

Endophytes – characteristics and possibilities of application in forest management

Dorota Hilszczańska 

Forest Research Institute, Department of Forest Ecology, ul. Braci Leśnej 3, Sękocin Stary, 05–090 Raszyn, Poland

Tel. +48 22 7150502, fax +48 22 227150504, e-mail: d.hilszczanska@ibles.waw.pl

Abstract. Endophytes are organisms that live within the plant tissue without usually causing any symptoms. In plants of natural ecosystems, endophytic fungi are in fact ubiquitous. This review summarizes research carried out on their biology emphasizing their functionality in terms of the host range, the colonization extent, the way of transmission between hosts and their influence on host fitness. The main focus will be on two classes of fungal endophytes, class 2 and 4 (Dark Septate Fungi), due to their potential for practical application in forestry. Raising awareness of the potential of endophytes to enhance the host's resistance to pathogens, insects and anthropogenic disturbances is a key factor in developing applications for forest management.

Keywords: endophytes, DSE, functionality, applications

1. Introduction

Endophytes are microorganisms which colonise plant tissues. They develop without any visible symptoms, at least for a major part of their life cycle. Fungi, bacteria or even viruses can be classified as endophytes. Among them, the most abundant are fungi endophytes which can be found on every plant irrespective of size, shape or taxonomy. Majority of those fungi belong to the Ascomycota group Hypocreales. Due to the range of colonized host-plants, there are four function types classified according to size of the colony, the mode of transmission between hosts and effects on host fitness (Rodriguez et al. 2009; Table 1).

Endophytes in Gramineae (grasses) belonging to the Ascomycota group Hypocreales (Clavicipitaceae) are the first class. They can show a range of interactions with plants, from parasitism to mutualism. The best recognized in this group are *Neotyphodium* which appear in anamorphic form (asexual form). Transmission of these endophytes is predominantly vertical, from one generation to the next, via mycelium born in plant's seeds.

Second class is composed mainly of Pezizomycotina endophytes (Ascomycota); only a few belong to Basidiomycete

(Basidiomycota). They colonize roots, shoots and leaves of both monocotyledon and dicotyledon plants, and form a separate ecological group especially prone to colonize plants which grow in stressful habitats (Watkinson 2016). There are two ways in which the fungi can spread: vertically (via infected seeds) and horizontally, using spores or hypha. Similar to other endophytes, they inhabit the plant tissues directly or by using apresoria. The endophytes are especially abundant in senescent plants.

Another class of endophytes comprises fungi which are characterized by their hyper-diversity. They are present in herbaceous and woody plants in a very wide spectrum, and are vastly diversified even in the case of individual plants. For instance, over 80 species of endophytes have been isolated from juniper (*Juniperus communis*) and oak (*Quercus petraea*). Contrary to the endophytes from class number 1 and 2, the representatives of this group form visible symptoms of their infections. In the third class, the Pezizomycotina and Saccharomycotina (Ascomycota) species, as well as Agaricomycotina, Pucciniomycotina and Ustilagomycotina (Basidiomycota), are numerous. They spread horizontally through spores and fragments of hypha.

Submitted: 2.03.2016, reviewed: 6.06.2016, accepted after revision: 10.06.2016.

Lastly, the fourth class belongs to endophytes inhabiting roots. This is a group of fungi recognized by their black hypha and dark septum known as DSE (Dark Septate Endophytes). DSE's presence has been acknowledged in over 600 plant species. DSE fungi belong mostly to the Ascomycota, such as: *Cadophora*, *Microdochium*, *Trichocladium*, *Phialocephala*, *Leptodontidium* and *Phialocephala* (Watkinson 2016). Some species, like those from *Cadophora*, form web structures in roots which resemble Hartig's net in ectomycorrhizae, and in fact fulfil the role of the latter. Mycorrhizal fungi usually colonize short unlignified roots, whereas endophytes can be found in all parts of the root structural system (Grunig et al. 2011). Hence, the role of DSE seems to be as substantial as the role of mycorrhizal fungi. Due to the common presence of this group of organisms in the tree roots, the next chapter is focused primarily on DSE endophytes.

2. Characteristic of DSE Endophytes

Fungi of this group can affect plants as parasites (Wilcox, Wang 1987; Stoyke, Currah 1993), symbionts (Newsham 1999; Usuki, Narisawa 2007; Upson et al. 2009; Wu et al. 2010). They cannot cause any reaction (Jumpponen 2001).

Among the tested hypotheses, conducted to unravel the positive impact of DSE on the plant, two seem to be the most convincing. Both of these methods are based on the stimulation of plant growth. The first one focuses on supplying the plant with nutrients just like in mycorrhizas (Jumpponen 2001; Mandyam, Jumpponen 2005; Upson et al. 2009; Newsham 2011), whereas the second helps in the production of phytohormones (Mucciarelli et al. 2002; Schulz, Boyle 2005; Schulz 2006). In the research by Haselwandter and Read (1982), the isolated DSE increased the rate of growth and stimulated the accumulation of phosphorous in two highland species of sedge (*Carex*). Similar results had been received in the case of Chinese medicinal plant *Saussurea involucrate* Kar. et Kir. ex Maxim (Wu, Guo 2008).

Meyerhofer et al. (2013) indicate that plant reaction depends on the type of colonizing endophyte. According to the

authors, plants inoculated with DSE belonging to the genus of *Phialocephala* reached lower biometric values than the plants which were not inoculated. At present, *P. fortinni* is the best known species of DSE. It was described for the first time by Melin (1921) and is known as *Mycelium radices artrovirens* (Melin 1922). Due to the rich body of literature (Grunig et al. 2004, 2008a,b; Queloz et al. 2005; Brenn et al. 2008), it is already known that this is not a single species but consists of multiple numbers, and has at least 14 different species [(*Phialocephala fortinii* s.l. – *Acephala appalantata* (PAC)]. These species are usually isolated from trees in North America and Europe (Jumpponen and Trappe 1998; Grunig et al. 2008b). Fungi belonging to the PAC complex are notoriously encountered endophytes in the roots of coniferous and heather plants growing in the forest and highland ecosystems (Addy et al. 2000; Grunig et al. 2006). They can be found in all parts of the root system, starting from the apex of the mycorrhiza to the root collar (Menkis 2005, Grunig et al. 2008b).

Many of the DSE species sampled from coniferous trees (Table 2) belong to the Helotiales group, the most diversified among Ascomycota with around 300 genera and over 2000 species (Kirk et al. 2001). DSE belonging to the Helotiales are divided into three main groups. One of these groups comprises species in teleomorphic stadium related to *Mollisia*, *Phaeomollisia* and *Vibrisea* (MPV), as well as species in anamorphic stadium related to *Phialocephala* and *Cystodendron*. In the last few decades, many new strains have been characterized (Kowalski, Kehr 1995; Wilson et al. 2004; Grunig et al. 2009; Munzerberger et al. 2009; Wang et al. 2009). Despite so many discoveries, the fungi taxonomy is still far from clarity.

The second DSE group is composed of fungi, such as: *Caldophorafinlandia* (Wang, Wilcox 1985), *Pezoloma* (*Rhizoscypha sericeae* and *Meliniomyces* spp.) (Hambleton, Sigler 2005). To the third DSE group has the fungi perceived as plant pathogens, for example, *Rhynchosporium secalis*, *Oculimaculayallundae*, *Pyrenopezabraceae*, *Leptodontidium orchidicola*, *Cadophoramalarum* and *C. fastigiata*

Table 1. Criteria depicting classes of fungal endophytes

Criteria	Class 1	Class 2	Class 3	Class 4
Host range	narrow	broad	broad	broad
Tissues colonised	shoot and rhizome	shoot, root and rhizome	shoot	root
In planta colonisation	extensive	extensive	limited	extensive
In planta biodiversity	low	low	high	unknown
Transmission	vertical and horizontal	vertical and horizontal	horizontal	horizontal

Table 2. The most common isolated endophytes DSE

Taxon	Host species	Literature
<i>Acephala appalanata</i>	<i>Picea abies</i>	Grünig, Sieber 2005
<i>Phialocephala fortinii</i> s.s.	<i>Pinus sylvestris</i>	Grünig et al. 2008a
<i>Acephala</i> sp. 1	<i>Cassiope mertensiana</i>	Grünig et al. 2009
<i>Vibrissea truncorum</i>	<i>Populus</i> sp.	Grünig et al. 2009
<i>Acephala</i> sp. 2	<i>Pinus sylvestris</i>	Grünig et al. 2009
<i>Acephala</i> sp. 2	<i>Sorbus aucuparia</i>	Grünig et al. 2009
<i>Acephala</i> sp. 3	<i>Vaccinium myrtillus</i>	Grünig et al. 2009
<i>Acephala</i> sp. 4	<i>Pinus banksiana</i>	Grünig et al. 2009
<i>Acephala macrosclerotiorum</i>	<i>Pinus sylvestris</i>	Münzerberger et al. 2009
<i>A. macrosclerotiorum</i>	<i>Picea abies</i>	Menkis et al. 2004
<i>Phialocephala glacialis</i>	<i>Vaccinium myrtillus</i>	Grünig et al. 2009
<i>P. glacialis</i>	<i>Picea abies</i>	Grünig et al. 2009
<i>Phialocephala sphaeroides</i>	<i>Aralia nudicaulis</i>	Wilson et al. 2004
<i>P. sphaeroides</i>	<i>Picea abies</i>	Grünig et al. 2009
<i>Phialocephala</i> sp. 8	<i>Carex aquatilis</i>	Grünig et al. 2009
<i>Phialocephala</i> sp. 9	<i>Myricaria prostrata</i>	Burri (niepublikowane)
<i>Cadophora finlandica</i>	<i>Pinus sylvestris</i>	Wang and Wilcox 1985
<i>Meliniomyces variabilis</i>	<i>Rhododendron albiflorum</i>	Hambleton, Sigler 2005
<i>M. variabilis</i>	<i>Tsuga heterophylla</i>	Hambleton, Sigler 2005
<i>Meliniomyces bicolor</i>	<i>Nothofagus procera</i>	Hambleton, Sigler 2005
<i>M. bicolor</i>	<i>Quercus robur</i>	Hambleton, Sigler 2005
<i>Meliniomyces vraolstadae</i>	<i>Betula pubescens</i>	Hambleton, Sigler 2005
<i>Meliniomyces</i> sp. 1	<i>Betula pubescens</i>	Hambleton, Sigler 2005
<i>Meliniomyces</i> sp. 2	<i>Pinus sylvestris</i>	Hambleton, Sigler 2005
<i>Meliniomyces</i> sp. 3	<i>Gaultheria shallon</i>	Hambleton, Sigler 2005
<i>Meliniomyces</i> sp. 3	<i>Vaccinium myrtillus</i>	Hambleton, Sigler 2005
<i>Meliniomyces</i> sp. 4	<i>Pinus sylvestris</i>	Hambleton, Sigler 2005
<i>Pezoloma ericae</i>	<i>Calluna vulgaris</i>	Read 1974
<i>P. ericae</i>	<i>Ledum groenlandicum</i>	Hambleton et al. 1999
<i>Leptodontidium orchdicola</i>	<i>Platanthera hyperborea</i>	Currah et al. 1987
<i>L. orchdicola</i>	<i>Pedicularis bracteosa</i>	Currah et al. 1987
<i>Cadophora malorum</i>	-	Harrington, Mcnew 2003
<i>Cryptosporiopsis ericae</i>	<i>Vaccinium membranaceum</i>	Sigler et al. 2005
<i>C. ericae</i>	<i>Picea abies</i>	Sigler et al. 2005
<i>Cryptosporiopsis brunnea</i>	<i>Gaultheria shallon</i>	Sigler et al. 2005

Taxon	Host species	Literature
<i>Cryptosporiopsis melanigena</i>	<i>Quercus petraea</i>	Kowalski et al. 1998
<i>Cryptosporiopsis radiculicola</i>	<i>Quercus robur</i>	Kowalski, Bartnik 1995
<i>Cryptosporiopsis rhizophila</i>	<i>Erica tetralix</i>	Verkley et al. 2003
<i>Chloridium paucisporum</i>	<i>Pinus resinosa</i>	Alberton et al. 2010
<i>Cladiophialophora chaetospira</i>	<i>Picea abies</i>	Crous et al. 2007
<i>Didymosphaeria</i> sp.	<i>Picea abies</i>	Brenn et al. 2008
<i>Monodictys arctica</i>	<i>Salix oppositifolia</i>	Day et al. 2006
<i>Macrophomina phaseolina</i>	<i>Solanum tuberosum</i>	Manici, Caputo 2009
<i>Microdochium bolleyi</i>	<i>Elymus farctus</i>	Sanchez Marquez et al. 2008
<i>Neonectria radiculicola</i>	<i>Tilia petiolaris</i>	Schroers et al. 2008
<i>Periconia macrospinosa</i>	<i>Holcus lanatus</i>	Sanchez Marquez et al. 2010
<i>Phoma chrysantemicola</i>	<i>Chrysanthemum morifolium</i>	Aveskamp et al. 2009
<i>Pseudocercospora cantuariensis</i>	<i>Saussurea involucrata</i>	Wu et al. 2010

(Harrington and Mcnew 2003). The next order is Pleosporales which comprises great number of DSE endophytes. DSE belonging to the Sordariales (*Trichocladium opacum*) or Pezizales also have a wide range of occurrence [(Wilcoxina spp.) (Grunig et al. 2011)].

3. Endophytes in forestry

The knowledge about biological diversity of endophytes provides us with a possibility to use their properties and improve the growth of plants due to the mutualistic symbiosis (Arnold 2007). Endophytes by process of selection can be used in forest management. However, this process is not easy, given the huge number of these organisms. Researchers facing this issue have to be aware of many obstacles. Firstly, the endophytes selected and inserted into the environment can be quite easily replaced by other competing species. Next possibility lies in the genetically changed succession traits of the host. The environment of the selected endophyte can occur to be quite different from the environment where the given endophyte is moved. Consequently, the results may be opposite to the expected, and the benefits rather marginal, if any.

To find the 'right' endophytes, it is essential to correlate the results achieved in the laboratory analytical research with the results of the field tests. The correlation can be approached in the traditional way by first obtaining assay-based results, followed with field experiments. Sometimes laboratory phase is omitted, so the researchers have to follow the basic requirements: the taxonomic identity and the

knowledge of the probable role of the organism in natural environment (Rodriguez et al. 2009). Forest nursery is the place where typical field tests take place and saplings inoculated with endophytes from the local populations are grown here. The aim of the observation is to obtain data on persistence, growth rate and susceptibility to diseases and pests such as insects. Usually, nursery-grown seedlings have lower number of endophytes than those from natural regeneration (Miller et al. 2002; Ganley, Newcombe 2006), thus it is justified to mimic natural processes and use the endophytes from local forest, just like in the process of mycorrhization.

Doubts regarding choosing and preparation of the right inoculum may be limited if the researchers follow the functionality of the specific organism chosen for inoculation. On the basis of taxonomic identity, it is easier to verify the functional role of an organism. For example, *Beauveria bassiana* endophyte isolated from *Pinus monticola* was expected to protect pine trees against insects. In case of *Trichoderma* isolates, it was vital to set the hypothesis that it will induce the host with a defence against pathogens (Bailey et al. 2006). Nevertheless, it is essential to remember that many fungi taxa are characterized by their functional diversity. Attempts to focus on function via taxonomy may be deceptive due to the extent of undescribed diversity among endophytes (Arnold et al. 2000; Arnold 2007).

Endophytes belonging to *Trichoderma* may be mycoparasitic (Bailey et al. 2008), thus this property might add to the potential of a defence mutualist. On the other hand, caution in this regard is needed since a mycoparasite could

conceivably work against a defence mutualist, as it is in case of *Hydropisphaera fungicola* (Rossman et al. 2008) which feeds on an endophytic *Ulocladium* that itself reduces the severity of leaf rust in *Populus* (Newcombe et al. 2010).

If the selection of endophytes was solely based on their functionality, then Pezizomycotina (Ascomycota) would seem like the logical choice. They are a separate ecological group that is able to colonize roots, shoots and both monocotyledonous and dicotyledonous plants (Watkinson, 2016). According to Rodriguez and co-authors (2009), a few of the examined species belonging to this group had a positive effect on the growth of plants. The authors claim that both plants and endophytes could not survive in difficult environmental conditions when growing alone. *Curvulariaprotrubate*, endophyte which colonises all tissues of geothermal plant *Dichanthelium lanuginosum* increases plant's ability to tolerate heat. Mutualistic relation makes a plant function in a temperature up to 65° C. Without the connection, both plant and endophyte cannot survive above 40° C. Similar effect can be observed in case of grass *Leymus mollis*, which, thanks to the presence of *Fusarium culmorum* in its tissues, is capable to grow in saline sea water.

Although the surveys of endophyte communities present in forest trees have largely been examined in shoot systems (Sieber 2007), roots have also been sampled in a number of tree genera endophytes (Stone et al, 2000). So far, no attempts have been made to compare these two congeries as individual hosts. Endophytes isolated from seeds of *Pinus smonticola* that included isolates of *Hormonema*, *Geomyces* and *Cladosporium* were also isolated from healthy needles (Ganley, Newcombe 2006). These fungi as second class endophytes with mutualistic potential merit further research.

4. Conclusion

Endophytes affect many different aspects of forest trees, such as their longevity, growth rate, resilience to pathogens and insect pests, and resistance to stressful conditions. Due to these values they can become very useful tools in forest management.

Studies on fungi endophytes, which affect trees growth and their healthy status, have not been conducted until recently. Publications focused on this topic started to appear more than ten years ago, and have been studied by many researchers ever since. The contemporary knowledge on fungi endophytes leads to the assumption that we have to change the way we define particular groups of fungi. Fungi can affect the plant and the strain of the plant itself based on many environmental factors, and therefore defining them as endophytes, pathogens or saprotrophs narrows the biology of investigated organisms (Unterseher, 2011). Concurring with

this kind of statement, it is essential to accept the ambiguity of the aforementioned categories for many fungal groups.

Conflict of Interests

Author declares no conflict.

Acknowledgements and funding sources

I am grateful to Kasia Sikora and Hania Szmidla for the inspiration they provided me to throw light on the role of endophytes in a plant's life through this article. This work was due to the project No 260102 granted by Forest Research Institute.

References

- Addy H.D., Hambleton S., Currah R.S. 2000. Distribution and molecular characterization of the root endophyte *Phialocephala fortinii* along an environmental gradient in the boreal forest of Alberta. *Mycological Research* 104: 1213–1221.
- Alberton O., Kuyper T.W., Summerbell R.C. 2010. Dark septate root endophytic fungi increase growth of Scots pine seedlings under elevated CO₂ through enhanced nitrogen use efficiency. *Plant and Soil* 328: 459–470.
- Arnold A.E. 2007 Understanding the diversity of foliar endophytic fungi: progress, challenges, and frontiers. *Fungal Biology Review* 21: 51–66.
- Arnold A.E., Maynard Z., Gilbert G.S., Coley P.D., Kursar T.A. 2000. Are tropical fungal endophytes hyperdiverse? *Ecology Letters* 3: 267–274.
- Aveskamp M.M., Verkley G.J.M., de Gruyter J., Murace M.A., Perelló A., Woudenberg J.H., Groenewald J.Z., Crous P.W. 2009. DNA phylogeny reveals polyphyly of *Phomasection Peyronellaea* and multiple taxonomic novelties. *Mycologia* 101:363–382.
- Bailey B.A., Bae H., Strem M.D., Roberts D.P., Thomas S.E., Crozier J., Samuels G.J., Choi I.Y., Holmes K.A. 2006. Fungal and plant gene expression during the colonization of cacao seedlings by endophytic isolates of four *Trichoderma* species. *Planta* 224: 1449–1464.
- Brenn N., Menkis A., Grünig C.R., Sieber T.N., Holdenrieder O. 2008. Community structure of *Phialocephala fortinii* s. lat. in European tree nurseries, and assessment of the potential of the seedlings as dissemination vehicles. *Mycological Research* 112: 650–662.
- Crous P.W., Schubert K., Braun U., Hoog G.S., de Hocking A.D., Shin H.D., Groenewald J.Z. 2007. Opportunistic, human-pathogenic species in the *Herpotrichiellaceae* are phenotypically similar to saprobic or phytopathogenic species in the *Venturiaceae*. *Studies in Mycology* 58: 185–234.
- Currah R.S., Sigler L., Hambleton S. 1987. New records and new taxa of fungi from the mycorrhizae of terrestrial orchids of Alberta. *Canadian Journal of Botany* 65: 2473–2482.

- Day M. J., Gibas C. F. C., Fujimura K. E., Egger K.N., Currah R.S. 2006. *Monodictysarctica*, a new hyphomycete from the roots of *Saxifraga oppositifolia* collected in the Canadian High Arctic. *Mycotaxon* 98:261–272.
- Ganley R.J., Newcombe G. 2006. Fungal endophytes in seeds and needles of *Pinus monticola*. *Mycological Research* 110: 318–327.
- Grünig C.R., Queloz V., Sieber T.N. 2011. Structure of Diversity in Dark Septate Endophytes: From Species to Genes, in: Endophytes of Forest Trees: Biology and Applications (eds. Pirtilä and Frank C.A.), 3–30. DOI 10.1007/978-94-007-1599-8_1.
- Grünig C.R., Sieber T.N. 2005. Molecular and phenotypic description of the widespread root symbiont *Acephala applanata* gen. et sp. nov., formerly known as dark septate endophyte type 1. *Mycologia* 97: 628–640.
- Grünig C.R., McDonald B.A., Sieber T.N., Rogers S.O., Holdenrieder O. 2004. Evidence for subdivision of the root-endophyte *Phialocephala fortinii* into cryptic species and recombination within species. *Fungal Genetics and Biology* 41: 676–687.
- Grünig C.R., Du'o A., Sieber T.N. 2006. Population genetic analysis of *Phialocephala fortinii* s. l. and *Acephala applanata* in two undisturbed forests in Switzerland and evidence for new cryptic species. *Fungal Genetics and Biology* 43: 410–421.
- Grünig C.R., Duo A., Sieber T.N., Holdenrieder O. 2008a. Assignment of species rank to six reproductively isolated cryptic species of the *Phialocephala fortinii* s. l.-*Acephala applanata* species complex. *Mycologia* 100: 47–67.
- Grünig C.R., Queloz V., Sieber T.N., Holdenrieder O. 2008b. Dark septate endophytes (DSE) of the *Phialocephala fortinii* s.l. – *Acephala applanata* species complex in tree roots – classification, population biology and ecology. *Botany* 86: 1355–1369.
- Grünig C.R., Queloz V., Duo A., Sieber T.N. 2009. Phylogeny of *Phaeomollisiapiceae* gen. sp. nov.: a dark septate conifer-needle endophyte and its relationships to *Phialocephala* and *Acephala*. *Mycological Research* 113: 207–221.
- Hambleton S., Huhtinen S., Currah R. 1999. *Hymenoscyphus ericae*: a new record from western Canada. *Mycological Research* 103: 1391–1397.
- Hambleton S., Sigler L. 2005. *Meliniomyces*, a new anamorph genus for root-associated fungi with phylogenetic affinities to *Rhizoscyphus ericae* (*Hymenoscyphus ericae*), Leotiomycetes. *Studies in Mycology* 53: 1–27.
- Harrington T., Mcnew D. 2003. Phylogenetic analysis places the *Phialophora*-like anamorph genus *Cadophora* in the Helotiales. *Mycotaxon* 87: 141–151.
- Haselwandter K., Read D.J. 1982. The significance of a root-fungus association in two *Carex* species of high-alpine plant communities. *Oecologia* 52:352–354.
- Jumpponen A. 2001. Dark septate endophytes – are they mycorrhizal? *Mycorrhiza* 11: 207–211.
- Jumpponen A., Trappe J.M. 1998. Performance of *Pinus contorta* inoculated with two strains of root endophytic fungus, *Phialocephala fortinii*: effects of synthesis system and glucose concentration. *Canadian Journal of Botany* 76: 1205–1213.
- Kowalski T., Kehr R.D. 1995. Two new species of *Phialocephala* occurring on *Picea* and *Alnus*. *Canadian Journal of Botany* 73: 26–32.
- Kowalski T., Bartnik C. 1995. *Cryptosporiopsis radicola* sp. nov. from roots of *Quercus robur*. *Mycological Research* 99: 663–666.
- Kowalski T., Halmschlager E., Schrader K. 1998. *Cryptosporiopsis melanigena* sp. nov., a root inhabiting fungus of *Quercus robur* and *Q. petraea*. *Mycological Research* 102: 347–354.
- Kirk P.M., Cannon P.F., David J.C., Stalpers J.A. (ed.) 2001. *Dictionary of the fungi*, 9th edn. CAB International, Oxon, 655 s.
- Mandyam K., Jumpponen A. 2005. Seeking the elusive function of the root-colonising dark septate endophytic fungi. *Studies in Mycology* 53: 173–189.
- Manici L.M., Caputo F. 2009. Fungal community diversity and soil health in intensive potato cropping systems of the east Po valley, northern Italy. *Annals of Applied Biology* 155: 245–258.
- Melin E. 1922. On the mycorrhizas of *Pinus sylvestris* L. and *Picea abies* Karst. A preliminary note. *Journal of Ecology* 9: 254–257.
- Menkis A. 2005. Root associated fungi of conifer seedlings and their role in afforestation of agricultural land. PhD thesis, Swedish University of Agricultural Sciences, Uppsala.
- Menkis A., Allmer J., Vasiliauskas R., Lygis V., Stenlid J., Finlay R. 2004. Ecology and molecular characterization of dark septate fungi from roots, living stems, coarse and fine woody debris. *Mycological Research* 108: 965–973.
- Miller J.D., Mackenzie S., Foto M., Adams G.W., Findlay J.A. 2002. Needles of white spruce inoculated with rugulosin producing endophytes contain rugulosin reducing spruce budworm growth rate. *Mycological Research* 106: 471–479.
- Münzenberger B., Bubner B., Wöllecke J., Sieber T. N., Bauer R., Fladung M., Hüttl R.F. 2009. The ectomycorrhizal morphotype *Pinirhiza sclerotia* is formed by *Acephala macrosclerotia* sp. nov., a close relative of *Phialocephala fortinii*. *Mycorrhiza* 19: 481–492.
- Mucciarelli M., Scannerini S., Berteau C., Maffei M. 2003. In vitro and in vivo peppermint (*Mentha piperita*) growth promotion by non-mycorrhizal fungal colonization. *New Phytologist* 158: 579–591.
- Newcombe G., Martin F., Kohler A. 2010. Defence and nutrient mutualisms in *Populus*, in: Jansson S., Groover A.T., Bhalerao R.P. (ed.) *Genetics and genomics of Populus*. Springer, New York, Dordrecht, Heidelberg, London, 247–278.
- Newsham K.K., Upson R., Read D.J. 2009. Mycorrhizas and dark septate endophytes in polar regions. *Fungal Ecology* 2: 10–20.
- Newsham K.K. 2011. A meta-analysis of plant responses to dark septate root endophytes. *New Phytologist* 190: 783–793. DOI 10.1111/j.1469-8137.2010.03611.x.
- Queloz V., Grünig C.R., Sieber T.N., Holdenrieder O. 2005. Monitoring the spatial and temporal dynamics of a community of the tree-root endophyte *Phialocephala fortinii* s. l. *New Phytologist* 168: 651–660.
- Read D.J. 1974. *Pezizella ericae* sp. nov., perfect state of a typical mycorrhizal endophyte of *Ericaceae*. *Transactions of the British Mycological Society* 63: 381.
- Rodriguez R.J., White J.F., Arnold A.E., Redman R.S. 2009. Fungal endophytes: diversity and functional roles. *New Phytologist* 182: 314–330. DOI 10.1111/j.1469-8137.2009.02773.x.

- Rossmann A.Y., Farr D.F., Platas G., Newcombe G. 2008. *Hydropisphaera fungicola* Rossmann, Farr & Newcombe, sp. nov. *Fungal Planet* 24: 1–2.
- Sanchez Marquez S., Bills G.F., Zabalgoitia I. 2008. Diversity and structure of the fungal endophytic assemblages from two sympatric coastal grasses. *Fungal Diversity* 33: 87–100.
- Sanchez Marquez S., Bills G.F., Dominguez Acuna L. et al. (2010) Endophytic mycobiota of leaves and roots of the grass *Holcus lanatus*. *Fungal Diversity* 41: 115–123.
- Schroers H.J., Zerjav M., Munda A., Halleen F. Crous P.W. 2008. *Cylindrocarpon pauciseptatum* sp. nov., with notes on *Cylindrocarpon* species with wide, predominantly 3-septate macroconidia. *Mycological Research* 112: 82–92.
- Schulz B., Boyle C. 2005. The endophytic continuum. *Mycological Research* 109: 661–686. DOI 10.1017/S095375620500273X.
- Sieber T.N. 2007. Endophytic fungi in forest trees: are they mutualists? *Fungal Biology Reviews* 21: 75–89.
- Sigler L., Allan T., Lim S.R., Berch S., Berbee M. 2005. Two new *Cryptosporiopsis* species from roots of ericaceous hosts in western North America. *Studies in Mycology* 53: 53–62.
- Stone J.K., Bacon C.W., White J.F. Jr 2000. An overview of endophytic microbes: endophytism defined. In: Bacon CW, White JF Jr (eds) *Microbial endophytes*. Marcel Dekker, New York, 3–29.
- Stoyke G., Currah R.S. 1991. Endophytic fungi from the mycorrhizae of alpine ericoid plants. *Canadian Journal of Botany* 69: 347–352.
- Unterseher M. 2011. Diversity of Fungal Endophytes in Temperate Forest Trees, in: *Endophytes of Forest Trees: Biology and Applications* (eds. Pirttilä and Frank C.A.), 3–30. DOI 10.1007/978-94-007-1599-8_2.
- Usuki F., Narisawa K. 2007. A mutualistic symbiosis between a dark septate endophytic fungus, *Heteroconium chaetospora*, and a nonmycorrhizal plant, Chinese cabbage. *Mycologia* 99: 175–184.
- Upton R., Newsham K.K., Bridge P.D., Pearce D.A., Read D.J. 2009b. Taxonomic affinities of dark septate root endophytes of *Colobanthus quitensis* and *Deschampsia antarctica*, the two native Antarctic vascular plant species. *Fungal Ecology* 2: 184–196.
- Verkley G., Zijlstra J., Summerbell R., Berendse F. 2003. Phylogeny and taxonomy of root-inhabiting *Cryptosporiopsis* species, and *C. rhizophila* sp. nov., a fungus inhabiting roots of several Ericaceae. *Mycological Research* 107: 689–698.
- Wang C.J.K., Wilcox H.E. 1985. New species of ectendomycorrhizal and pseudomycorrhizal fungi: *Phialophora finlandia*, *Chloridium paucisporum*, and *Phialocephala fortinii*. *Mycologia* 77: 951–958.
- Wang W., McGhee D., Gibas C.F.C. Tsuneda A., Currah R.S. 2009. *Phialocephala urceolata*, sp. nov., from a commercial, water-soluble heparin solution. *Mycologia* 101: 136–141.
- Watkinson S.C. 2016. Mutualistic symbiosis between fungi and autotrophs, in: *The Fungi. Third Edition* (eds. S.C. Watkinson, L. Boddy, N.P. Money), 234–239. DOI 10.1016/B978-0-12-382034-L00007-4.
- Wilcox H.E., Wang C.J.K. 1987. Mycorrhizal and pathological associations of dematiaceous fungi in roots of 7-month-old tree seedlings. *Canadian Journal of Forest Research* 17: 884–899.
- Wilson B.J., Addy H.D., Tsuneda A. Hambleton S., Currah R.S. 2004. *Phialocephala sphaeroides* sp. nov., a new species among the dark septate endophytes from a boreal wetland in Canada. *Canadian Journal of Botany* 82: 607–617. DOI 10.1139/cjb-76-7-120.
- Wu L., Guo S. 2008. Interaction between an isolate of dark septate fungi and its host plant *Saussurea involucreata*. *Mycorrhiza* 18: 79–85. DOI 10.1007/s00572-007-0159-9.
- Wu L.Q., Lv Y.L., Meng Z.X., Chen J., Guo S.X. 2010. The promoting role of an isolate of dark-septate fungus on its host plant *Saussurea involucreata* Kar. et Kir. *Mycorrhiza* 20: 127–135.