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Dark septate endophytes: a review of facultative biotrophic root-colonizing fungi

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SUMMARY

Dark septate root endophytes (DSE) are conidial or sterile fungi (Deuteromycotina, Fungi Imperfecti) likely to be ascomycetous and colonizing plant roots. They have been reported for nearly 600 plant species representing about 320 genera and 100 families. DSE fungi occur from the tropics to arctic and alpine habitats and comprise a heterogeneous group that functionally and ecologically overlaps with soil fungi, saprotrophic rhizoplane-inhabiting fungi, obligately and facultatively pathogenic fungi and mycorrhizal fungi. Numerous species of undescribed sterile and anamorphic taxa may also await discovery. Although DSE are abundant in washed root and soil samples from various habitats, and are easily isolated from surface-sterilized roots of ecto-, ectendo-, endo- and non-mycorrhizal host species, their ecological functions are little understood. Studies of DSE thus far have yielded inconsistent results and only poorly illustrate the role of DSE in their natural habitats. These inconsistencies are largely due to the uncertain taxonomic affinities of the strains of DSE used. In addition, because different strains of a single anamorph taxon seem to vary greatly in function, no clear generalizations on their ecological role have been drawn. This paper reviews the current literature on DSE and the ecology and discusses the need for and direction of future research.

Key words: Dark septate endophytes, deuteromycetes, ecology, fungi, mycorrhizas, root endophytes.

INTRODUCTION

Fungi have a variety of symbiotic interactions with plant roots, ranging from antagonism to mutualism. Fungal colonizations that do not fit the identified categories of mutualistic or pathogenic symbiosis have been referred to in a variety of ways (Table 1). Some researchers (Lewis, 1973; Smith & Smith, 1990) have approached the problem from a more functional point of view by characterizing root–fungus interactions based on uni- or bidirectional flow of resources (nutrients, carbohydrates, etc.).

Because a fungus and its hosts may have associations that occupy different positions on the 'mutualism–parasitism continuum', depending on environmental conditions (Johnson, Graham & Smith, 1997), the associations may not always be clearly defined. This is predictable when fungi of unknown identity produce structures of unknown function when colonizing host roots. Nevertheless, it is essential to acknowledge the potentially important ecological role of these associations, however poorly known they might currently be.

The objective of this paper is to review the literature of miscellaneous, root-associated, dark septate endophytic (DSE) fungi. Despite several studies addressing various aspects of DSE and their associations with colonized hosts, very little is known of their taxonomic affinity, host range and ecology. In this context, we refer to endophytic fungi in a broad sense: they colonize living plant organs without causing any apparent, overt negative effects (Hirsch & Braun, 1992). In a taxonomical sense, we attempt to include those conidial or sterile fungi (Deuteromycotina, Fungi Imperfecti) that frequently colonize living plant roots and are likely to be ascomycetous. Because very little is known what comprises *Mycelium radicis atrovirens* (MRA; Melin, 1922, 1923), we include those MRA that seem to fulfil these requirements, all hereafter termed DSE. We recognize that an unknown number of fungal taxa (anamorphic and/or teleomorphic) are involved, and that a considerable functional and ecological overlap might exist between soil fungi, saprotrophic rhizoplane-inhabiting fungi, strictly pathogenic fungi, mycorrhizal fungi and fungal endophytes. Because Richard & Fortin (1974) reviewed the

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Table 1. *Terms that have been used to describe fungal colonization that do not fit the identified categories of mutualistic or pathogenic symbiosis*

Term for fungal colonization	Reference
Casual mycorrhizal	Burges (1936)
Endophytic	Currah *et al.* (1987); Stoyke & Currah (1991); Stoyke *et al.* (1992); Väre *et al.* (1992)
Pseudomycorrhizal	Melin (1923); Thomas (1943); Robertson (1954); Kowalski (1970; 1973); Wang & Wilcox (1985); Wilcox & Wang (1987*a*)
Weakly pathogenic	Wang & Wilcox (1985); Egger & Paden (1986*a*); Wilcox & Wang (1987*a*)
Dark septate	Haselwandter & Read (1982); Haselwandter (1987); Cázares (1992); Väre *et al.* (1992)
Rhizoctonia-like	Peyronel (1924); Haselwandter & Read (1980)
Septate endophytes	O'Dell *et al.* (1993)

literature on MRA, we only cover briefly the earlier work, and emphasize what has been published since.

EARLY OBSERVATIONS ON DSE

In his initiating work, Frank (1885) referred to ectomycorrhizas of trees. Gallaud (1905) first reported another type of root colonization by septate endophytes on *Allium sphaerocephalum* L. and *Ruscus aculeatus* L. Peyronel (1922) observed similar fungal structures on the roots of *Triticum aestivum* L. He subsequently noted another type of root colonization, later termed 'endomycorrhizas' (Peyronel, 1922, 1923). While isolating ectomycorrhizal fungi and aseptically resynthesizing mycorrhizas, Melin (1922, 1923) isolated brown, or blackish, 'pseudomycorrhizal' fungi. He called these sterile, root-associated fungi *Mycelium radicis atrovirens* (MRA) and *Rhizoctonia sylvestris*. Neither formed ectomycorrhizas; *R. sylvestris* produced sclerotia on the root surfaces, whereas MRA produced them intracellularly. No taxonomic affinity for these 'pseudomycorrhizal' fungi was suggested at that time. MRA has since been applied to any sterile, dark and septate fungi isolated from roots or soil.

Peyronel documented colonization by pigmented root endophytes on 135 species of angiosperms (Peyronel, 1924). He referred to the observed structures as '*Rhizoctonia*-like', but was convinced that more than one fungal taxon – not necessarily *Rhizoctonia* spp. – was involved in these root colonizations (Peyronel, 1924). He described the root colonization as simple, branched hyphae that occasionally produced short, branched, clavate, barrel-shaped segments similar to chlamydospores of *Oidium* or *Monilia*. Within the cortical cells of the host root, the hyphae aggregated into groups of thick-walled stromatic nodules (Peyronel, 1924).

Melin (1925 and references therein) reported similar structures in several members of Pinaceae referring to them as 'pseudomycorrhizas'. He concluded that the 'pseudomycorrhizas' represented a parasitic rather than mutualistic behaviour (Melin, 1924). He insisted on the term 'pseudomycorrhiza' because the colonization could be observed under conditions where ectomycorrhizal associations did not develop at all.

Melin might not have realized, however, that DSE coexist with mycorrhizal fungi. Endophytic and ectomycorrhizal fungi colonize roots concurrently (Hatch, 1934; Manka & Truszkowska, 1958; Trappe, 1962; Sengupta, Chakraborty & Chaudhuri, 1989; Dhillion, 1994; Horton, Cázares & Bruns, 1998), as can arbuscular and ectomycorrhizal fungi (Blaschke, 1991; Cázares & Trappe, 1993; Dhillion, 1994; Horton *et al.*, 1998). Recording the endophytes may be difficult when the ectomycorrhizas are covered by fungal mantle. Melin (1922, 1923, 1925) reported that host roots were intracellularly colonized and that neither Hartig net nor mantle was present. Morphological studies of colonized roots have since revealed, however, that DSE occasionally develop a partial Hartig net and a thin mantle only a few cell layers thick (O'Dell, Massicotte & Trappe, 1993; Fernando & Currah, 1996).

HOSTS AND GEOGRAPHICAL RANGES

Richard & Fortin (1974) pointed out that DSE fungi are widely distributed in coniferous boreal forests. Morphologically similar root colonizations had also been described elsewhere, e.g. from Australian Liliaceae (Burges, 1936). Colonization resembling DSE has been noted in approx. 600 plant species representing about 320 genera and 114 families (Table 2). These include species and genera usually considered arbuscular, ericoid, orchid and ecto- and non-mycorrhizal. There seems to be no rule governing the species DSE colonize. They have been observed in plant families with quite different life strategies, suggesting little or no host specificity. Table 2 contains observations from habitats ranging from South African coastal plains and lowlands to tropical, temperate, subalpine, alpine, maritime Antarctic, and arctic zones.

Most authors (see http://www.cup.cam.ac.uk/SPECIES_TABLE.html) observed root endophytes with darkly pigmented, septate hyphae that, in most cases, formed intracellular structures similar to those termed microsclerotia by Read & Haselwandter (1981). The sterile dark mycelium seems ubiquitous in soil and root systems; it dominated in studies of fungi from washed soil or root samples from the

Table 2. *Number of plant species within 144 families reported to be colonized by DSE*

The colonized 587 species include any reports of dark, septate hyphae observed in the root systems. For list of species and references, please see http://www.cup.cam.ac.uk/SPECIES_TABLE.html. Nomenclature follows Database of North American Plants (USDA-NRCS) (available at http://www.ars-grin.gov/npgs/tax/index.html) and new provisional Global Plant Checklist (available at http://gbbm3.bgbm.fuberlin.de/IOPI/GPC/query.htm) where applicable.

Plant taxon	No. of reported species
ANGIOSPERMAE	
DICOTYLEDONEAE	
Aceraceae	1
Aizoaceae	4
Anacardiaceae	1
Apocynaceae	2
Asclepiadaceae	1
Avicenniaceae	3
Betulaceae	5
Bignoniaceae	3
Boraginaceae	4
Buddlejaceae	1
Cactaceae	3
Campanulaceae	7
Caprifoliaceae	2
Caryocaraceae	1
Caryophyllaceae	18
Chenopodiaceae	2
Cistaceae	2
Compositae	37
Connaraaceae	1
Convolvulaceae	1
Cornaceae	1
Crassulaceae	15
Cruciferae	14
Empetraceae	1
Ericaceae	25
Euphorbiaceae	1
Fabaceae	1
Fagaceae	1
Geraniaceae	1
Gentianaceae	4
Guttiferaceae	1
Juglandaceae	1
Labiatae	7
Lauraceae	1
Leguminosae-Caesalpiniaceae	11
Leguminosae-Mimosoideae	3
Leguminosae-Papilionoideae	34
Malpighiaceae	1
Melastomataceae	1
Moraceae	2
Myrtaceae	6
Ochnaceae	1
Onagraceae	4
Oleaceae	2
Oxalidaceae	3
Papaveraceae	2
Pedaliaceae	1
Piperaceae	1
Plantaginaceae	3
Plumbaginaceae	1
Polemoniaceae	2
Polygonaceae	7
Portulacaceae	1
Primulaceae	8
Ranunculaceae	18
Rhizophoraceae	2
Rosaceae	20
Rubiaceae	4
Rutaceae	2
Salicaceae	16
Santalaceae	1
Saxifragaceae	16
Scrophulariaceae	18
Solanaceae	6
Sterculiaceae	1
Theaceae	2
Tiliaceae	1
Ulmaceae	1
Umbelliferae	7
Urticaceae	1
Violaceae	6
Vitaceae	1
Zygophyllaceae	1
MONOCOTYLEDONAE	
Alliaceae	3
Aloeaceae	1
Amaryllidaceae	1
Araceae	1
Asparagaceae	1
Asphodelaceae	1
Colchicaceae	1
Colvallariaceae	5
Cyperaceae	15
Graminaceae	59
Haemodoraceae	1
Hyacinthaceae	1
Iridaceae	7
Juncaceae	8
Liliaceae	3
Melanthiaceae	3
Orchidaceae	9
Palmae	2
Ruscaceae	1
Smilacaceae	1
Trilliaceae	1
GYMNOSPERMAE	
Cupressaceae	6
Pinaceae	25
EQUISETOPSIDA	
Equisetaceae	4
LYCOPSIDA	
Lycopodiaceae	4
Selaginellaceae	2
POLYPODIOPSIDA	
Adiantaceae	2
Aspleniaceae	4
Blechenaceae	1
Cyatheaceae	1
Dennstaedtiaceae	1
Dryopteridaceae	3
Hymenophyllaceae	3
Marattiaceae	3
Matoniaceae	1
Ophioglossaceae	2
Polypodiaceae	1
Pteridiceae	1
Schizaeaceae	1
Woodsiaceae	5
PSILOTOPSIDA	
Psilotaceae	1
Total – 144	587

Table 3. *Host species reported to be colonized by the five described anamorphic taxa of DSE*
Reports include notations of DSE isolated from the root systems (natural) or inoculated and shown to colonize a host plant (aseptic/open pot cultures). Nomenclature follows Database of North American Plants (USDA-NRCS) (available at http://www.arsgrin.gov/npgs/tax/index.html) and new provisional Global Plant Checklist (available at http://bgbm3.bgbm.fuberlin.de/IOPI/GPC/query.html) where applicable.

Species of endophyte	Host species	Location	Conditions	Reference
Chloridium paucisporum	*Betula alleghansis*	—	Aseptic	Wilcox & Wang (1987*b*)
	Picea rubens	—	Aseptic	Wilcox & Wang (1987*b*)
	Pinus resinosa	NY, U.S.A.	Natural	Wang & Wilcox (1985)
Leptodontidium orchidicola	*Abies balsamea*	Alberta, Canada	Natural	Fernando & Currah (1996)
	Achillea sp.	Alberta, Canada	Natural	Fernando & Currah (1996)
	Artemisia norvegica	Alberta, Canada	Natural	Fernando & Currah (1995)
	Betula pumila	—	Aseptic	Fernando & Currah (1995)
	Calypso bulbosa	Alberta, Canada	Natural	Currah *et al.* (1988); Currah & Sherburne (1992); Currah *et al.* (1987)
	Carex sp.	Alberta, Canada	Natural	Fernando & Currah (1995)
	Castilleja sp.	Alberta, Canada	Natural	Fernando & Currah (1996)
	Coeloglossum viride	Alberta, Canada	Natural	Currah & Sherburne (1992); Currah *et al.* (1987); Fernando & Currah (1995)
	Corallorhiza maculata	Alberta, Canada	Natural	Currah & Sherburne (1992); Currah *et al.* (1987)
	C. trifida	Alberta, Canada	Natural	Currah *et al.* (1990); Fernando & Currah (1995)
	Dryas octopetala	—	Open pot culture	Fernando & Currah (1996)
	Erigeron sp.	Alberta, Canada	Natural	Fernando & Currah (1996)
	Heracleum lanatum	Alberta, Canada	Natural	Fernando & Currah (1996)
	Listera borealis	Alberta, Canada	Natural	Currah *et al.* (1990)
	Pedicularis bracteosa	Alberta, Canada	Natural	Fernando & Currah (1995)
	Picea glauca	—	Aseptic	Fernando & Currah (1995)
	Piperia unalascensis	Alberta, Canada	Natural	Fernando & Currah (1995)
	Platanthera hyperborea	Alberta, Canada	Natural	Currah & Sherburne (1992); Currah *et al.* (1987); Fernando & Currah (1995)
	Potentilla fruticosa	—	Aseptic/Open pot culture	Fernando & Currah (1995); Fernando & Currah (1996)
	Rubus sp.	Alberta, Canada	Natural	Fernando & Currah (1996)
	Salix glauca	—	Aseptic/Open pot culture	Fernando & Currah (1996)
	Spiranthes lacera	Alberta, Canada	Natural	Fernando & Currah (1995)
	Trollius albiflorus	Alberta, Canada	Natural	Fernando & Currah (1996)
Phialocephala dimorphosphora	sp.	Schwarzwald, Germany	Natural	Courtois (1990)
	Picea mariana	?	Natural	Richard & Fortin (1973, 1974)
	P. rubens	—	Aseptic	Wilcox & Wang (1987*b*)
	Pinus resinosa	—	Aseptic	Wang & Wilcox (1985); Wilcox & Wang (1987*b*)
Phialocephala fortinii	*Abies alba*	Switzerland	Natural	Ahlich & Sieber (1996)
	Alnus rubra	Canada	Natural	Ahlich & Sieber (1996)
	Amerorchis rotundifolia	Alberta, Canada	Natural	Currah *et al.* (1987)
	Andromeda polifolia	Alberta, Canada	Natural	Hambleton & Currah (1997)
	Calluna vulgaris	Switzerland	Natural	Ahlich & Sieber (1996)
	Calypso bulbosa	Alberta, Canada	Natural	Currah *et al.* (1988); Currah *et al.* (1987)
	Cassiope mertensiana	Alberta, Canada	Natural	Currah & Tsuneda (1993); Hambleton & Currah (1997)
	C. tetragona	Alberta, Canada	Natural	Hambleton & Currah (1997)
	Chamaedaphne calyculata	Alberta, Canada	Natural	Hambleton & Currah (1997)
	Dryas octopetala	—	Open pot culture	Fernando & Currah (1996)
	Empetrum nigrum	Alberta, Canada	Natural	Hambleton & Currah (1997)
	Fagus sylvatica	Switzerland	Natural	Ahlich & Sieber (1996)
	Gaultheria humifusa	Canada	Natural	Hambleton & Currah (1997)
	G. shallon	Canada	Natural	Ahlich & Sieber (1996)

Table 3. (*cont.*)

Species of endophyte	Host species	Location	Conditions	Reference
	Kalmia microphylla	British Columbia, Canada	Natural	Currah & Tsuneda (1993)
	K. polifolia	Alberta, Canada	Natural	Hambleton & Currah (1997)
	Loiseleuria procumbers	Alberta, Canada	Natural	Hambleton & Currah (1997)
	Luetkea pectinata	Alberta, Canada	Natural	Currah & Tsuneda (1993)
	Lupinus latifolius	Washington, U.S.A.	Natural	O'Dell *et al.* (1993)
	Menziesia ferruginea	Alberta, Canada	Aseptic, Natural	Hambleton & Currah (1997); Stoyke & Currah (1993)
	Picea abies	Germany; Switzerland; Sweden	Natural	Ahlich & Sieber (1996); Dahlberg *et al.* (1997)
	Pinus contorta	—	Aseptic/Growth Pouch/Open pot culture	Jumpponen *et al.* (1998); O'Dell *et al.* (1993)
	P. resinosa	—	Aseptic	Wilcox & Wang (1987*a*)
	P. sylvestris	Finland; Germany; Switzerland	Natural	Ahlich & Sieber (1996); Wang & Wilcox (1985)
	Potentilla fruticosa	—	Open pot culture	Fernando & Currah (1996)
	Phyllodoce empetriformis	Alberta, Canada	Natural	Hambleton & Currah (1997)
	P. glanduliflora	Alberta, Canada	Natural	Hambleton & Currah (1997)
	Rhododendron albiflorum	Alberta, Canada	Natural	Hambleton & Currah (1997)
	R. brachy-carpum	—	Aseptic	Currah *et al.* (1993)
	R. obtusum	Tottori, Japan	Natural	Currah & Tsuneda (1993)
	Salix glauca	—	Aseptic/Open pot culture	Fernando & Currah (1996)
	Vaccinium membranaceum	Alberta, Canada	Natural	Hambleton & Currah (1997)
	V. myrtilloides	Alberta, Canada	Natural	Hambleton & Currah (1997)
	V. myrtillus	Switzerland	Natural	Ahlich & Sieber (1996)
	V. scoparium	Alberta, Canada	Natural	Hambleton & Currah (1997)
	V. uliginosum	Alberta, Canada	Natural	Hambleton & Currah (1997)
	V. vitis-idaea	Alberta, Canada	Natural	Hambleton & Currah (1997)
Phialophora finlandia	*Betula alleghansis*	—	Aseptic	Wilcox & Wang (1987*a*, *b*)
	Picea rubens	—	Aseptic	Wilcox & Wang (1987*a*, *b*)
	Pinus resinosa	—	Aseptic	Wilcox & Wang (1987*a*, *b*)
	P. sylvestris	Suonenjoki, Finland	Natural	Wang & Wildox (1985)

subantarctic (Heal, Bailey & Latter, 1967), boreal coniferous forests in Canada (Summerbell, 1988, 1989), temperate and boreal forests in Northern and Central Europe (Holdenrieder & Sieber, 1992; Ahlich & Sieber, 1996) and exotic pine plantations in New Zealand (Chu-Chou, 1979; Chu-Chou & Grace, 1982). Courtois (1990) reported *Phialophora dimorphospora* and another unidentified *Phialophora* sp. in addition to several sterile isolates from spruce-roots and 'root-free' soil collected in the Black Forest region in Germany. It is currently unclear whether the isolates from soil indicate omnipresence of saprotrophic dark-pigmented fungi or extra-matrical mycelium of facultative biotrophic DSE extending into the soil from host roots.

Isolating and identifying the asexual fungi is laborious. Few attempts to identify the root endophytes from field samples have been reported (Table 3). However, these and additional reports from inoculation bioassays indicate wide host ranges for some anamorphic species. None of the known fungal endophytes appears to express any host specificity. For example, *P. fortinii* colonizes more than 20 plant species in either natural or experimental conditions (Table 3).

DSE appear to be found wherever they are sought. Their abundance in different habitats and on different hosts is still largely unknown. It is important to bear in mind that the observations of colonized hosts have been incidental to other work and only a few studies have attempted to identify the endophytic taxa. No systematic surveys focusing on DSE have been conducted. *Phialocephala fortinii* is the only taxon allowing inferences about its distribution: it has been observed in eastern and western North America, Europe, and Japan,

suggesting a global distribution (Table 3). As more attention is paid to other fungi in this group, their distribution is likely to prove global as well. The profusion of DSE in soil and roots of host species that belong to various plant families suggests not only a globally ubiquitous presence and lack of host specificity, but also a role of importance in natural ecosystems. The function of DSE – when present in soil or colonizing host roots – is still unknown and conclusions from the previous research are contradictory, as will be discussed below.

Since Melin's (1922–1925) characterization of 'pseudomycorrhizas', studies on conifer roots have yielded additional reports (Rayner & Levisohn, 1941; Levisohn, 1954; Laiho, 1965; Mikola, 1965; Kowalski, 1973). In most of those studies unfortunately, the fungi colonizing the roots remained sterile and unidentified. Consequently, it has been difficult to discern their potential functions and ecological roles. Mikola (1965) addressed the unknown ecological role and the uncertain taxonomic affinity of root-colonizing – yet not necessarily mycorrhizal – fungi, by suggesting the use of 'non-mycorrhizal roots' as a category that would include roots either colonized solely intracellularly or completely free of any fungal colonization. This approach, however, leaves frequently observed fungal colonization of plant roots beyond recognition. Also, it deprives the unknown symbiotic (*sensu* de Bary, 1887) fungi, that do not form any 'typical' mycorrhizal structures (see Harley & Smith, 1983), of appropriate terminology for describing their manifestations in natural ecosystems.

Asexual reproductive structures of DSE were ultimately described by Wang & Wilcox (1985), Currah, Sigler & Hambleton (1987) and Fernando & Currah (1996), enabling identification of some of the root endophytic fungi, as well as experimental inoculations for studies on the comparative morphology of roots colonized by known strains. The morphology of DSE-colonized roots had been reported to resemble ectomycorrhizas (Wilcox & Wang, 1987*b*; O'Dell *et al.* 1993), ectendomycorrhizas (Wilcox & Ganmore-Neumann, 1974; Wang & Wilcox, 1985; Wilcox & Wang, 1987*a*), and pseudomycorrhizas (Wang & Wilcox, 1985). In some cases the structures in the colonized root suggested a pathogenic association (Wang & Wilcox, 1985; Wilcox & Wang, 1987*a*). The variety of root morphologies observed has made it difficult to sort out the fungal endophytes and their effects on hosts. Morphological structures of DSE-colonized roots do not fall clearly into any previously described category of mycorrhizal, parasitic or pathogenic associations. The terms consequently introduced to describe the patterns of this root–fungus association were: 'dark septate' (Read & Haselwandter, 1981) or 'septate' endophytes (O'Dell *et al.*, 1993).

MORPHOLOGY OF ROOTS COLONIZED BY DSE

The pattern of DSE colonization is similar in roots of different plant species that are otherwise mainly considered as arbuscular, ericoid, orchid or ectomycorrhizal (see Peyronel, 1924; Väre, Vestberg & Eurola, 1992; Currah, Tsuneda & Murakami, 1993; O'Dell *et al.*, 1993; Stoyke & Currah, 1993). Plants that do not form mycorrhizas also have similar fungal structures when colonized by DSE (Haselwandter & Read, 1982; Cázares, 1992; Väre *et al.*, 1992). Root colonization by *Phialocephala fortinii* exemplifies DSE colonization and has been described in detail by several authors. Consequently, we briefly summarize the general pattern of *P. fortinii* colonization here. Initial colonization is usually characterized by superficial hyphae (Currah & Van Dyk, 1986; Figs 1, 2) that have also been called 'runner hyphae' (McKeen, 1952; Deacon, 1973). The individual hyphae usually grow along the depressions between adjacent epidermal cells and can colonize the space between cortical cells along the main axis of the root (Currah *et al.*, 1993). 'A loose hyphal network on the root surface' (Stoyke & Currah, 1993) or 'loose wefts of hyphae' (O'Dell *et al.*, 1993) can develop during the superficial colonization. The hyphae eventually penetrate into the outer cortical cells (Stoyke & Currah, 1991; O'Dell *et al.*, 1993; Stoyke & Currah, 1993). Penetration into the root hairs has been observed and might be a way to enter the cortical layer (O'Dell *et al.*, 1993; Fig. 3). Once into the epidermal layer, the hyphae can grow parallel to the main axis of the host root and from cell to cell within the epidermis, usually causing no distortion of the host roots (Currah *et al.*, 1993; O'Dell *et al.*, 1993; Fig. 4). The hyphae pass through adjoining epidermal cell walls by narrow penetration tubes (Currah *et al.*, 1993; Fig. 4), which occasionally arise from inflated, appressorium-like structures (Fig. 4).

During intracellular colonization, endophytes might form clusters of inflated, rounded, thick-walled cells within the cortical cells (Fig. 2) referred to as 'thick pseudoparenchymatic mass' (Melin, 1923; Robertson, 1954), 'sclerotia' (Melin, 1923; Hatch, 1934; Stoyke & Currah, 1991; O'Dell *et al.*, 1993; Stoyke & Currah, 1993; Fernando & Currah, 1995), 'microsclerotia' (Haselwandter & Read, 1980; Read & Haselwandter, 1981; Haselwandter, 1987; Jumpponen, Mattson & Trappe, 1998) or 'sclerotial bodies' (Levisohn, 1954; Wilcox & Wang, 1987*b*). The clusters of fungal cells within root cells have been described as filled with 'closely packed, thick-walled cells' (McKeen, 1952), 'groups of swollen cells' (Deacon, 1973), 'intracellular sclerotia of compact, darkly pigmented and irregularly lobed, thick-walled hyphae' (Stoyke & Currah, 1991), or 'thick-walled, irregularly lobed and compacted cells

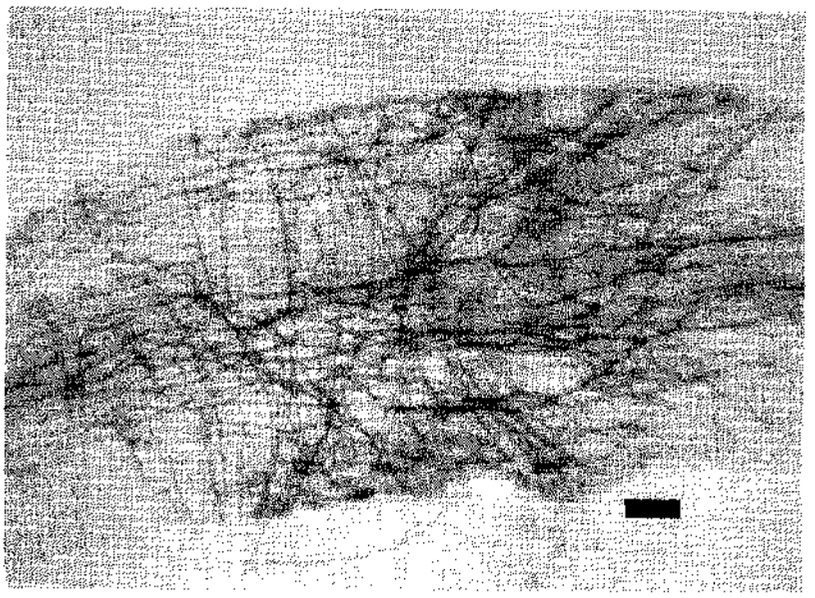

Figure 1. Superficial hyphal net of *Phialocephala fortinii* on lateral roots of *Pinus contorta*. Inoculation experiment conducted in open pot culture using strain isolated by O'Dell *et al.* 1993. Strain currently maintained in the USDA Forest Service PNW Research Station (Cortallis, OR, USA). Bar, 0·1 mm.

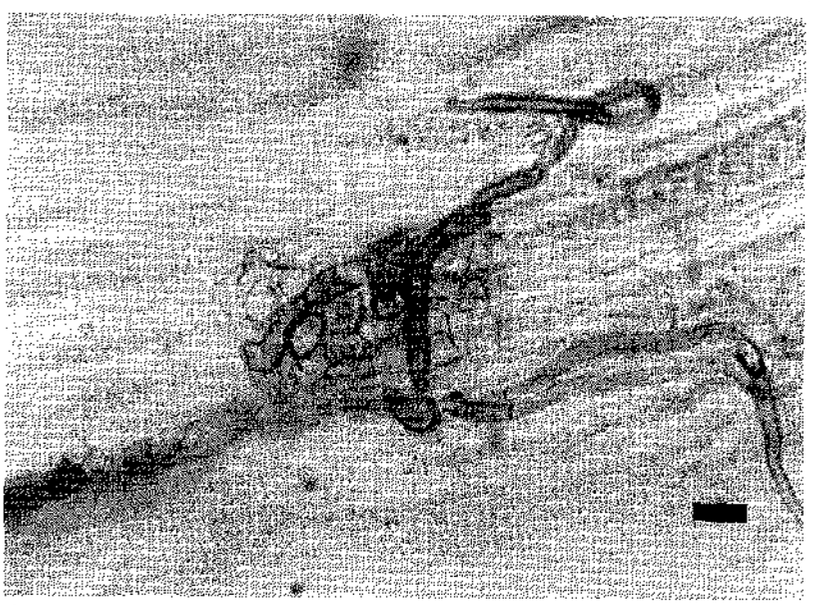

Figure 2. Superficial hyphae of *Phialocephala fortinii* and a cell filled with microsclerotia on roots of *Pinus contorta*. For details, see Fig. 1 legend. Bar, 20 μm.

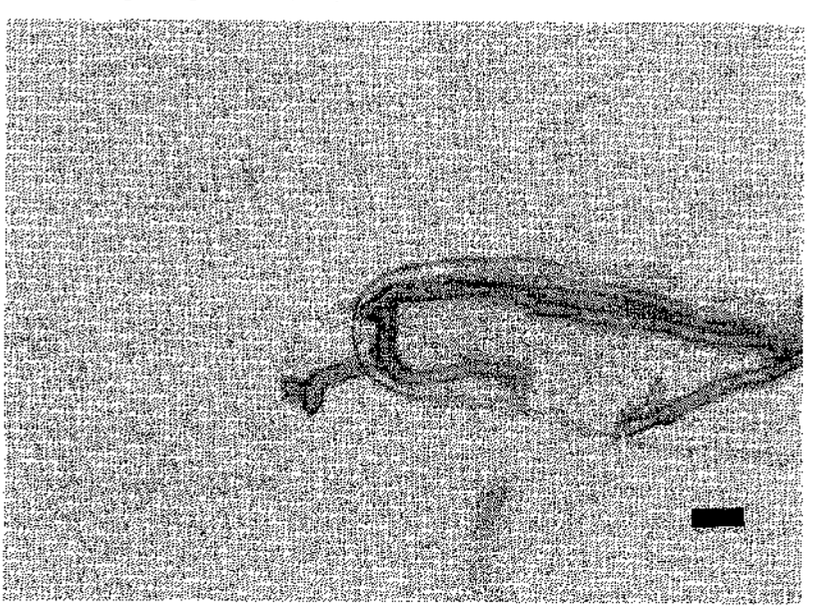

Figure 3. Hyphae of *Phialocephala fortinii* colonizing a root hair of *Pinus contorta*. For details, see Fig. 1 legend. Bar, 25 μm.

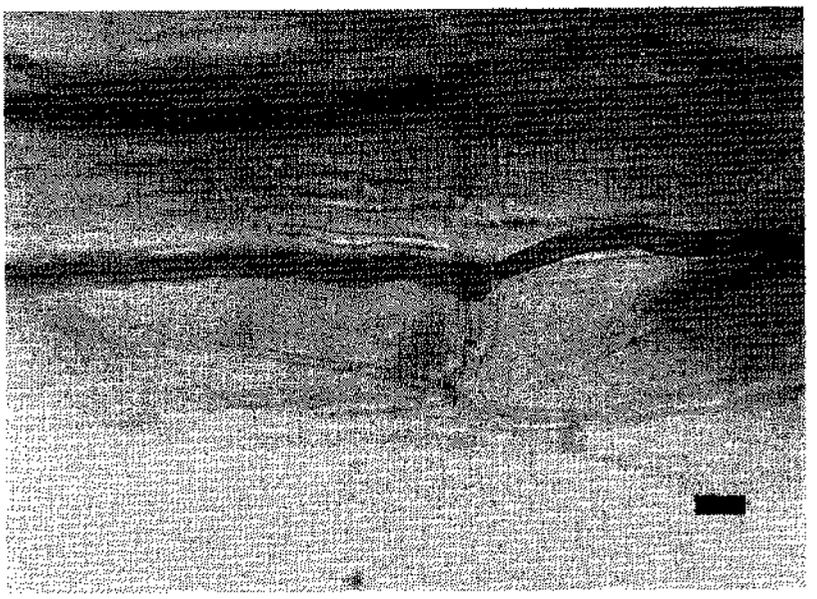

Figure 4. Hyphae of *Phialocephala fortinii* penetrating through the cell wall in the root of *Pinus contorta*. Note the narrow penetration tube and swollen appressorium-like structure. For details, see Fig. 1 legend. Bar, 15 μm.

which sometimes formed sheets several cells thick' (O'Dell *et al.*, 1993).

Occasionally structures resembling ectomycorrhizas can also occur with ectomycorrhizal host plants. O'Dell *et al.* (1993) reported 'labyrinthine tissue (similar to Hartig net tissue)' in roots of *Pinus contorta* when inoculated with *Phialocephala fortinii*. Similarly, Fernando & Currah (1996) reported a Hartig net and a thin, patchy mantle when *Salix glauca* was inoculated with *P. fortinii*. In addition, occasional hyphal coils (Haselwandter & Read, 1980) or peloton-like structures of coiled or looped, branched hyphae within root cells have been reported when DSE colonized ericaceous hosts (Currah *et al.*, 1993). Stoyke & Currah (1991) pointed out that none of their DSE isolates from alpine ericaceous plants displayed dense coiling similar to that frequently observed in ericoid mycorrhizas.

Wilcox & Wang (1987*a*) suggest that the morphology of the colonized root is mainly controlled by the host plant. Morphology might also change with time (Wilcox & Ganmore-Neumann, 1974). Wilcox & Ganmore-Neumann (1974) described the morphology of *Pinus sylvestris* roots inoculated with 'a black imperfect fungus'. While observing inoculated seedlings at 2-month intervals, they reported the structures changing from a combination of intracellular and intercellular invasion to those more typical of ectendomycorrhizas, including a continuous or discontinuous Hartig net and a discontinuous, patchy mantle similar to that observed by O'Dell *et al.* (1993) in an inoculation trial with *Phialocephala fortinii* and *Pinus contorta*.

When describing the colonization by DSE, it is necessary to allow adequate time for the structures to develop. Some basic structures seem constant for DSE colonization regardless of the host species. The presence of sparse superficial mycelium, penetration into the cortical layer and subsequent occasional formation of chlamydospore-like, rounded cells within the cortical cells of the host root seem common to known form-taxa of DSE fungi. *Phialocephala fortinii*, *Phialophora finlandia*, *Leptodontidium orchidicola*, isolates of Pezizales, as well as several unidentified isolates, all developed structures similar to those described above when colonizing a variety of host plants (Wilcox & Ganmore-Neumann, 1974; Read & Haselwandter, 1981; Egger & Paden, 1986*b*; Wilcox & Wang, 1987*a*, *b*; Currah *et al.*, 1993; O'Dell *et al.*, 1993; Stoyke & Currah, 1993; Fernando & Currah, 1995, 1996). More data are needed, however, to validate whether DSE are morphologically or phylogenetically uniform. The current evidence seems not to favour such uniformity, as will be discussed below. A standardized vocabulary, however, is necessary to describe the DSE colonization. For this purpose, we propose the following terms: 'runner hyphae' for the individual, superficial fungal strands following the depressions between epidermal cells; 'superficial net' for the superficial colonization shown on Figure 1; 'appressorium' for the swollen structure preceding penetration through a host cell wall (Fig. 4): 'penetration tube' for the thin structure penetrating through the cell wall (Fig. 4); 'microsclerotia' for the intracellular groups of rounded, thick-walled cells (Fig. 2).

TAXONOMIC AFFINITIES OF DSE

Only a few taxonomic affinities of DSE have been recognized. Most are classified within deuteromycetes and their relation to teleomorphic taxa is unknown. Some DSE are fairly easy to isolate and maintain in pure culture. Conidiogenesis and sporulation of the cultures is usually necessary for identification (but see Jumpponen & Trappe, 1996;

Table 4. *The sampled taxa and their GenBank accession numbers in the neighbour-joining analyses (Fig. 5)*

Taxon	GenBank accession. number
Pleoporales	
Herpotrichia diffusa	U42484
Herpotrichia juniperi	U42483
Leptosphaeria doliolum	U04205
Ophiobolus herpotrichus	U43453
Pleospora herbarum	U43458
Microascales	
Microascus trigonosporus	L36987
Xylariales	
Xylaria hypoxylon	U20378
Pezizales	
Morchella esculenta	U42642
Morchella elata	U42641
Verpa bohemica	U42645
Dothideales	
Botryosphaeria ribis	U42477
Dothidea insculpta	U42474
Leotiales	
Cudonia confusa	Z30240
Monilinia laxa	Y14210
Sclerotinia sclerotiorum	L37541
Spathularia flavida	Z30239
Chaetothyriales	
Capronia pilosella	U42473
Elaphomycetales	
Elaphomyces maculatus	U45440
Eurotiales	
Talaromyces bacillisporus	D14409
Onygenales	
Blastomyces dermatitidis	M63096
Saccharomycetales	
Debaryomyces castellii	X83819
Debaryomyces hansenii	X62649
Saccharomyces rosinii	X99524
Neolectales	
Neolecta vitellina	Z27393
Taphrinales	
Taphrina deformans	U20376
Mitosporic taxa	
Alternaria alternata	U05194
Aspergillus parasiticus	D63699
Coccidiodes immitis	M55627
Cochliobolus heterostrobus	L36994
Exophiala mansonii	U20382
Leptodontidium orchidicola[a]	AF056374
Leptodontidium quercuum	AF056375
Phialocephala fortinii	L76626
Phialocephala fortinii[b]	AF055885
Phialophora finlandia	L76625
Phialophora finlandia[c]	AF056373
Phialophora verrucosa	L36999
Nonsporulating cultures	
Unknown 1[d]	AF056369
Unknown 2[e]	AF056370
Unknown 3[f]	AF056371
Unknown 4[g]	AF056372

[a] Strain UAMH8151, isolated from *Artemisia norvegica*, courtesy of Lynne Sigler and Randy Currah (Fernando & Currah, 1995).

[b] Strain SE24, isolated from *Lupinus latifolius* (O'Dell *et al.*, 1993)

[c] Strain UAMH8322, isolated from *Pinus strobus* mycorrhizas, courtesy of Lynne Sigler and Randy Currah.

[d] Strain stthb, isolated from *Stipa thurbeniana*, courtesy of Marcia Wicklow.

[e] Strain WB12, isolated from *Betula papyrifera*, courtesy of Kathleen Ann Johnson.

[f] Strain cc3, isolated from *Carex* sp., courtesy of Kurt Haselwandter (Haselwandter & Read, 1982).

[g] Strain A12b2, isolated from *Alnus* sp.

Hambleton & Currah, 1997). Conidiogenesis typically is infrequent and some strains sporulate only after extended incubation in low temperatures (Richard & Fortin, 1973; Wang & Wilcox, 1985; Fernando & Currah, 1995; Ahlich & Sieber, 1996). Usually, conidiogenesis can only be induced in a few isolates; most remain sterile and unidentifiable (see Stoyke, Egger & Currah, 1992; Ahlich & Sieber, 1996).

The identity and number of fungal (anamorphic or teleomorphic) species included in DSE are uncertain. The isolates typically do not sporulate or, when they do, produce only scanty conidia. The difficulty of identifying the root endophytes led researchers to use various names to describe similar root-fungus associations. For example, Peyronel (1924) called such colonization that he observed on 135 taxa of angiosperms 'Rhizoctonia-like'. Several researchers have referred to isolates of sterile non-Rhizoctonia fungi from orchids as 'Rhacodium spp.' (Harvais & Hadley, 1967; Harvais, 1974) or given them names within *Rhizoctonia* (e.g. Curtis, 1939). The true taxonomic affinity of these fungi is obviously uncertain.

Despite Melin's (1923) accurate description of his sterile isolates, it was the 1960s before any taxonomic identities of root or soil associated fungi in the MRA complex were suggested. Gams (1963) identified two cultures of MRA isolated from soil as *Phialocephala dimorphospora* Kendrick. Richard & Fortin (1973) were able to identify 15 of the 41 strains of MRA they isolated from roots of various woody plants in central and northern Europe as *P. dimorphospora*. *P. dimorphospora* commonly appears to be associated with decaying wood, soil and pseudomycorrhizas or ectomycorrhizas (Kendrick, 1961; Gams, 1963; Richard & Fortin, 1973). Richard & Fortin (1973), however, were somewhat uncertain of the accuracy of their identification: 'the conidiophores of *P. dimorphospora* isolates were generally darker and the collarette more conspicuous'. Still, they felt that their sporulating isolates were, indeed, *P. dimorphospora*. When studying Richard & Fortin's cultures, Wang & Wilcox (1985) pointed out a possibility of misidentification in the previous work and concluded that at least some of the *P. dimorphospora* isolates might actually have been one of the later described anamorphic species, *Phialocephala fortinii*.

Additional anamorphic species from the MRA

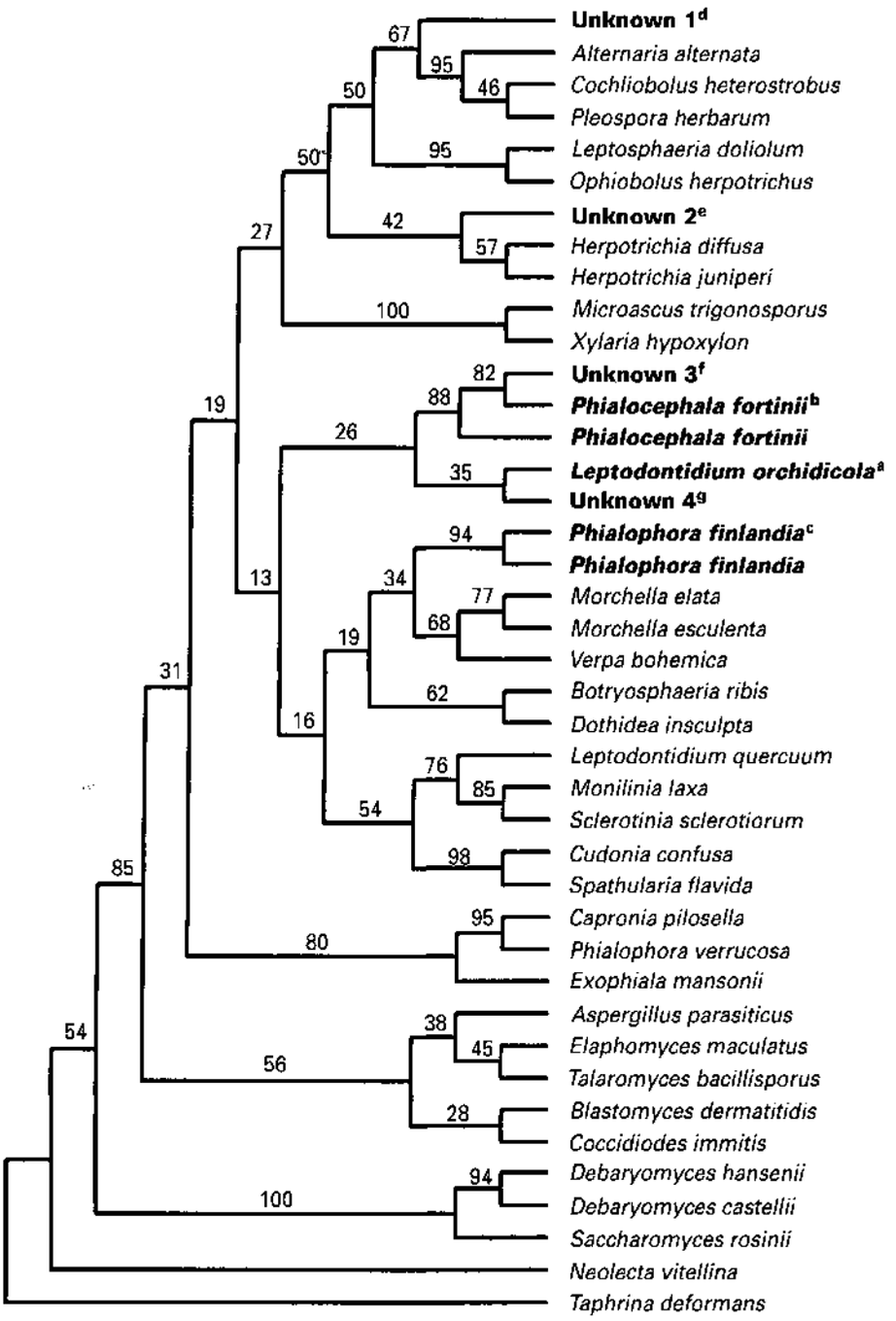

Figure 5. A 50% majority rule consensus of 1000 bootstrapped neighbour-joining trees (PAUP*, with permission from David Swefford) based on partial sequences of small subunit of the ribosomal rRNA gene aligned at 586 positions. Taxas shown in bold colonized *Pinus contorta* intracellularly in aseptic synthesis. Numbers above branches indicate bootstrap values. Accession numbers of the sampled taxa are shown in Table 4. Footnotes as in Table 4.

complex were described: *Phialocephala fortinii*, *Phialophora finlandia*, *Chloridium paucisporum* (*Want & Wilcox*, 1985) *and Leptodontidium orchidicola* (Currah *et al.*, 1987). We decided to exclude *Phialophora radicicola* Cain (Cain, 1952) from this discussion. It is thought to be a non-pathogenic (or parasitic) fungus that colonizes roots of grasses and cereals possessing characteristics typical of the DSE colonization (see Deacon, 1973), but observations are sparse and usually from agricultural fields. The above four species have all been isolated, identified and reported from various hosts and habitats (Table 3).

Establishing connections between DSE and sexually reproducing taxa, i.e., anamorph–teleomorph relationships, would be helpful for inferring the possible systematic and functional relationships between genera, species and strains of DSE. Currently the terms MRA and DSE, as employed by many investigators, represent a heterogeneous mix of strains of form taxa. Many DSE are likely ascomycetous. Our preliminary analysis of the small subunit of the nuclear ribosomal RNA gene (18S) clearly placed all the included DSE within ascomycetes (Fig. 5). Similarly, an analysis by Lobuglio, Berbee & Taylor (1996) showed clear

ascomycetous affinity for *Phialocephala fortinii* and *Phialophora finlandia*. Currah & Sherburne (1992) concluded that *Leptodontidium orchidicola* has a likely ascomycetous affinity, as judged by the septal ultrastructure.

The placement of DSE within ascomycetes is still an open question. Their placement is poorly resolved and appears polyphyletic; two of the DSE isolates that remained sterile were placed within Pleosporales, whereas others were placed close to Pezizales (operculate discomycetes) or Leotiales (inoperculate discomycetes) (Fig. 5). The 18S data by Lobuglio *et al.* (1996) positioned *Phialocephala fortinii* close to Leotiales. Currah *et al.* (1993) reported small aggregations of apothecium-like structures on the surface of the substrate in cultures in which colonization brachycarpum was inoculated with *Phialocephala fortinii*. Even though these ascomata remained sterile and never matured, the observed characteristics also suggest an affiliation with inoperculate discomycetes. *Phialophora finlandia*, however, was placed either with Leotiales or Pezizales (LoBuglio *et al.*, 1996). In our analysis, *P. finlandia* appeared more closely affiliated with Pezizales (Fig. 5). Another line of evidence also suggests that some of the DSE may be related to the Pezizales. Several species within the Pezizales have been shown to colonize roots of woody plants (Danielson, 1984; Egger & Paden, 1986*a*, *b*). Some of these, such as *Sphaerosporella brunnea*, may be ecto- or ectendomycorrhizal (Danielson, 1984; Egger & Paden, 1986*b*). Others, e.g. *Geopyxis carbonaria* and *Trichophaea hemisphaerioides*, formed patchy, discontinuous mantles and extensively colonized epidermal and cortical cells (Egger & Paden, 1986*b*), resembling structures described by O'Dell *et al.* (1993) in the roots of *Pinus contorta* colonized by *Phialocephala fortinii*. Most other species studied by Egger & Paden (1986*a*, *b*), however, were clearly pathogens on their test plant, *Pinus contorta*.

Sequencing and cladistic analyses will doubtless be powerful in identifying DSE. Genetic markers and their applications have been shown to be useful in identifying taxa and strains of DSE (Stoyke *et al.*, 1992; Yan, Rogers & Wang, 1995; Jumpponen & Trappe, 1996). They can in part replace the time-consuming morphological identification. Moreover, they can be used for studying the phylogenetic relationships among the form taxa (e.g. Yan *et al.*, 1995). For example, RFLP data of the ribosomal RNA gene indicates that *P. fortinii* and similar isolates vary substantially (Stoyke *et al.*, 1992; Harney, Rogers & Wang, 1997), suggesting taxa previously identified on the basis of morphological characteristics are heterogeneous. Similarly, Yan *et al.* (1995) found disagreement between morphological and molecular identification of *Phialophora* sp.

It is not surprising that the ecology of DSE is poorly understood, given that several taxa of ascomycetes from different families and even orders are involved. As Allen & Allen (1992, p. 465) explained: 'Unfortunately, few field data exist which allow definitive statements regarding the importance of different fungi on plant communities. In part this is due to frequent inability to recognize the vegetative state of fungi associated with plants in the field.' Description and identification of new taxa of DSE establish a starting point for a better understanding of their interactions with hosts (see Kendrick, 1961; Wang & Wilcox, 1985; Currah *et al.*, 1987, Fernando & Currah, 1995). Molecular and morphological systematic studies of DSE fungi (Kendrick, 1961; Wingfield, van Wyke & Wingfield, 1987; Currah & Tsuneda, 1993; Fernando & Currah, 1995) and re-evaluation of the taxa will open avenues for separating fungi with different ecological functions by accommodating morphologically or genetically distinct groups.

EFFECTS OF DSE ON THEIR HOSTS

Melin (1922) first described 'pseudomycorrhizas' and MRA, differentiating the structures 'harmful to seedlings and trees' from 'ectotrophic mycorrhiza which is a necessary condition for their normal development'. He reported that, after forming thin mycorrhizas, the MRA overgrew and killed the host plant, appearing as parasites (Melin, 1923). Robertson (1954) and Hatch & Hatch (1933) confirmed these results in their pure culture syntheses. However, because of the presence of dark mycelium on the surfaces of 'healthy elongating' roots of pines in the field samples, Robertson (1954) concluded that these fungi attack roots only under special physiological conditions, such as during senescence, and that they are not pathogenic 'to healthy roots in natural soils'.

The early observations indicating that MRA strains can be pathogenic resulted in further tests. Unidentified cultures of dark-pigmented, sterile fungi were inoculated on host plants: *Picea abies* (Schönhar, 1984), *Pinus sylvestris* (Schönhar, 1984), *Chamaecyparis nootkatensis* (Hennon, Shaw & Hansen, 1990) and *Fragaria vesca* (Wilhelm, Nelson & Ford, 1969). Results were, not surprisingly, inconsistent: the strains varied from strongly pathogenic (Wilhelm *et al.*, 1969) to weakly pathogenic (Schönhar, 1984) or non-pathogenic (Hennon *et al.*, 1990). Haselwandter & Read (1982) inoculated two *Carex* species with unidentified indigenous dark, septate strains from the European Alps. They reported increased biomass and phosphorus levels after inoculation and concluded that 'the root–fungus association appeared to be of a mutualistic rather than a parasitic nature'. One of Haselwandter & Read's (1982) isolates (unknown 3; Table 4) was

included in the preliminary molecular phylogenetic analysis. It appeared closely related to the type culture of *Phialocephala fortinii* and some other strains identified as *P. fortinii* (Fig. 5). It is essential to note that the association between a fungus and its host is dependent on the species of both the fungus and the host, as well as the experimental conditions. Meaningful conclusions about host–fungus relationships must therefore be based on correctly identified fungi and hosts.

With the description of a few species of DSE (Kendrick, 1961; Wang & Wilcox 1985; Currah *et al.*, 1987), interest increased in determining the nature of the association between the host and fungal endophyte in specific host–endophyte combinations. Wilcox & Wang (1987*a*) inoculated four species on *Pinus resinosa*, *Picea rubens*, and *Betula alleghaniensis*. The results were variable and host response depended on the host–fungus combination. They concluded that *Phialocephala dimorphospora* was pathogenic, *P. fortinii* pseudomycorrhizal or pathogenic, *Chloridium paucisporum* ectendomycorrhizal or pseudomycorrhizal, and *Phialophora finlandia* ectomycorrhizal or ectendomycorrhizal, depending on the host species. Their conclusions were based on the visual appearance of the seedlings rather than biomass accumulation, nutrient acquisition, or fitness. When they further studied the positive association between the same hosts and *P. finlandia*, they concluded that the fungal colonization increased growth (Wilcox & Wang, 1987*b*).

Additional inoculation assays with specific host–fungus combinations were conducted. Stoyke & Currah (1993) inoculated *Menziesia ferruginea* with *Phialocephala fortinii* on cellulose agar in Petri dish cultures. *P. fortinii* physically overgrew the seedlings in the absence of competition by other fungi under aseptic conditions. O'Dell *et al.* (1993), however, saw no adverse reaction or extensive degradation of *Pinus contorta* tissue in response to colonization by *P. fortinii* in an open system that received small amounts of fertilizer with watering, but no additional carbohydrates.

Several possible reasons could account for the inconsistent results of these studies. Fernando & Currah (1996) pointed out obvious strain-specific differences in the growth responses in bioassays where *P. fortinii* was inoculated on several hosts in aseptic and open pot cultures. The resynthesis system, as well as the media used in assays, can produce incongruent results. Duddridge & Read (1984) and Duddridge (1986) demonstrated a change in the behaviour of ectomycorrhizal fungi in the presence of exogenous carbohydrate. The nutritional status of the fungal endophyte might therefore be an explanation for the controversial earlier results: Wilcox & Wang (1987*a*) and Stoyke & Currah (1993) used a growing medium with readily available carbohydrates, double-strength MMN (Marx & Zak, 1965) and cellulose agar (Warcup, 1973), respectively. By contrast, O'Dell *et al.* (1993) used a method in which the seedlings were grown in a 'growth pouch' to which nutrients, but no carbohydrates, were added. Whatever the reasons for observed inconsistencies in the host response to inoculation, it is obvious that results from any pure culture synthesis should be viewed with some caution.

DSE involvement in host nutrient acquisition has also been hypothesized. Jumpponen *et al.* (1998) grew seedlings of *P. contorta* in nitrogen-limited glacier soil in a fully factorial design with three treatments: inoculation with a strain of *Phialocephala fortinii*, addition of organic matter, and N. The *P. fortinii*-inoculation alone did not affect growth, but significantly increased the foliar phosphorus concentration regardless of the N treatment. The combination of inoculation and N amendment resulted in a > 50% larger increase in *Pinus contorta* biomass than did the N amendment alone. Haselwandter & Read (1982) grew seedlings of *Carex firma* and *C. sempervirens* inoculated with two strains of DSE. Inoculated seedlings consistently had a significantly higher foliar P concentration, while only *C. firma* growth was stimulated. Taken together these results suggest that at least some strains of DSE may be involved in host nutrient acquisition and therefore may indeed have a mutualistic, mycorrhiza-like relationship with their host plants.

ECOLOGY

Even if the effects of DSE on host plants vary with hosts and growth conditions, their abundance in some natural environments (see Berch, Gamiet & Deom, 1988; Hennon *et al.*, 1990; Cázares, 1992; Holdenrieder & Sieber, 1992) and ubiquitous global presence (see http://www.cup.cam.ac.uk/SPECIES_TABLE.html) suggest an important ecological role. Intercellular and intracellular colonization, as well as the ability to colonize a wide variety of host plants, have led researchers to propose that non-mycorrhizal root endophytes such as *Rhizoctonia* sp. (Warcup, 1985) and *Phialocephala fortinii* (Jumpponen & Trappe, 1996) can form mycelial connections between plant individuals of the same or even different species. These connections could be involved in photosynthate or nutrient transport as suggested for ectomycorrhizal systems (Simard *et al.*, 1997*a*, *b* and references therein).

Several different enzymatic activities have also been detected in DSE (see Ahlich Schlegel, 1997). Bååth & Söderström (1980) showed cellulolytic and proteolytic activity in an unidentified darkly pigmented fungus. Ahlich Schlegel (1997) showed that strains of DSE possessed laccases, lipases, amylases and polyphenol oxidases. The activities and their relative strengths, however, varied drastically be-

tween the strains. Based on a similar enzymatic activity assay Caldwell, Trappe & Jumpponen (1996) concluded that *Phialocephala fortinii* and other sterile isolates of DSE similar to *P. fortinii* can process common detrital carbon and P polymers. Polyphenol oxidases, which may be involved in processes such as lignin degradation, have been shown to be produced by *Leptodontidium orchidicola* (Fernando & Currah, 1995) and *P. fortinii* (Currah & Tsuneda, 1993; Ahlich Schlegel, 1997). Despite their enzymatic activities, it remains unclear whether DSE fungi actually decompose organic debris in their natural environment. Hutchinson (1990) speculated that these enzymes may be involved in fungal resistance to antifungal compounds rather than in decomposition. Furthermore, penetration through host cell walls may require lignolytic and cellulolytic enzymes.

Colonization by DSE has also been observed to occur simultaneously with arbuscular mycorrhizal (Thoen, 1987; Sengupta *et al.*, 1989; Horton *et al.*, 1998) or ectomycorrhizal fungi (Trappe, 1962; Horton *et al.*, 1998). DSE are also frequently isolated from root tips colonized by ectomycorrhizal fungi (Hatch, 1934; Trappe, 1962; Holdenrieder & Sieber, 1992). Concurrent occupation by different root-associated fungi might indicate the dynamic nature of the root-colonizing fungal community. DSE colonization appears more frequent in older parts of the root system (Robertson, 1954; Livingston & Blaschke, 1984), suggesting that DSE prefer aging root tissue or that DSE are recycling nutrients from senescent or dead root cells back into the active roots. On the other hand, DSE might function as mutualistic fungi taking part in nutrient and water acquisition, especially in unfavourable environments (Sengupta *et al.*, 1989; Jumpponen *et al.*, 1998). The concurrent colonization by DSE and ectotrophic or endotrophic mycorrhizal fungi would thus provide a back-up system during periods when mycorrhizal fungi are inhibited by the environmental conditions. These hypotheses need to be tested, preferably in natural environments.

Another interesting question is the role and presence of melanins in the hyphae of DSE. Melanins develop in large quantities in organisms that live in unfavourable environments (Bell & Wheeler, 1986). They might play an important role in discouraging grazing on soil micro-organisms by other soil microfauna and enable the organisms to withstand desiccation and microbial lysis (Kuo & Alexander, 1967; Bell & Wheeler, 1986). Melanins might protect DSE hyphae from extreme temperatures and drought, and so broaden their ecological niche, as suggested for the strongly melanized *Cenococcum geophilum* (Trappe, 1962). Cázares (1992) and Jumpponen & Trappe (1996) isolated several DSE from an alpine glacier foreland in northern Washington, USA, which is frequently exposed to frost and midsummer droughts. Resistance to cold and desiccation may play a significant role for the organisms able to persist at the site from year to year.

Currah *et al.* (1993) hypothesized that the intracellular sclerotial bodies of *Phialocephala fortinii*, also heavily melanized, can be effective dispersal propagules. As the colonized roots mature, the epidermal cells frequently loosen and slough off the root. The sloughed-off cells can then disperse with the soil movement like the spores of arbuscular mycorrhizal fungi (Allen, 1991). Melanins would improve the persistence and survival of the DSE propagules in soil. According to Currah *et al.* (1993), persistent propagules, such as the sloughed-off cortical cells filled with sclerotial bodies, could explain why DSE fungi are frequently isolated from surface-sterilized or washed roots and mycorrhizas (Summerbell, 1989; Stoyke & Currah, 1991; Holdenrieder & Sieber, 1992; Stoyke *et al.*, 1992; Jumpponen & Trappe, 1996).

The reproduction and dispersal of DSE are almost completely unknown. As described above, mycelial fragmentation is among the suggested means of dispersal (Currah *et al.*, 1993). Dispersal by conidiospores is also possible. Despite the fact that to date no anamorph–teleomorph connections have been established, sexual reproduction is possible. Currah *et al.* (1993) described immature ascomata in a pot culture synthesis. Jumpponen & Trappe (1996) hypothesized, based on the high genetic diversity observed in a population assay, that a large number of asexual individuals or frequent sexual recombination would be required to explain the large number of distinct phenotypes found on their small study site on a glacier forefront. However, more data are needed to understand how the populations of DSE disperse and maintain themselves.

CONCLUSIONS

Sterile root endophytes are ubiquitous in various habitats. Harley (1950) pointed out that 'one is definitely in a position to state that such sterile septate mycelia are to be expected in the external tissues and on the surface of roots of almost any plant...'. These endophytes, DSE fungi, have been reported from various habitats and from a wide range of hosts. Hosts include species known to be arbuscular, ericoid, orchid, ecto- or non-mycorrhizal. In most studies to date, all but the most conventional types of root colonization have been ignored. Including root endophytes in mycorrhizal studies adds laborious steps to the already time-consuming enumeration of mycorrhizas, but it would yield valuable data about the importance and frequency of other root colonizers.

DSE clearly comprise a heterogeneous group of known, and possibly unknown and undescribed, taxa

of deuteromycetes. The inconsistencies and disagreements among results from various studies of DSE partly result from the uncertain identities of the strains used. Phylogenetic analyses of DSE may be essential to shed light on questions of their origin and provide further help in solving the functional aspects of the fungi in this group.

The ecology of DSE is largely unknown and hypotheses are based on sparse evidence. Root–fungus association might diverge from easily classifiable, morphologically identifiable mycorrhizal types and yet function physiologically as mycorrhizas under natural conditions (Kope & Warcup, 1986). Thus, a primary research focus should be on the functional aspects of the interaction between the two organisms involved in the association.

With the recent development of molecular tools and the availability of type culture material, as well as fungal sequences in international nucleotide databases, more emphasis should be put on identifying the true affinity of the fungi, even if only on a generic or familial level. Understanding the relationships within DSE, as well as the relationship of DSE to known teleomorphic genera and families, will help elucidate the true nature and ecological importance of these poorly known root-colonizing fungi. A detailed understanding of the systematics and taxonomy of DSE may unearth valuable clues to the interaction between DSE and their host plants.

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