in this paper is that outlined by Kirk et al. (2001) in the *Dictionary of the Fungi*, integrated following Eriksson et al. (2001) for the Ascomycota and various sources for the Basidiomycota (see the notes to specific taxa). Taxa belonging to the same order and family (not shown) are listed consecutively. The taxonomic status and/or position of some of the listed genera, such as *Genabea*, *Astraeus*, and *Wakefieldia*, is controversial

*Specific or typical *Cistus* mycobiont

(?) Dubious or suspect record

[a]Vila and Llimona (1999, 2002) consider *A. cistetorum* as a variety of *A. vaginata*

[b]Secotioid relative of *Amanita* (Moncalvo et al. 2002)

[c]Ortega and Esteve-Raventós (1999) have proposed the conspecificity of *H. erumpens* and *H. theobrimum* Quadr. with *H. truncatum*, which, on the other hand, is generally believed to be one of the few *Hebeloma* species with a saprophytic lifestyle (Hacskaylo and Bruchet 1972; Marmeisse et al. 1999)

[d]According to recent molecular studies by Peintner et al. (2001), different *Hymenogaster* species show affinities with either *Cortinarius* or *Hebeloma*, hinting to the possible polyphyletic origin of this group of sequestrate, hypogeous fungi

[e]Within the Agaricales, several recent molecular studies (e.g., Peintner et al. 2001, Moncalvo et al. 2002) have questioned the validity of classic taxonomy, especially what concerns the delimitation of families. *Inocybe*, for example, was traditionally placed in the Cortinariaceae, but molecular data have excluded its close relationship with *Cortinarius* and *Hebeloma* (Peintner et al. 2001, Moncalvo et al. 2002). Also, the inclusion of *Hygroporus* and *Laccaria* in the Tricholomataceae is not supported by molecular evidence (Bruns et al. 1998; Moncalvo et al. 2002)

[f]The taxonomical validity of this species is dubious, being considered by many authors a form of *L. laccata*

[g]The mycorrhizal status of *C. piperatus* has not been confirmed and was recently questioned (Högberg et al. 1999)

[h]*Leccinum arenicola* was originally described from coastal sand dunes in New Brunswick, Canada, as a putative mycorrhizal symbiont of *Hudsonia tomentosa*, Cistaceae (Redhead and Watling 1979)

[i]Sequestrate relative of *Russula* (Miller et al. 2001)

[j]In rare cases, *C. albidus* (Vila and Llimona 1998) and *C. salvifolius* (Sarnari 1998) have been reported as additional potential hosts

[k]Sarnari (1993) has questioned the classification of some specimens of *Russula* collected in Sardinia in association with *Cistus* sp. and identified as *R. werneri*. In his opinion, these specimens would belong to a taxon close to *R. pseudoaeruginea* (Romagn.) Kuyper and Vuure fo. *galochroa* Sarnari, and *R. werneri* would not establish mycorrhizal symbiosis with *Cistus* (Sarnari 1998)

characterization of the ectomycorrhizas formed by *Tuber* spp. on *C. incanus* (Fontana and Giovannetti 1979; Giovannetti and Fontana 1982), and in several other preliminary and/or not exhaustive descriptions of mycorrhizal morpho-anatomical details (Chevalier et al. 1975; Fusconi 1983; Leduc et al. 1986; Wenkart et al. 2001; Roth-Bejerano et al. 2003). For basidiomycetes, descriptions of the mycorrhizas formed by *L. laccata* and *Boletus rhodoxanthus* on *C. ladanifer* (Torres et al. 1995; Hahn 2001), by *Hebeloma sacchariolens* on *C. salvifolius* (Rosell 1981) and, more recently, by *Lactarius tesquorum* on *Cistus* sp. (Nuytinck et al. 2004), are available.

Common host-dependent features of all the ectomycorrhizal types described so far on *Cistus* spp. are (for the specific terminology used to characterize ectomycorrhizae, see Agerer 1986, 1987–1998, 1991): simple or monopodial-pinnate ramification systems; small diameter of ectomycorrhizal tips; thin mantle thickness; cortical cells generally present in two rows, tangentially rectangular, either radially rectangular orientated or square to radially rectangular orientated; Hartig net generally uniseriate, surrounding one–two rows of cortical cells and rarely reaching the endodermis ("cortical Hartig net", for a description of this peculiar structure, see Smith and Read 1997).

In addition to the ectomycorrhizal types mentioned above, very recent observations of *Cistus* roots excavated in Sardinia (Italy) have led to the isolation of ectomycorrhizas of *Lactarius cistophilus* and of a morphotype unequivocally formed by a sebacinoid mycobiont (Rinaldi and Comandini, unpublished observations). The latter finding adds to the increasing evidence that members of the Sebacinaceae, a family assigned to the heterobasidiomycetous order Auriculariales, are common symbionts in various ectomycorrhizal communities. Typical ectomycorrhizas formed by these fungi have been recently detected by both molecular and morphological analyses on several temperate deciduous and coniferous trees, including *Carpinus*, *Corylus*, *Fagus*, *Tilia*, *Picea*, and *Abies* (Selosse et al. 2002; Urban et al. 2003; Comandini, unpublished observations), and also in Australian *Eucalyptus* Mediterranean-type forests (Glen et al. 2002).

In recent years, the application of a range of molecular tools has greatly enhanced our knowledge of ectomycorrhizal communities, expanding well beyond classic morphotyping our possibilities to track and identify ectomycorrhizas and to compare the above- and below-ground mycorrhizal fungal components of ecosystems (Horton and Bruns 2001). Unfortunately, this "revolution" has only marginally impacted research on *Cistus* ectomycorrhizas. To date, indeed, only the mycorrhizas of *Lactarius tesquorum* on *Cistus* sp. have been fully characterized from both a molecular and morphological point of view (Nuytinck et al. 2004). Clearly, the confirmation of many putative *Cistus* mycobionts and the unambiguous identification of their mycorrhizas await a more general recourse to molecular methods.

Comparing ectomycorrhizal diversity in different ecosystems

In addition to forming extensive patches of pure shrublands, *Cistus* is also a significant presence in other vegetation communities. These communities include the mixed Mediterranean maquis or garrigue, where *Cistus* occurs together with other sclerophyllous (not-ectomycorrhizal) scrubs, such as *Olea*, *Phyllirea*, *Pistacia*, *Erica*, *Arbutus*, and some *Quercus* and *Pinus*-dominated communities, where *Cistus* is an element of the undercanopy vegetation and colonizes clearings and open areas. The data gathered in this study indicate that the number of ectomycorrhizal fungal species associated with *Cistus* is significant, and support the importance of this symbiosis in these Mediterranean ecosystems. On the other hand, when compared to other better-known host plants such as *Pseudotsuga menziesii*, which associates with some 2000 fungal species in North America (Trappe 1977), the ectomycorrhizal diversity of *Cistus* might look rather poor.

However, it should be stressed that comparing lists of fungal associates drafted by different authors might be biased to some extent by personal choices for inclusion or exclusion of those fungal genera for which the mycorrhizal status is uncertain or not fully confirmed. Focusing on the information available for other better-studied Mediterranean-type ecosystems, some 660 fungal associates, many of which are endemic, have been recorded for *Eucalyptus* in natural environments of Australia (Castellano and Bougher 1994; Bougher 1995). *Eucalyptus* is also believed to have the potential to associate with the richest flora of host genus-specific ectomycorrhizal fungi in the world (Molina et al. 1992), while diversity in its plantations is considerably lower in both Australian and exotic areas (Lu et al. 1998a,b; Giachini et al. 2000) (an extensive account of *Eucalyptus* ectomycorrhizal fungi can be found at http://www.ffp.csiro.au/research/mycorrhiza/eucfungi.html). *Eucalyptus* and *Cistus* share a small contingent of associated fungi, included in the genera *Pisolithus*, *Scleroderma*, and *Laccaria*, with the characteristics of "early stage" species. These mycobionts appear in the early phases of fungal successions and represent, in some cases, pioneer fungi, being often typical of disturbed habitats with young trees and shrubs, or may occur even in freshly cleared areas and often associate with a diversity of hosts. Some *Hebeloma* listed in Table 1 are also well known early stage fungi.

What needs to be done

Our knowledge of *Cistus* mycorrhizal ecology is too limited to draw any simple conclusions for this host plant and its associated fungi as for many key aspects mentioned above. However, information acquired from studies of other ecosystems may help to highlight priority areas for future research. In particular, the pattern and role of host specificity, possibly for each fungal species, in *Cistus* ectomycorrhizal communities should be investigated, as the importance of host specificity in other ectomycorrhizal communities has been underlined (Bruns et al. 2002).

Examining the plant-fungal associations for *Cistus* would also serve to elucidate mycobiont–host distribution and mycobiont–host species relationships (Newton and Haigh 1998), to see if they have a general validity or, and eventually how, they change in specialized environments. Many of the *Cistus*-specific symbionts listed here, e.g., *Cortinarius* spp. and *Inocybe* spp., have been identified only very recently, which highlights the need for in-depth taxonomical surveys of these and other fungal genera in *Cistus* maquis over the entire host geographic range. Belowground ectomycorrhizal diversity in *Cistus* natural communities should also be explored to see if it reflects the *Cortinariaceae* and *Russulaceae* dominance detected aboveground, and the morphological and molecular characterization of the prevailing ectomycorrhizal types should be performed.

Work aimed at confirming the identity of putative mycobionts and extending their number would certainly be easier if carried out in pure *Cistus* stands, rather than in areas where it grows mixed with other ectomycorrhizal hosts. However, the exploration of diversity and biology of *Cistus* mycorrhizas in mixed plant communities could provide key information on the structure of both the plant and fungal components of these communities in Mediterranean-type ecosystems. Doubtlessly, molecular tools will play a major role in tackling these complex issues. As data on the succession of mycorrhizal fungi in *Cistus* ecosystems are totally lacking, community level studies should also be conducted to address this important aspect, as well as the impact of mycorrhizal colonization upon the fitness of *Cistus* and its resilience to natural and anthropogenic disturbances, such as strong water limitation, fire, overcutting, and grazing.

Considering the ecological niches occupied by *Cistus* and the intermediate position of this host genus in the vegetation series leading to evergreen *Quercus* or *Pinus* climax forests on one side, and to impoverished pastures and/or desertified lands on the other, a deeper knowledge of *Cistus* ectomycorrhizal fungal communities may well prove to be of wider significance and to contribute to understand the role and dynamics of mycorrhizas in inherently unstable ecosystems, especially if integrated into broader ecological investigations. These studies may also provide valuable tools to help shape future programs of protection and management of natural resources in vast areas across the Mediterranean basin. In general, *Cistus* holds the potential to develop into an alternative model to assess the role of mycorrhizal symbiosis in ecosystem functioning of Mediterranean-climate shrublands throughout the world. Clearly, we are just at the beginning of this research journey.

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