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ECTOMYCORRHIZA FORMATION IN *EUCALYPTUS*

I. PURE CULTURE SYNTHESIS, HOST SPECIFICITY AND MYCORRHIZAL COMPATIBILITY WITH *PINUS RADIATA*

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SUMMARY

Ectomycorrhiza formation by 11, geographically distinct *Eucalyptus* species and *Pinus radiata* with 23 diverse ectomycorrhizal fungi was examined in pure culture syntheses. Few differences occurred between the *Eucalyptus* species in their ability to form ectomycorrhizas with several fungi, thus indicating no evidence for host–fungus specificity within *Eucalyptus*. *Pinus radiata* and most *Eucalyptus* species formed ectomycorrhizas in common with several broad-host-ranging fungi. However, fungus species which are known to associate exclusively with members of the Pinaceae, *e.g.* *Suillus* and *Rhizopogon* species, did not form ectomycorrhizas with any *Eucalyptus* species and vice versa. Possible incompatibility between several host–fungus combinations was characterized by host accumulation of phenolic compounds in epidermal and cortical cells. These results are discussed relevant to better understanding degrees and processes of ectomycorrhiza host–fungus specificity and compatibility and to practical considerations in reforestation of exotic plantations.

INTRODUCTION

The Australian genus *Eucalyptus* contains many timber-producing forest species and is the major forest crop in Australia. Many species grow rapidly and have been extensively planted around the world (Penfold and Willis, 1961). Similarly, *Pinus radiata* D. Don, a conifer native to the California coast, has become popular as an exotic in Australia and New Zealand in extensive reforestation programmes (Mirov, 1967).

Ectomycorrhizas are typical of both the eucalypts and *P. radiata* in both indigenous forests (Samuels, 1926; Smith and Thiers, 1964; Chilvers, 1973; Thiers, 1975; Ashton, 1976) and exotic plantings (Smith and Pope, 1934; Birch, 1937; Rawlings, 1951; Levisohn, 1958; McNabb, 1968; Trappe and Molina, unpublished data). Successful establishment of exotic plantings in most cases has required inoculation of seedlings with ectomycorrhizal fungi. *P. radiata* growth in Australia can be stimulated in growth by inoculation with litter containing mycorrhizal fungus symbionts (Kessell, 1923; Kessell and Stoat, 1936). Pryor (1956a,

1959) attributed failure of eucalypt plantings in the Northern Hemisphere to mycorrhizal deficiency.

Many studies have shown ectomycorrhizas to be essential for adequate uptake of minerals such as phosphorus, sulphur, and zinc by trees (*P. radiata* – Bowen, 1973; *Eucalyptus* – Malajczuk, McComb and Loneragan, 1975). Certain mycorrhizal fungi are more effective in this role than others under given circumstances (Trappe, 1977). Yet, little is known of specific fungal symbionts of either eucalypts or *P. radiata*, let alone their particular function(s). Most information on the symbionts has been from field observation of association between sporocarps and hosts; few have been demonstrated by synthesis in pure culture (Tables 1 and 2). Most fungi reported to associate with *P. radiata* are different from those found in eucalypt forests. Chilvers (1973) and Malajczuk (1975) found that pine isolates, *Rhizopogen luteolus* and *Suillus granulatus*, formed ectomycorrhizas with *P. radiata* but not with eucalypts in pure culture syntheses. Pryor (1956b), Bakshi (1966), and Thapar, Singh and Bakshi (1967) indicate that the eucalypt subgenera apparently differ little in ability to form ectomycorrhizas. Uhlig (1968) reports a similar conclusion and suggests that some eucalypts are more dependent on mycorrhizas than others. Chilvers (1973) detected little evidence for the specificity of particular fungi to the eucalypt subgenera, although his study was primarily a comparison of ectomycorrhizal types rather than identification of fungal symbionts.

Clearly, host specificity to particular fungi both within *Eucalyptus* and between *Pinus* and *Eucalyptus* needs additional study. Since *P. radiata* is often planted on to former *Eucalyptus* forest sites, the ability of *P. radiata* to form ectomycorrhizas with *Eucalyptus* symbionts is of practical significance. Similarly, with the advent of the practice of artificially inoculating tree seedlings with pure cultures of ectomycorrhizal fungi, the ability of these different hosts to associate with selected fungi should be known. The study reported here was accordingly designed to (1) evaluate the ability of taxonomically and geographically differing eucalypts to form, in pure culture, ectomycorrhizas with diverse ectomycorrhizal fungi of known host associations, and (2) determine if eucalypt-associated fungi can form mycorrhizas with *Pinus radiata* and vice versa.

MATERIALS AND METHODS

The fungi used in this study (Table 3) were all isolated from sporocarp tissue except for *Cenococcum geophilum*, which was isolated from a surface sterilized sclerotium. *Hydnangium carneum* and *Hymenogaster albellus* were isolated from sporocarps fruiting beneath plantations of *Eucalyptus* spp. in western Oregon and northern California. The other isolates were associated with various northwestern American trees, and all previously formed mycorrhizas in pure culture syntheses (Molina and Trappe, 1982). They were selected to include both broad-host-ranging and host-specific mycorrhiza formers.

The seeds of the 11 *Eucalyptus* spp. used (Table 4) were representatives from different subgenera as well as from diverse geographic locations. *Pinus radiata* seed was from plantations in Australia.

Molina's (1979) pure culture synthesis technique – large glass test tubes containing autoclaved peat moss plus Vermiculite moistened with modified Melin-Norkrans nutrient solution (Marx, 1969) – was used for all host–fungus syntheses. All seeds were surface sterilized with 30% H_2O_2 for the following

Table 1. *Ectomycorrhizal Fungi Reported for* Pinus radiata*

Amanita muscaria (L. ex Fr.) Pers. ex Hook. – Benito-Martinez and Torres-Juan, 1965; Birch, 1937; **Chu-Chou, 1979**; Fisch, 1959; Purnell, 1957; Rawlings, 1951, 1960.
A. phalloides (Vaill. ex Fr.) Secr. – Takacs, 1961a.
Boletus auriporus Peck – Mikola, 1970.
B. piperatus Bull. ex Fr. – **Chu-Chou, 1979**; McNabb, 1968; Rawlings, 1951, 1960.
Cantharellus cibarius Fr. – Benito-Martinez and Torres-Juan, 1965.
Cenococcum geophilium Fr. (*C. graniforme*) – Bowen, 1965; **Henderson and Stone, 1968**; **Lamb and Richards, 1970, 1971**, Mejstrik, 1970, 1971; **Mejstrik and Krause, 1973**; **Trappe, 1962**, 1964.
Chroogomphus rutilus (Schaeff. ex Fr.) Miller (*Gomphidius rutilus*) – Pilát and Dermek, 1974; Singer, 1949.
Chroogomphus vinicolor (Peck) Miller – Singer, 1946 and 1964.
Endogone flammicorona Trappe and Gerd. – Gerdemann and Trappe, 1974.
E. lactiflua Bk. and Br. – Trappe, unpublished data.
Hebeloma crustuliniforme (Bull. ex St. Am.) Quél. – **Chu-Chou, 1979**; Gibson, 1963.
Hysterangium separabile Zell. – Trappe, unpublished data.
Inocybe lacera (Fr.) Kumm. – Trappe, 1961.
Laccaria laccata (Scop. ex Fr.) Berk. and Br. – **Chu-Chou, 1979**; **Henderson and Stone, 1968**; Rawlings, 1951, 1960.
Lactarius deliciosus (L. ex Fr.) S. F. Gray – Benito-Martinez and Torres-Juan, 1965; Fisch, 1945; Mikola, 1969; Purnell, 1957.
Pisolithus tinctorius (Pers.) Cok. and Couch (*P. arhizus*) – **Henderson and Stone, 1968**; Lamb and Richards, 1974.
Rhizopogon luteolus Fr. and Nordh. – Bowen, 1965, 1968; **Chilvers, 1973**; **Chu-Chou, 1979**; Donald, 1975; Kessell, 1927; Lamb and Richards, 1971; Purnell, 1957; Rawlings, 1960; Reid and Bowen, 1979; **Skinner and Bowen, 1974**; Theodorou, 1971; Theodorou and Bowen, 1970, 1973.
R. ochraceorubens Smith – Trappe, unpublished data.
R. roseolus (Corda) Holl. – **Henderson and Stone, 1968**; **Lamb and Richards, 1970, 1971**, 1978; **Richards and Voight, 1964**; Walker, 1931.
R. rubescens Tul. and Tul. – Birch, 1937; Cunningham, 1934; Rawlings, 1960; Rayner, 1938.
R. subcaerulescens Smith – Trappe, unpublished data.
Scleroderma bovista Fr. – Birch, 1937; Cunningham, 1931; Gibson, 1963; Khan, 1980; Rawlings, 1960; Rayner, 1938.
S. citrinum Pers. (*S. aurantium*) – Benito-Martinez and Torres-Juan, 1965; **Chu-Chou, 1979**; Takacs, 1961a, b.
S. verucosum Vaill. ex Pers. – **Chu-Chou, 1979**.
Suillus acerbus Smith and Thiers – Smith and Thiers, 1964; Thiers, 1975.
S. bovinus (L. ex Fr.) Kuntze – Benito-Martinez and Torres-Juan, 1965; Pilát and Dermek, 1974.
S. brevipes (Peck) Kuntze – McNabb, 1968.
S. granulatus (L. ex Fr.) Kuntze – Benito-Martinez and Torres-Juan, 1965; Bowen, 1965; **Chilvers, 1973**; **Chu-Chou, 1979**; Cromer, 1935; **Lamb and Richards, 1971**, 1978; McNabb, 1968; Mikola, 1969; Puppi and Rambelli, 1972, Purnell, 1957; Takacs, 1961a, b; Theodorou and Bowen, 1970; Walker, 1931; Young, 1936.
S. grevillei (Klotzsch) Sing. – **Henderson and Stone, 1968**.
S. luteus (L. ex Fr.) Gray – Birch, 1937; **Chu-Chou, 1979;** Fisch, 1945, 1959; Gibson, 1963; **Henderson and Stone, 1968**; McNabb, 1968; **Mejstrik and Krause, 1973**; Purnell, 1957; Rawlings, 1960; Rayner, 1938; **Stone, 1950**; Theodorou and Bowen, 1970; Walker, 1931.
S. pungens Thiers and Smith – Smith and Thiers, 1964; Thiers, 1975.
S. subacerbus McNabb – McNabb, 1968.
S. subaureus (Peck) Snell – Singer, 1964; Singer and Digilio, 1960.
Thelephora americana Lloyd – Trappe, unpublished data.

* References in bold-face report pure culture syntheses, others are field observations.

durations: *E. camaldulensis*, *E. dalrympleana*, 10 min; *E. calophylla*, *E. obliqua*, *E. sieberi*, *E. st.-johnii*, *E. regnans*, 15 min; *E. diversicolor*, *E. microcorys*, *E. marginata*, 20 min; *E. maculata*, 25 min; *P. radiata*, 30 to 40 min. Seeds were then germinated on nutrient agar in small vials to screen for contamination and contaminated vials discarded. *Eucalyptus* seed needed no stratification; germination

Table 2. *Ectomycorrhizal Fungi Reported for* Eucalyptus *spp.**

E. archeri Maid. and Blakeley
- *Hydnangium carneum* Wallr. – Trappe, unpublished data.
- *Hymenogaster albellus* Mass. and Rodw. – Trappe, unpublished data.
- *Scleroderma albidum* Pat. and Trab. – Trappe, unpublished data.

E. bridgesiana Bak.
- *Pisolithus tinctorius* – **Chilvers, 1973.**

E. calophylla Brown ex Lindl.
- *Ramaria sinapicolor* (Clel.). Corn. – **Malajczuk, 1975.**

E. camuldulensis Dehnh.
- *Cenococcum geophilum* – Anderson, 1966.
- *Pisolithus tinctorius* – Neumann, 1959
- *Scleroderma verrucosum* – Bakshi, 1966; Thapar *et al.*, 1967.

E. citriodora Hook.
- *Scleroderma verrucosum* – Bakshi, 1966; Thapar *et al.*, 1967.

E. dalrympleana Maid.
- *Hydnangium carneum* – Trappe, unpublished data.
- *Pisolithus tinctorius* – Chilvers, 1973.

E. deglupta Blume
- *Scleroderma verrucosum* – Bakshi, 1966; Thapar *et al.*, 1967.

E. dives Schau.
- *Octaviania densa* (Rodw.) Cunn. – Chilvers, 1973.
- *Scleroderma cepa* Vaill. ex Pers. (*S. flavidum*) – Pryor, 1956a, b.

E. erythrocorys Muell.
- *Lycoperdon gemmatum* Batsch – **Rambelli, 1962a, b.**
- *Tricholoma pardinum* Quél. – **Rambelli, 1962a, b (**as *T. tigrinum*).

E. fastigiata Deane and Maid.
- *Octaviania densa* – Chilvers, 1973.
- *Pisolithus tinctorius* – **Chilvers, 1973.**

E. forrestiana Diels.
- *Lycoperdon gemmatum* – **Rambelli, 1962a, b.**
- *Tricholoma pardinum* – **Rambelli, 1962a, b (**as *T. tigrinum*).

E. gigantea Hook.
- *Cenococcum geophilum* – Trappe, 1964.

E. glaucescens Maid. and Blakely
- *Hydnangium carneum* – Trappe, unpublished data.

E. globulus Lab.
- *Cenococcum geophilum* – Anderson, 1966.
- *Hydnangium carneum* – Trappe, unpublished data
- *Hymenogaster albellus* – Trappe, unpublished data.
- *H. albus* (Klotzch) Berk. and Br. – Trappe, unpublished data.
- *Hysterangium incarceratum* Mal. – Trappe, unpublished data.

E. gomphocephala DC.
- *Scleroderma verrucosum* – Bakshi, 1966; Levisohn, 1968; Thapar *et al.*, 1967.

E. grandis Hill in Maid.
- *Cenococcum geophilum* – Anderson, 1966.
- *Macrolepiota procera* (Scop. ex Fr.) Sing. – Anderson, 1966.
- *Octaviania densa* – Chilvers, 1973.
- *Pisolithus tinctorius* – Marx, 1977.
- *Scleroderma verrucosum* – Bakshi, 1966; Thapar *et al.*, 1967.
- *Tricholoma pardinum* – Anderson, 1966; Rambelli, 1962c (as *T. tigrinum*).

E. gummifera (Gaertn.) Hochr.
- *Pisolithus tinctorius* – **Mullette, 1976.**

E. gunnii Hook.
- *Hydnangium carneum* – Trappe, unpublished data.

E. kirtoniana Muell.
- *Scleroderma verrucosum* – Bakshi, 1966; Thapar *et al.*, 1967.

E. leucoxylon Muell.
- *Pisolithus tinctorius* – **Chilvers, 1973.**

E. macrorrhyncha Muell.
- *Scleroderma cepa* (*S. flavidum*) – Pryor, 1956a, b.

Table 2 (*cont.*)

E. maculata Hook.
Pisolithus tinctorius – **Chilvers, 1973**.
E. marginata Smith
Ramaria sinapicolor (Clel.) Corn. – **Malajczuk, 1975**.
E. microcorys Muell.
Pisolithus tinctorius – Marx, 1977.
E. niphophylla Maid. and Blakely
Hydnangium carneum – Trappe, unpublished data.
Hymenogaster albellus – Trappe, unpublished data.
E. nitens Maid.
Hydnangium carneum – Trappe, unpublished data.
E. odorata Behr and Schlecht.
Scleroderma verrucosum – Bakshi, 1966; Thapar *et al.*, 1967.
E. paniculata Smith
Scleroderma verrucosum – Bakshi, 1966; Thapar *et al.*, 1967.
E. pauciflora Sieb.
Scleroderma cepa (*S. flavidum*) – Pryor, 1956a, b.
E. perriniana Muell. in Rodw.
Hydnangium carneum – Trappe, unpublished data.
Hymenogaster albellus – Trappe, unpublished data.
H. albus (Klotzsch) Berk. and Bk. – Trappe, unpublished data.
E. pilularis Smith
Octaviania densa – Chilvers, 1973.
E. polyanthemos Schauer
Pisolithus tinctorius – **Chilvers, 1973**.
E. pulverulenta Sims
Hydnangium carneum – Trappe, unpublished data.
Hymenogaster albellus – Trappe, unpublished data.
E. punctata DC.
Scleroderma verrucosum – Bakshi, 1966; Thaper *et al.*, 1967.
E. pyriformis Turcz.
Lycoperdon gemmatum – **Rambelli, 1962a, b**.
Tricholoma pardinum – **Rambelli, 1962a, b** (as *T. tigrinum*).
E. radiata Sieb. ex DC.
Pisolithus tinctorius – **Chilvers, 1973**.
E. regnans Muell.
Agaricus xanthodermus Gen. – **Ashton, 1976**.
Cenococcum geophilum – Chilvers, 1968; Chilvers and Pryor, 1965.
Cortinarius fragilipes Clel. – Ashton, 1976.
C. ochraceus Clel. – **Ashton, 1976**.
C. purpurascens Fr. – Ashton, 1976.
C. radicatus Clel. – **Ashton, 1976**.
C. subcinnamomeus Clel. – Ashton, 1976.
Gymnopilus pampeanus (Speg.) Sing. (*Flammula eucalyptorum* Clel.) – Ashton, 1976.
Hygrophorus coccineus (Schaeff. ex Fr.) Fr. – Ashton, 1976.
Hymenogaster violaceus Mass. and Rodw. (*Gymnoglossum violaceum*) – Ashton, 1976.
Hysterangium inflatum Rodw. – Ashton, 1976.
Mesophellia arenaria Berk. – **Ashton, 1976**.
Inocybe olivaceofulvus Clel. – Ashton, 1976.
Naematoloma fasciculare (Huds. ex Fr.) Karst. – **Ashton, 1976**.
Russula purpureoflava Clel. – Ashton, 1976.
Tricholoma coarctatum (Cooke and Mass.) Sacc. – Ashton, 1976.
E. robusta Smith
Octaviania densa – Chilvers, 1973.
Pisolithus tinctorius – Marx, 1977.
Scleroderma verrucosum – Bakshi, 1966; Thapar *et al.*, 1967.
E. rossii Bak. and Smith
Octaviania densa – Chilvers, 1973.
E. rudis Endl.
Octaviania densa – Chilvers, 1973.
Scleroderma verrucosum – Bakshi, 1966; Thapar *et al.*, 1967.

Table 2 (*cont.*)

E. sieberi Johns.
Pisolithus tinctorius – Chilvers, 1973.
E. st.-johnii Bak.
Pisolithus tinctorius – **Chilvers, 1973**.
Scleroderma cepa (*S. flavidum*) – Pryor, 1956a, b.
E. tereticornis Smith
Scleroderma verrucosum – Bakshi, 1966; Thapar *et al.*, 1967.
E. torelliana Muell.
Scleroderma verrucosum – Bakshi, 1966; Thapar *et al.*, 1967
E. viminalis Lab.
Octaviania densa – Chilvers, 1973.
Eucalyptus spp.
Cenococcum geophilum – Chilvers, 1968; Chilvers and Pryor, 1965.
Boletus portentosus Berk. and Br. – Fisch, 1945.
Cortinarius archeri Berk. – Moser, 1968.
C. microarcheri Clel. – Moser, 1968.
Hydnangium carneum – Thiers, 1979 (as *H. soederstromii*).
Hymenogaster albus – Gross, 1980.
Hysterangium incarceratum – Gross, 1980.
Lycoperdon gemmatum – Rawlings, 1951.
Pisolithus tinctorius – Bijl, 1918 (as *Polysaccum crassipes*); Marx, 1977; Mikola, 1969; Smith and Pope, 1934.
Scleroderma albidum – Guzmán and Varela, 1978.
S. bovista – Rawlings, 1951.
S. cepa – Thapar *et al.*, 1967.

* References in bold-face report pure culture syntheses, others are field observations. As our paper went to press Chu-Chou and Grace (1982) published additional ecualypt–fungus associations from New Zealand.

commenced after 3 to 6 days under artificial light. *P. radiata* seed was stratified at 3 °C for 30 days to yield uniform germination. Germinants were then aseptically planted into the sterilized synthesis tubes, inoculated with approximately 15 ml of a previously prepared mycelial slurry, and then placed in a water bath under fluorescent-incandescent lighting, 11 500 lx set for a 15 h day, for the duration of the experiment.

After 4 months, seedlings were removed intact from the synthesis tubes. The roots were gently washed and examined by stereomicroscopy for ectomycorrhiza formation. Squash mounts of fine roots showing fungal colonization were examined under the compound microscope for evidence of Hartig net penetration.

RESULTS

Except for *Hydnangium carneum* and *Hymenogaster albellus*, all fungi that formed ectomycorrhizas with eucalypts were those previously observed as broad-host-ranging (Molina and Trappe, 1982): *Laccaria laccata*, *Amanita muscaria*, *Hebeloma crustuliniforme*, *Cenococcum geophilum*, *Pisolithus tinctorius*, *Paxillus involutus*, *Scleroderma laeve* and *Astraeus pteridis*. But some broad-host-ranging fungi did not form ectomycorrhizas with eucalypts: *Lactarius deliciosus*, *Boletus edulis* and *Thelephora terrestris*. Because these readily initiated ectomycorrhizas with *P. radiata*, the cultures were clearly capable of mycorrhiza formation. *Hydnangium carneum* and *Hymenogaster albellus*, isolated from sporocarps collected from beneath eucalypt plantings in the United States and probably introduced from Australia on roots of imported eucalypt seedings, formed ectomycorrhizas only with the eucalypts. Mycorrhizas were formed by these two fungi on all eucalypts

Table 3. *Ectomycorrhizal fungus isolates tested in pure culture sunthesis for ectomycorrhiza formation with different* Eucalyptus *species and* Pinus radiata

Isolate	Fungus*	Year isolated	Associated hosts†
S-276	*Alpova diplophloeus* (Zeller & Dodge) Trappe & Smith (H)	1976	Alru, Psme
S-230	*Amanita muscaria* (L. ex Fr.) Pers. ex Hooker	1976	Abpr
S-237	*Astraeus pteridis* (Shear) Zeller	1976	Psme
S-329	*Boletus edulis* Bull. ex Fr.	1976	Pisi
A-145	*Cenococcum geophilum* Fr.	1974	Psme
S-166	*Hebeloma crustuliniforme* (Bull ex St. Am.) Quél.	1971	Psme, Tshe
S-475	*Hydnangium carneum* Wallr. in Dietr. (H)	1978	Eugl
S-493	*Hymenogaster albellus* Mass. & Rodw. (H)	1979	Eusp
S-238	*Laccaria laccata* (Scop. ex Fr.) Bk. & Br.	1976	Tsme
S-229	*Lactarius deliciosus* (L. ex Fr.) S. F. Gray	1976	Pipo, Psme
S-385	*Melanogaster intermedius* Zeller & Dodge (H)	1977	Psme
S-403	*Paxillus involutus* (Batch ex Fr.) Fr.	1977	Coav
S-216	*Pisolithus tinctorius* (Pers.) Coker & Couch	1976	Psme
S-297	*Rhizopogon occidentalis* Zeller & Dodge (H)	1976	Pico
A-153	*R. vinicolor* Smith (H)	1975	Psme, Tshe
S-218	*R. vulgaris* (Vitt.) M. Lange (H)	1976	Abgr, Tsme
S-308	*Scleroderma laeve* Lloyd	1976	Coav
S-223	*Suillus brevipes* (Peck) O. Kuntze	1976	Pico, Psme
S-255	*S. grevillei* (Klotzsch) Singer	1976	Laoc
S-243	*S. lakei* (Murr.) Smith & Thiers	1976	Psme
S-222	*S. tomentosus* (Kauffm.) Sing., Snell & Dick	1976	Pico
S-142	*Thelophora terrestris* (Ehrh.) Fr.	1965	Psme
S-273	*Truncocolumella citrina* Zeller (H)	1976	Psme

* Vouchers numbers for most isolates are listed in Molina (1979). (H) signifies a hypogeous fruiting habit.
† Alru, *Alnus rubra* Bong.; Abgr, *Abies grandis* (Dougl.ex D. Don) Lindl.; Abpr, *Abies procera* Rehder; Coav, *Corylus avellana* L.; Eusp, *Eucalyptus* species; Eugl, *Eucalyptus globulus* Labill.; Laoc, *Larix occidentalis* Nutt.; Pisi, *Picea sitchensis* (Bong.) Carr.; Psme, *Pseudotsuga menziesii* (Mirbel) Franco; Pico, *Pinus contorta* Dougl. ex Loud.; Pipo, *Pinus ponderosa* Dougl. ex Laws.; Tshe, *Tsuga heterophylla* (Raf.) Sarg.; Tsme, *Tsuga mertensiana* (Bong.) Carr.

Table 4. *Geographic distribution and taxonomic affinites of* Eucalyptus *species tested for ectomycorrhiza formation in pure culture with selected fungal isolates*

	Geographical* distribution	Taxonomical† affinities (subgenus)
E. calophylla B. Br. ex Lindl	WA	Corymbia
E. camaldulensis Dehnh.	WA NT QLD NSW VIC SA	Symphyomyrtus
E. dalrympleana Maiden.	TAS VIC NSW	Symphyomyrtus
E. diversicolor F. Muell.	WA	Symphyomyrtus
E. maculata Hook.	QLD NSW	Corymbia
E. marginata Donn ex Sm.	WA	Monocalyptus
E. microcorys F. Muell.	QLD NSW	Symphyomyrtus
E. obliqua L'Her.	QLD NSW VIC TAS SA	Monocalyptus
E. regnans F. Muell.	VIC TAS	Monocalyptus
E. sieberi Johns.	NSW VIC TAS	Monocalyptus
E. st.-johnii Bak.	NSW VIC	Symphyomyrtus

* WA, Western Australia; SA, South Australia; VIC, Victoria; TAS, Tasmania; NSW, New South Wales; QLD, Queensland; NT, Northern Territory.
† According to Pryor and Johnson, 1971.

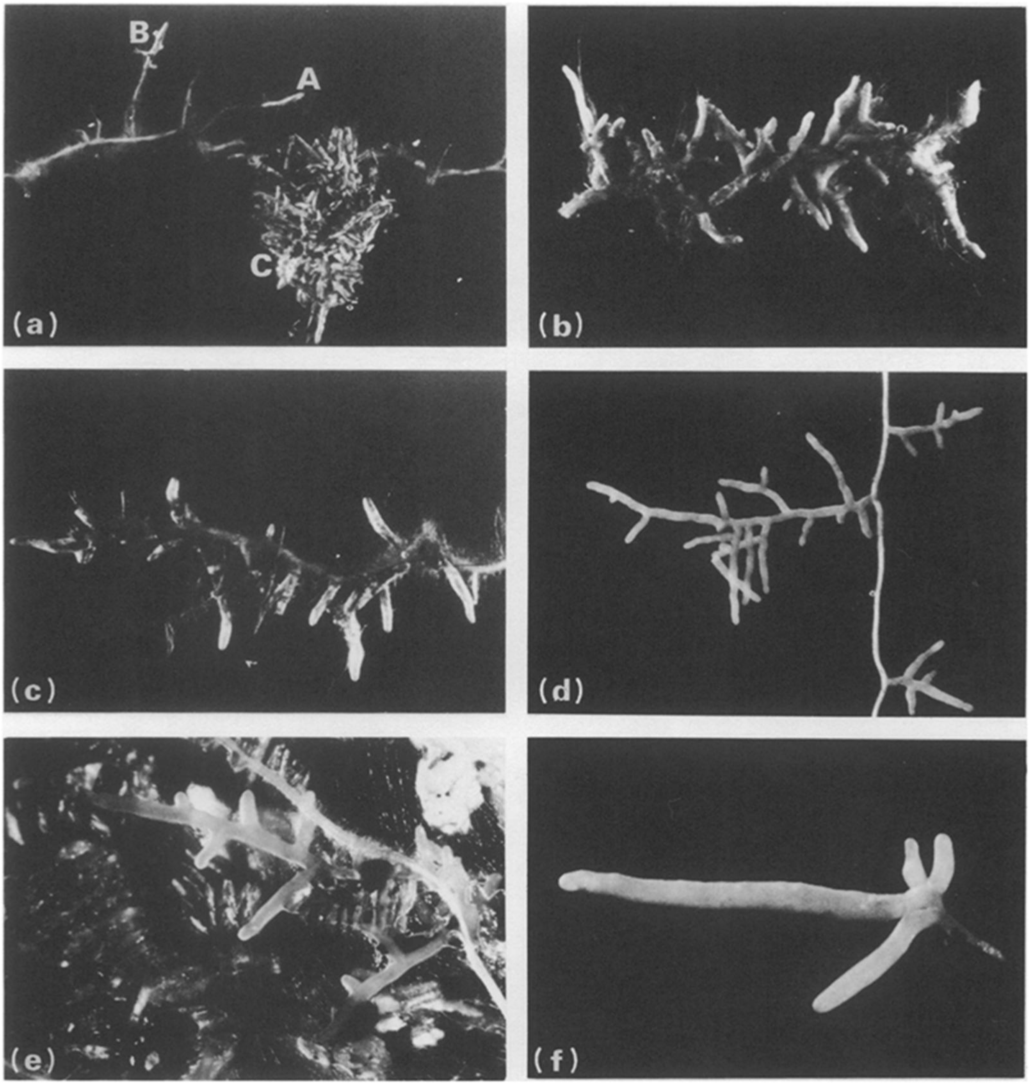

Fig. 1. Synthesized eucalypt ectomycorrhizas. (a) *Eucalyptus maculata* + *Paxillus involutus* showing developmental stages. A, Single tip; B, simple branching; C, multiple branching. ×2·5. (b) *Eucalyptus maculata* + *Astraeus pteridis*. ×5. (c) *Eucalyptus maculata* + *Melanogaster intermedius*. ×5. (d) *Eucalyptus camaldulensis* + *Hydnangium carneum*. ×4. (e) *Eucalyptus sieberi* + *Hydnangium carneum*. ×5·5. (f) *Eucalyptus obliqua* + *Hymenogaster albellus*. ×7·5.

tested except *E. marginata*, which formed no ectomycorrhizas with *H. albellus* and only weak colonization with *H. carneum* (Table 5).

The ecualypt ectomycorrhizas illustrated in Figures 1 and 2(a) represent a range of morphological characteristics. Figure 1(a) shows the sequential development of ectomycorrhizas initiated by *P. involutus*, from simple sheathing of a short root (A) to complex branching (C). A similar pattern resulted with *Amanita muscaria* [Fig. 2(a)]. *Astraeus pteridis* , *Cenococcum geophilum* and *Melanogaster intermedius*

Table 5. *Ectomycorrhiza formation by* Eucalyptus *and* Pinus radiata *with selected ectomycorrhizal fungi in pure culture synthesis**

Fungi	Hosts†											
	Pira	Eumar	Eumac	Eucam	Eusi	Euob	Eust	Eucal	Eumi	Eure	Eudi	Euda
Alpova diplophloeus	−	−	−	−	−	−	−	−	−	−	−	−
Amanita muscaria	+++	+	+	+	+	+	+	+	+	+++	+	+
Astraeus pteridis	+++	+	+++	+++	+	+	++	+	+	+++	+++	+++
Boletus edulis	++	−	−	−	−	−	−	−	−	−	−	−
Cenococcum geophilum	+	+	+	+	+	+	+	+	+	+	+	+
Hebloma crustuliniforme	+++	+	++	+++	+	++	+++	NS	+	+++	+++	+++
Hydnangium carneum	−	+	++	+++	+	+	+	+	++	++	+	++
Hymenogaster albellus	−	−	NS	+++	+++	NS	NS	NS	NS	NS	NS	NS
Laccaria laccata	++	+	+	+	+	+	++	+	++	++	+	++
Lactarius deliciosus	+	−	−	−	−	−	−	−	−	−	−	−
Melanogaster intermedius	+++	+	+++	−	−	+	+	+	−	+++	+	++
Paxillus involutus	+++	+	+++	++	+	NS	+	+	+	+++	+++	+
Pisolithus tinctorius	+	++	++	+	+	+	+	+	+	++	++	+
Rhizopogon occidentalis	+	−	−	−	−	−	−	−	−	−	−	−
R. vinicolor	+	−	−	NS	−	−	−	−	−	−	−	−
R. vulgaris	++	−	−	−	−	−	−	−	−	−	−	−
Scleroderma laeve	+	+	+	+	+	+	+	+	++	+	+	+
Suillus brevipes	+++	−	−	−	−	−	−	−	−	−	−	−
S. grevillei	+	−	−	−	−	−	−	−	−	−	−	NS
S. lakei	+++	−	−	−	−	−	−	−	−	−	−	−
S. tomentosus	+	−	−	−	−	−	−	−	−	−	−	−
Thelephora terrestris	+++	−	−	−	NS	−	−	−	−	−	−	−
Truncocolumella citrina	+++	−	−	−	−	−	−	−	−	−	−	−

* Mycorrhizal intensity: +++, 70–100% short roots colonized; ++, 30–69% short roots colonized; +, 1–29% short roots colonized; −, no mycorrhizal formation; NS, no synthesis.

† Host abbreviations: Pira, *Pinus radiata*; Eumar, *Eucalyptus marginata*; Eumac, *E. maculata*; Eucam, *E. camaldulensis*; Eusi, *E. sieberi*; Euob, *E. obliqua*; Eust, *E. st.-johnii*; Eucal, *E. calophylla*; Eumi, *E. microcorys*; Eure, *E. regnans*; Eudi, *E. diversicolor*; Euda, *E. dalrympleana*.

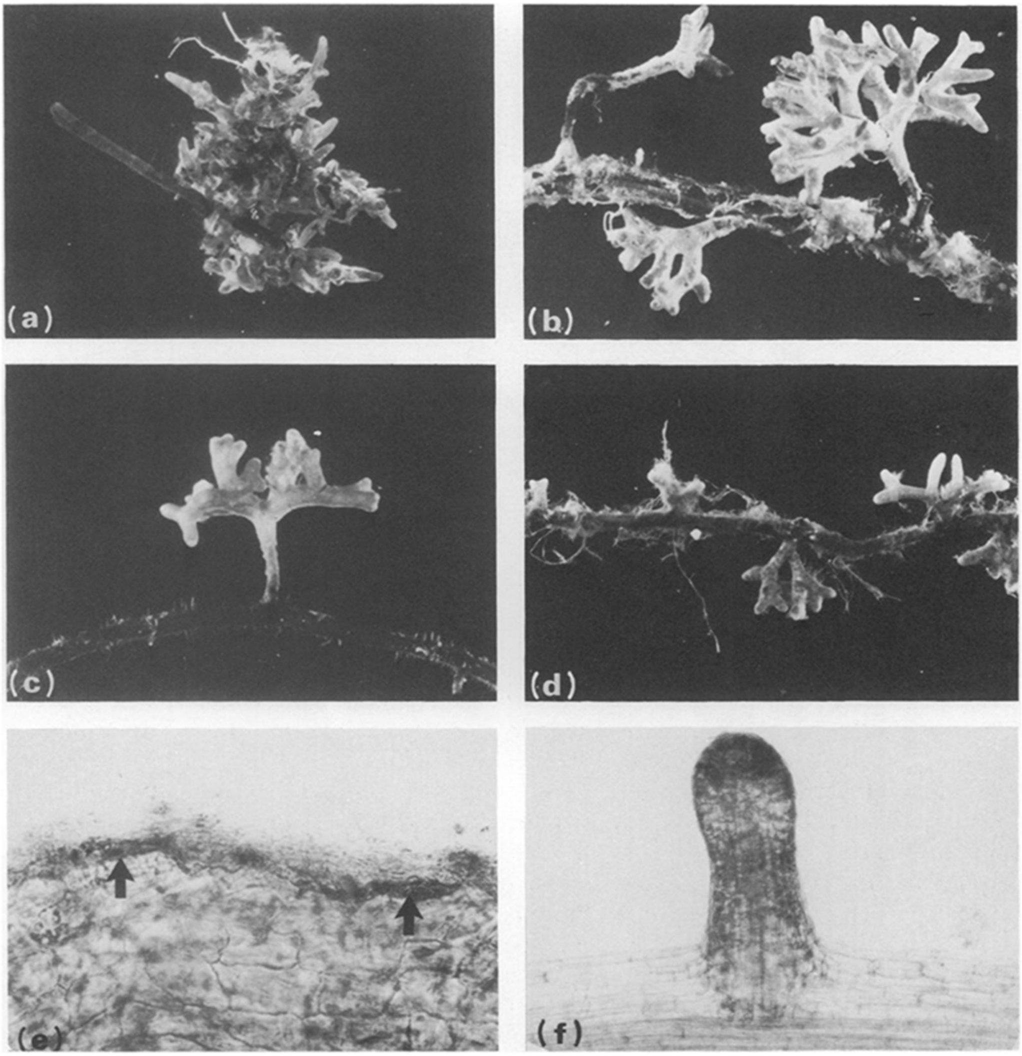

Fig. 2. (a) Synthesized eucalypt ectomycorrhiza, *Eucalyptus diversicolor* + *Amanita muscaria*. × 5. (b) to (d) Synthesized *Pinus radiata* ectomycorrhizas. (b) *P. radiata* + *Amanita muscara*. × 6. (c) *P. radiata* + *Boletus edulis*. × 5. (d) *P. radiata* + *Suillus brevipes*. × 5. (e) Probable phenolic deposits beneath the fungal mantle (arrowed) in ectomycorrhizas of *Eucalyptus marginata* formed with *Pisolithus tinctorius*. × 100. (f) Intense probable phenolic deposits in epidermal and cortical cells of short roots of *Eucalyptus camaldulensis* when grown together with an incompatible ectomycorrhizal fungus, *Suillus brevipes*. × 25.

ectomycorrhizas of eucalypts were invariably unbranched; lateral roots were often encased with a fungal mantle [Fig. 1(b) and (c)]. *Hydnangium carneum* and *Hymenogaster albellus* mycorrhizas were pinnately branched, smooth and hyaline [Fig. 1(d), (e) and (f)].

No isolates reported as conifer-specific formed ectomycorrhizas on the eucalypts. Most eucalypts reacted to isolates of *Rhizopogon* and *Suillus* spp. with a darkening of epidermal and cortical cells of short roots [Fig. 2(f)] probably due to an accumulation of phenolic compounds. *E. marginata* seedlings reacted more intensely than other species, in that first order laterals also darkened, even in the stele, and seedlings died within 2 months. No reaction in eucalypt roots was observed, however, to the other incompatible fungi *Thelephora terrestris*, *Boletus edulis* and *Lactarius deliciosus*, or to the *Alnus*-specific symbiont *Alpova diploploeus*. Eucalypt ectomycorrhizas initiated by *Pisolithus tinctorius*, *Melanogaster intermedius* and *Astraeus pteridis* also had dark depositions in and/or above epidermal cells which were in contact with the fungal mantle [Fig. 2(e)].

All the conifer-specific and broad-host-ranging fungi formed ectomycorrhizas with *P. radiata*. Typical bifurcated ectomycorrhizas are shown in Fig. 2(b), (c) and (d), including simple branching with *Rhizopogon* and *Suillus* spp. and complex branching with *A. muscaria* and *B. edulis*. The *Alnus*-specific fungus, *Alpova diplophloeus*, and the *Eucalyptus* isolates, *Hydnangium carneum* and *Hymenogaster albellus*, did not initiate ectomycorrhiza formation. Pine reacted to its incompatible fungi as did the eucalypts, with darkening of cortical and epidermal cells.

Discussion

All eucalypts, irrespective of geographic distribution or taxonomic affinities, formed ectomycorrhizas in pure culture with a number of broad-host-ranging fungi from the United States; however, no ectomycorrhizas formed with any conifer-specific fungal isolates, e.g. *Suillus*, *Rhizopogon* or *Truncocolumella*. Similarly, the two eucalypt-specific fungal isolates (*Hydnangium carneum* and *Hymenogaster albellus*) did not initiate formation on *P. radiata* or other conifer hosts (Molina, unpublished). This supports the conclusion of Chilvers (1973), that ectomycorrhizal fungi show specificity at the host genus level rather than at the host species level. The fungi that initiated ectomycorrhizas on eucalypts included not only species with a world wide distribution, e.g. *Pisolithus tinctorius*, *Cenococcum geophilum*, *Paxillus involutus* and *Laccaria laccata* (Trappe, 1962, 1964), but also species endemic to the Northern Hemisphere, e.g. *Amanita muscaria*, *Astraeus pteridis* and *Melanogaster intermedius*. In addition, some Douglas-fir and larch isolates unexpectedly formed mycorrhizas with *P. radiata*. Grand (1968) and Molina (1979, 1981) earlier concluded that some fungi can form ectomycorrhizas with a wider range of hosts, at least in pure culture, than predicted from their sporocarp association with specific hosts in the field. Whether such synthesized combinations can form in natural soil remains to be learned.

Hydnangium carneum has been collected in many parts of the world outside the native range of eucalypts. Singer (1962) regards the commonly collected species as *H. soederstroemii*, but variation in individual collections of ours encompasses his concepts of both species, so we regard *H. soederstroemii* as a synonym of *H. carneum*. The most common notation for these collections is 'under eucalypts' or in eucalypt–conifer mixes. Collections for which no associated hosts are noted are usually from botanical gardens or areas where eucalypts have been extensively planted. In light of these collection data and the failure of *H. carneum* to form mycorrhizas with pine in our experiments, we infer that this fungus is native to Australia and has been introduced elsewhere on roots of seedlings of imported Australian hosts. A similar conclusion can be drawn for *Hymenogaster albellus*, although collection data for it are relatively scanty.

Hydnangium carneum is hypogeous; but by all other characters, it is closely related to the genus *Laccaria* (Pegler and Young, 1979). Its colonies in pure culture and the mycorrhizas it forms with eucalypts closely resemble those of *Laccaria laccata*. *L. laccata* is broad-host-ranging, however, whereas *H. carneum* seems to be host-specific to eucalypts (although it remains to be seen whether it can form mycorrhizas with other ectomycorrhizal host genera native of Australia). Comparisons of the physiology of these phylogenetically related fungi and their interactions with hosts and non-hosts could reveal much about the physiological nature of ectomycorrhizal host-specificity.

That *Eucalyptus* spp. and *P. radiata* both became mycorrhizal with several broad-host-ranging fungi, yet were unable to form mycorrhizas with fungi host specific to each other, indicates that a variety of recognition phenomena may be determining compatibility or incompatibility between these symbionts. Such recognition phenomena have been demonstrated for legume–*Rhizobium* symbioses (Bohlool and Schmidt, 1974; Schmidt, 1979), but we are unaware of such information for ectomycorrhizal hosts and fungi. Molina (1981) presented evidence for a response mechanism by *Alnus* to ineffective ectomycorrhiza formation by *Paxillus involutus*. In this case, epidermal and cortical cells in immediate contact with the mantling mycelium accumulate polyphenolic compounds. Since phenolic compounds are associated with host reactions to pathogen invasion (Kosuge, 1969), he speculated that this reaction may be indicative of incompatibility. An examination of short roots of the *Eucalyptus* species inoculated with incompatible ectomycorrhizal fungi (i.e. conifer-specific symbionts) showed intense accumulations of probable phenolic compounds in the epidermal and cortical cells Fig. 2(f)], even without fungal mantling of short roots. Ling-Lee *et al.* (1977) have described the presence of various phenolic compounds in both mycorrhizal and non-mycorrhizal roots of *Eucalyptus fastigiata* Deane and Maiden and suggested that accumulation of phenols in the epidermal cells of mycorrhizas is a response to the presence of the fungal symbiont. Our observations support this suggestion but further indicate that phenolic production by the host may differ depending on the colonizing fungus, particularly between compatible and incompatible ectomycorrhizal fungi. Perhaps this accumulation in non-compatible host-plant/fungus relationships represents a form of hypersensitive reaction typical of incompatible host-root/pathogen reactions (Deverall, 1977). Clearly further research is needed on how host phenolics may influence ectomycorrhiza formation, as well as host–fungus specificity and compatibility.

The success of eucalypts and *P. radiata* in establishment of exotic plantations and as invaders of indigenous communities (Bowen, 1963; Burdon and Chilvers, 1977; Lamb, 1979) can be attributed in part to their compatibility with broad host-ranging fungi. Successful, long-term development of exotic plantations of these hosts, however, is generally accompanied by appearance of host-specific fungi. We suggest that in native stands of eucalypts and *P. radiata* a natural succession of mycorrhizal fungi occurs as stands mature, and that this succession tends over time from broad-host-ranging fungi towards dominance by host-specific fungi. In plantations of ectomycorrhizal exotics, this succession is qualitatively and perhaps quantitively restricted by the depauperate mycoflora of host-specific fungi originally introduced with planting stock. If this hypothesis is correct, its implications to problems in exotic plantations, e.g. second rotation decline, urgently need to be explored.

These results have ecological implications in reforestation and plant succession. That both eucalypts and *P. radiata* form ectomycorrhizas both with broad-host-ranging and host-specific fungi helps explain their success as exotics and as invaders of indigenous communities (Bowen, 1963; Burdon and Chilvers, 1977; Lamb, 1979). Field observations of fungal fruiting (Tables 1 and 2), however, suggest that successful, long-term development of exotic stands of these hosts is largely related to appearance of host-specific ectomycorrhizal fungi rather than broad-host-ranging fungi. Because effort in selecting the 'right' fungi for eucalypt plantings in the Northern Hemisphere and *P. radiata* in the Southern Hemisphere has been minimal, further research is urgently needed on optimal fungus–host combinations if maximum gains are to be achieved from current forestation programmes with exotics.

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