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COMMENT

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Dark septate endophytes – are they mycorrhizal?

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Abstract Dark septate endophytes (DSE) are a miscellaneous group of ascomycetous anamorphic fungi that colonize root tissues intracellularly and intercellularly. The limited selection of studies quoted here exemplifies the range of host responses to symbiotic DSE fungi. Like mycorrhizal associations, DSE associations vary from negative to neutral and positive when measured by host performance or host tissue nutrient concentrations. This range of host responses is partially attributable to variation between different fungus taxa and strains. Similarly, hosts differ in their responses to a single DSE strain. Experimental conditions may also govern the nature of the symbiotic association. It is concluded that DSE are capable of forming mutualistic associations functionally similar to mycorrhizas. If the variation in host response to mycorrhizal fungi is considered to represent a continuum ranging from parasitism to mutualism, DSE symbiosis must be considered mycorrhizal, at least under some conditions.

Keywords Mutualism · Mycorrhiza · Parasitism · Symbiosis

Dark septate endophytes (DSE) comprise a miscellaneous group of root-inhabiting fungi. A recent review (Jumpponen and Trappe 1998a) defined DSE as conidial or sterile ascomycetous fungi that colonize living plant roots without causing apparent negative effects such as tissue disorganization. This definition is likely to include a plethora of fungi whose functions and taxonomic affinities remain unknown. Fungi typically forming ectendomycorrhizas of conifers may also be included. Ectendomycorrhizas share structural similarities with ectomycorrhizas: they are characterized by a thin mantle and Hartig net. However, the two types of mycorrhizas differ in that ectendomycorrhizas penetrate intracellular space to a greater extent than ectomycorrhizas (Harley and Smith 1983). DSE often fail to form a complete mantle or Hartig net when colonizing a susceptible ectomycorrhizal host but colonize intracellular spaces forming microsclerotial structures (O'Dell et al. 1993). Nonetheless, some studies on morphology of roots colonized by DSE have described such associations as ectendomycorrhizal (Wilcox and Wang 1987a, b). Therefore, DSE likely include fungi which can be considered as ectendomycorrhizal symbionts, but appear able to colonize a great variety of hosts which are not ecto- or ectendomycorrhizal (Jumpponen and Trappe 1998a). In summary, DSE are a diverse group of fungi and may include a number of fungi forming ectendomycorrhizas. Because of the greater variety of hosts which DSE are capable of colonizing, they probably overlap only partially with the ectendomycorrhizal fungal symbionts.

Molecular data indicate the diverse origin of DSE. In a neighbor-joining analysis based on partial sequences of the small subunit of the ribosomal RNA (rRNA) gene, non-sporulating fungus isolates found capable of colonizing seedlings of *Pinus contorta* were clearly polyphyletic (Jumpponen and Trappe 1998a). The known and unknown DSE isolates represented Pleosporales and poorly resolved groups likely related to either Pezizales or Leotiales (Jumpponen and Trappe 1998a). Earlier analyses using longer sequences of the rRNA gene than those used by Jumpponen and Trappe (1998a) also support a polyphyletic origin of DSE fungi (LoBuglio et al. 1996). Taken together, all these observations indicate DSE to be a poorly defined group of fungi. The term DSE seems to be liberally applied whenever melanized, septate hyphae are observed colonizing roots either intercellularly or intracellularly.

Because of the difficulty in clearly defining DSE, their biotrophic nutritional mode may be questioned. DSE have been reported to possess a range of enzymatic capabilities (Caldwell et al. 2000; Currah and Tsuneda 1993; Fernando and Currah 1995; Haselwandter 1983). Caldwell et al. (2000), for example, concluded that DSE are able to utilize some of the major organic detrital nutrient pools. However, the ubiquitous presence of DSE on living plant roots (Ahlich and Sieber 1996; Ahlich

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et al. 1998; Jumpponen and Trappe 1998a), and the frequently observed intercellular and intracellular interfaces (Barrow and Aaltonen 2001) strongly suggest that a biotrophic nutritional mode is of importance for DSE fungi. Smith and Smith (1990) argue that the heterotrophic partner typically obtains organic carbon from the host when intercellular or intracellular interfaces are present in parasitic and mutualistic symbioses. Although such carbohydrate flow has not been shown directly for DSE, it may be inferred that the fungal partner is biotrophic. However, it remains an open question whether this biotrophic symbiosis is mycorrhizal. It has been suggested that DSE are mycorrhizal (e.g., Lewis 1987; Treu et al. 1996) but there is currently no consensus on this topic. This commentary concentrates on the published evidence of whether or not the symbiotic association between DSE fungi and their hosts is mycorrhizal, i.e., whether or not the colonized roots can function as mycorrhizas.

The mycorrhizal symbiosis has been viewed frequently to be synonymous with mutualistic symbiosis: the fungi benefit by obtaining carbohydrates from hosts and the hosts, in turn, benefit by improved growth and more efficient nutrient acquisition (for a further description of the benefits of mycorrhizal symbiosis, see Newsham et al. 1995). However, the fungal structures formed by DSE when colonizing host roots differ from those observed in typical mycorrhizal associations. Because of these unusual fungal structures and the lack of any demonstration of benefit to hosts, DSE associations have not been considered mycorrhizal. Notwithstanding, Trappe (1996), modifying earlier definitions proposed by Gerdemann (1970) and Harley (1992), defined a mycorrhiza functionally and structurally as “dual organs of absorption formed when symbiotic fungi inhabit healthy absorbing organs (roots, rhizomes, or thalli) of most terrestrial plants and many aquatics and epiphytes”. He also suggested that mutualism should be the defining functional criterion for a mycorrhiza: if a fungus is mutualistic in some situations and pathogenic in others, it would be mycorrhizal if the roots remained healthy but pathogenic when demonstrated to cause disease. Defining mycorrhizal symbiosis by mutual benefit may be an oversimplification. Although mycorrhizas are a classical example of mutualism, neutral and negative host responses, i.e., non-mutualistic responses, to colonization by mycorrhizal fungi are frequent (see references in Johnson et al. 1997; Smith and Smith 1996).

What causes fungal symbionts to deviate from the expected mutualism? Several authors (e.g., Francis and Read 1995; Johnson et al. 1997; Smith and Smith 1996) have addressed this issue, listing a variety of potential causes including plant developmental factors, experimental or environmental conditions, or (in)compatible host/fungus genotypes. Obviously, hosts and their root-inhabiting fungi vary in their associations as measured by host performance or fitness. The symbiotic association may be further modified by the environmental factors under which the association is observed. To acknowledge this problem, Johnson et al. (1997) suggested accepting the dynamic plant responses to mycorrhizal associations, yet considering them mainly mutualistic with occasional excursions toward commensalism or parasitism.

The mycorrhizal symbiosis may also imply a long-term improvement in fitness and fecundity. Clearly, improved nutrition of a host plant may indicate that a given individual is doing well, especially if size is not compromised. Whether the advantages of mycorrhizal symbiosis are transferred to the following generations has been measured only rarely. Some studies have shown that mycorrhizas can increase host reproductive investment as measured by seed size and seed nutrient content (e.g., Koide et al. 1988; Stanley et al. 1993). These traits may improve offspring vigor and, therefore, enhance recruitment (Koide and Lu 1992). Indeed, Stanley et al. (1993) observed more emerging, second-generation seedlings in the mycorrhizal than in the non-mycorrhizal treatments. In addition to the mainly positive effects on the current generation, the above observations show that the mycorrhizal symbiosis may have long-term effects only visible on the community level and over extended periods of time.

Clearly, DSE form symbiotic associations with the roots of their host plants; the fungal symbionts inhabit the absorbing organs of the host forming the dual organ as described by Trappe (1996). The questions that remain include whether this dual organ is an organ of absorption and whether the DSE associations can be considered mutualistic with occasional instances of parasitism. With these questions in mind, the few reports that have used identified DSE fungi to determine the nature of their symbiotic association will be examined here. I do not attempt to provide a comprehensive review of this topic. Rather, I will use a limited selection of studies exemplifying variation in host response to colonization by DSE and draw some parallels to observations in systems that are clearly recognized as mycorrhizal. I include examples that demonstrate host growth responses to DSE and briefly discuss the evidence for the involvement of DSE in nutrient absorption.

Root colonization by DSE fungi has been reported to cause a variety of host growth responses (see review by Jumpponen and Trappe 1998a). Undoubtedly, some of the observed variation is attributable to the great diversity of unknown fungi that may be included in DSE. Wilcox and Wang (1987b), for example, inoculated four DSE fungi (*Chloridium paucisporum*, *Phialocephala fortinii*, *Phialophora dimorphospora*, and *Phialophora finlandia*) on three ectomycorrhizal species of trees (*Betula alleghaniensis*, *Picea rubens*, *Pinus resinosa*). Based mainly on the morphology of the colonized roots and visual appearance of the tree seedlings, they concluded that some DSE fungi were either weak or serious pathogens, whereas others were structurally similar to ectendo- or ectomycorrhizal fungi and appeared to improve host growth. In other words, different mitotic DSE taxa formed associations ranging from pathogenic to mutualistic.

Different strains of DSE have also been shown to vary in their effects on hosts. Fernando and Currah

Table 1 Reported growth responses of hosts to *Phialocephala fortinii* inoculation

Host family	Host response		
	Positive	Negative	Neutral
Pinaceae	Jumpponen et al. (1998); Jumpponen and Trappe (1998b)	Wilcox and Wang (1987b)	Wilcox and Wang (1987b); Jumpponen et al. (1998); Jumpponen and Trappe (1998b); Fernando and Currah (1996)
Cyperaceae	Haselwandter and Read (1982)[a]	–	Haselwandter and Read (1982)[a]
Ericaceae	–	Stoyke and Currah (1993)	–
Salicaceae	–	–	Fernando and Currah (1996)
Rosaceae	Fernando and Currah (1996)	Fernando and Currah (1996)	Fernando and Currah (1996)

[a] One of the isolates isolated by Haselwandter and Read was clustered within a clade containing *Phialocephala fortinii* in Jumpponen and Trappe (1998a)

(1996) inoculated *Picea glauca* and *Potentilla fructicosa* with four strains of *Leptodontidium orchidicola*. *Potentilla fructicosa* shoot biomass increased when inoculated with one of the four strains but decreased when inoculated with two different strains. *Picea glauca* biomass, however, increased when inoculated with the two strains that resulted in a decrease in *Potentilla fructicosa* growth. In summary, both host and fungus genotypes (on either the species or individual level) appear to govern whether the symbiosis is mutualistic. The variation in symbiotic associations between anamorphic fungal taxa or strains and various host species is not unexpected; such differences have been observed in mycorrhizal systems. Dependency on mycorrhiza varies between host species (Francis and Read 1995; Wilson and Hartnett 1998). Francis and Read (1995) provide an example: in their experiment, only one species (*Plantago lanceolata*) showed a typical mutualistic response to arbuscular mycorrhizal fungi, whereas eight additional species showed a converse response of growth inhibition. Similarly, when inoculated on a single host, mycorrhizal fungus strains or species can result in an increase, decrease, or no effect on host biomass accumulation (see references in Fitter 1985; Johnson et al. 1997; Smith and Smith 1996). In conclusion, observations on the range of host responses to DSE colonization appear similar to those made in mycorrhizal systems.

To avoid the problems resulting from differences between DSE taxa, Table 1 lists reported growth responses to inoculation with just one taxon, *Phialocephala fortinii*. Even when confining observations to *P. fortinii*, host growth responses range from negative through neutral to positive. In addition to variation between strains, experimental conditions may influence the outcome of the symbiotic association, as was shown for mycorrhizal associations (see references in Johnson et al. 1997; Smith and Smith 1996). Some experiments showed a clearly pathogenic association between *P. fortinii* and the host plant: inoculation increased host mortality (Stoyke and Currah 1993; Wilcox and Wang 1987b). Stoyke and Currah (1993), however, provide a possible explanation for the observed pathogenic behavior of *P. fortinii* in their experiment. They used an axenic culture system involving petri dishes with cellulose agar. In the absence of competition from other fungi, *P. fortinii* was able to overgrow the hosts. Seedlings that did not die after inoculation seemed to develop normally. Ectomycorrhizal fungi also have been shown to behave unexpectedly in resynthesis systems. Duddridge and Read (1984) observed *Pinus sylvestris* roots being killed by a compatible ectomycorrhizal symbiont, *Suillus bovinus*, in a resynthesis system with a medium containing glucose at high concentrations.

Another example demonstrates the contrasting effect of experimental systems on DSE associations. Soil nutrient levels, as controlled by N fertilization, changed *Pinus contorta* growth response to *Phialocephala fortinii* inoculation from neutral to positive (Jumpponen et al. 1998). In the absence of N fertilization, no effects of *Phialocephala fortinii* inoculation on *Pinus contorta* growth were observed, whereas host growth increased when inoculation was combined with fertilization. This observation is contrary to reports on arbuscular mycorrhizal systems. High nutrient levels (usually P) frequently decrease the growth of mycorrhizal plants (e.g., Buwalda and Goh 1982; Graham et al. 1996; Mosse 1973). The negative growth effects of mycorrhizal colonization under high nutrient levels have been attributed to either carbon drain under non-limiting nutrient levels (Buwalda and Goh 1982) or toxic effects of high nutrient levels (Amijee et al. 1989). There are two likely explanations why the conclusions from the N fertilization study with *Phialocephala fortinii* differ. First, a reasonable N application (100 kg N/ha) that removed N limitation may have allowed the host to benefit from the presence of the fungal partner through the improved nutrient status and growth hormones possibly produced by the fungus. Second, the levels of N applied were not likely to be toxic. In conclusion, as with mycorrhizal associations, the experimental system may affect the DSE symbiotic association. Some observations on the DSE and symbiotic associations resulting in either positive or negative host growth responses are likely to have been influenced by the experimental conditions.

Increased host foliar P concentration, in addition to increased yield, is considered a “typical” result of functioning mycorrhizas (Harley and Smith 1983; Smith and Read 1997). There is no direct evidence of DSE involve-

ment in host nutrient acquisition. Furthermore, only a limited number of studies have addressed the effects of DSE on host tissue nutrient content. Two examples suggest that DSE may improve P uptake by the host. First, Haselwandter and Read (1982) observed increased shoot P concentrations in two *Carex* sp. (members of the typically non-mycorrhizal family Cyperaceae) when inoculated with two unknown DSE strains. One isolate was later included in a neighbor-joining analysis using rRNA (Jumpponen and Trappe 1998a) and formed a well-supported clade with two sporulating strains of *Phialocephala fortinii*. Therefore, it is likely that the strain resulting in improved P status in the two species of *Carex* is conspecific to *Phialocephala fortinii*. Second, and similar to the report by Haselwandter and Read (1982), Jumpponen et al. (1998) recorded increased foliar P concentration in *Pinus contorta* seedlings as a result of inoculation with a strain of *Phialocephala fortinii*. In conclusion, DSE are capable of increasing host P concentration under some experimental conditions.

As briefly mentioned above, mycorrhizal symbiosis may also provide long-term benefits by improving the fitness of an individual or a species. Mycorrhizal symbiosis has been reported to result in increased quantity or quality of seed, which in turn improves offspring vigor and performance and increases offspring number (Koide and Lu 1992; Koide et al. 1988; Stanley et al. 1993). Quantity and quality of offspring may be of particular importance when interspecific competition and plant community dynamics are taken into account. Furthermore, experimental manipulations have shown that mycorrhizal symbiosis may regulate successional change in plant communities by allowing facilitation by non-mycotrophic plants and enhancement of the establishment of later successional mycorrhizal species (Allen and Allen 1984, 1988). To my knowledge, no studies addressing the effects of DSE on either plant fitness or community dynamics exist at this time. However, Jumpponen (1999) hypothesized that *Phialocephala fortinii* affects the community dynamics in two different ways. First, similarly to the mycorrhizal systems, DSE may provide the shared mycelial infrastructure necessary for facilitation by common root-inhabiting fungi. In a study assessing spatial distribution of DSE phenotypes (Jumpponen 1999), individuals of different plant species were observed to be colonized by one fungal phenotype. It remained unanswered in that study whether the mycelium colonizing plant individuals was continuous or comprised several genetically identical, discontinuous ramets. Second, colonization by DSE fungi with broad host range may alter the competitive balance and provide a greater competitive advantage to only few species or individuals in a plant community. The differing competitive advantages might be expressed through improved vigor or greater reproductive investment of some species, resulting in shifts in the plant community structure due to DSE colonization. However, due to the paucity of data, the community level effects of DSE fungi are currently only speculative.

DSE may form mutualistic associations with their hosts. However, various soil fungi, or fungi occupying root surfaces (epirhizal or contact fungi in Iyer et al. 1980; Wilde et al. 1956), which do not colonize roots have also been shown to have positive effects on host performance, improving host growth by production of growth-promoting agents, excretion of antibiotic compounds, or enhancement of nutrient uptake (see Kucey 1987; Linderman 1988; Shivanna et al. 1994; Vassilev et al. 1996, 1997). How are DSE different from these soil organisms? As discussed above, DSE possess interfaces that indicate a biotrophic nutritional mode probably allowing carbon transfer between the host and its symbiotic fungi. They are also likely to possess extramatrical mycelia that allow access to resources beyond those provided by the host. According to Lewis (1973), whenever an heterotrophic symbiont has access to resources outside of the symbiosis, there is the possibility of bidirectional nutrient movement and development of a mutualistic symbiosis. The interfaces formed by DSE differ from the conventional types of interfaces observed in mycorrhizal symbioses. Nevertheless, DSE seem capable of forming the interfaces and infrastructure that allow mutualistic symbiosis with autotrophic hosts (Barrow and Aaltonen 2001). Reasonable evidence also exists to show that DSE fungi can, under some environmental or experimental conditions, enhance host growth and nutrient uptake, hence functioning in a manner typical of mycorrhizal associations. Enhanced growth and improved nutritional status indicate better performance resulting from DSE colonization. It remains unanswered whether DSE colonization also results in increased fecundity or fitness in the long term. Because of the wide range of fungi that may be included under the term DSE, it is likely that only some of them can form mutualistic associations. If it is accepted that mycorrhizal fungi cause host responses varying from parasitic to mutualistic without taking long-term fitness into account, the DSE association should be included when the diversity of mycorrhizal symbioses and responses is considered.

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