# The Use of Symbiotic Fungal Associations with Crops in Sustainable Agriculture

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Agriculture in the 21st century faces the daunting task of satisfying the unceasingly increasing demand for food in a context of continuous depletion of natural resources and the need to respect international environmental standards. Among the alternatives to conventional agriculture developed in this context, symbiotic fungal association with crops shows considerable promise because of its effectiveness, habit-specific mode of action, and ability to provide multiple benefits. Known as endophytism, this association represents a new area of research based on the benefits of mutualistic interactions between host crops and nonpathogenic fungi. The advantages conferred by endophytic fungi include their ability to promote plant growth and tolerance of both abiotic stresses (e.g., salt, drought, heat) and biotic stresses (e.g., insects, plant diseases). As such, the practical applications of endophytes as potential sources of bioorganic nutrients and as biocontrol agents can significantly improve yields in an environmentally sound way. Moreover, the ability of fungal endophytes to improve plant tolerance of salt, drought, and heat stress make it possible to grow crops on previously uncultivable land. Thus, fungal endophytes should be included among alternative modern technologies to support food production.

Key words: Symbiotic association, sustainability, endophytes, biocontrol

#### Introduction

The world population is expected to reach 9.2 billion by 2050 (UN, 2007), creating a growing demand for food. At the same time, the rapid economic growth in many Asian countries is creating demand for a higher quality diet (Brown, 2005; FAO, 2008), further heightening global food demand, while rising oil prices are making it difficult for developing countries to afford the modern agricultural techniques capable of meeting this demand. Agriculture in the 21st century therefore faces the daunting task of satisfying this increasing food demand while still respecting increasingly strict global environmental standards. To achieve these objectives, it will be necessary to integrate the economic, social, and environmental functions of agriculture to produce a sustainable agricultural system (FAO, 1999). Taking advantage of natural processes, such as symbioses between plants and various microorganisms, will greatly support efforts to achieve these objectives.

Although symbioses between nitrogen-fixing rhizobacteria and plants and between soil-dwelling fungi and plants have been known for more than a century (Krings *et al.*, 2007; Saikia and Jain, 2007; Peterson *et al.*, 2008), fungal symbioses have not yet been widely studied or used in agriculture. Symbiotic fungal associations with crops (endophytism) have been discovered that improve crop growth and yield without requiring the use of expensive chemical fertilizers, while simultaneously improving the ability of these crops to tolerate a range of biotic and abiotic stresses (Arnold *et al.*, 2003; Hesse *et al.*, 2003; Rodriguez *et al.*, 2008). These endophytes thus seem to offer a solution to

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several of the problems facing modern agriculture. In this paper, we review some recent advances in the use of endophytes to promote plant growth, provide biological control of insect pests and plant diseases, and improve plant tolerance of abiotic stresses (salt, drought, and heat stress).

# Understanding Symbiotic Fungal Associations with Crops

Symbiosis can be defined as an association between unlike organisms that generally persists for long periods (Kirk *et al.*, 2008). Often, there is a mutualistic interaction between the two partners that offers benefits to each partner. Such mutualistic associations between fungi and plants are referred to as "endophytism." Fungal endophytes are microfungi that cause symptomless infections of their host plants (Suryanarayanan *et al.*, 2003). Fungal endophytes colonize their hosts in a range of different ways. Here, we discuss a typical class of endophyte in which colonization of the host by fungal hyphae is limited to the epidermal cells of the roots, leaving the vascular cylinder tissues intact (Fig. 1).

Fungal endophytes play important ecological roles in their natural environments through a habitatspecific symbiosis (Rodriguez *et al.*, 2008). Practical applications of this mutualism in agriculture have been proposed based on these ecological roles. The benefits that have been observed from these symbiotic associations include improved plant growth and tolerance of abiotic and biotic stresses.

# **Plant Growth Promotion**

As a result of the green revolution, there has been a significant increase in fertilizer consumption worldwide, with total consumption estimated at 163.9 Mt in 2006/2007 (Heffer and Prud'homme, 2007). Fungal endophytes, with their potential to promote plant growth without requiring the use of these fertilizers (Fig. 2), can make the chemicalintensive modern crop production system more sustainable by reducing dependence on synthetic fertilizer. The mechanism and efficiency of the growth promotion effect depend strongly on the species or isolate of the endophyte, as well as on the host and the study conditions. For example, the root endophyte *Heteroconium chaetospira*, (Grove) M.B. Ellis significantly increased (by more than 800%) the

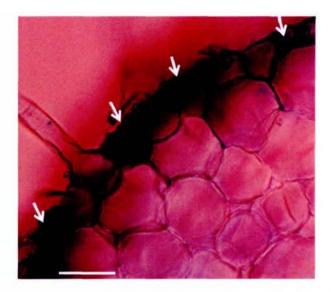


Fig. 1. Cross-section of a cucumber root stained with 50% acetic acid plus 0.005% cotton blue, showing colonization of the root by the endophyte *Pseudosigmoidea* sp. Arrows indicate hyphae that have only penetrated the root epidermal cells. Bar =  $60 \,\mu$ m.

biomass of inoculated Chinese cabbage (Brassica rapa chinensis) by means of nitrogen transfer to the host in exchange for carbohydrates (Usuki and Narisawa, 2007). In addition to the nitrogen transfer, improved host uptake of phosphorus conferred by the endophytic fungus Cladorrhinum foecundissimum in cotton roots increased plant height by 50% compared with control plants (Gasoni and De Gurfinkel, 1997). Piriformospora indica is another root endophyte that has been shown to promote the growth of both food crops (e.g., maize) and shrubs (e.g., Artemisia annua L.), with increases of up to 50% of their fresh biomass (Varma et al., 1999), and it has been shown to promote the formation of adventitious roots in cuttings of pelargonium cv. "Isabell", and poinsettia cv. "Cortez Red" (Druege et al., 2007). Plant growth promotion has also been caused by endophytic yeast due to production of auxins, as in the case of Williopsis saturnus in maize roots (Nassar, 2005).

The merit of these symbionts lies in their potential to increase production in the absence of synthetic fertilizers, the ability to culture the symbiotes on artificial media, and the presence of symbiotes with a range of degrees of host specificity. However, despite these promising results under controlled



**Fig. 2.** Compared with uninfected control plants (A), cucumber plants infected by the endophyte *Pseudosigmoidea* sp. (B) show growth promotion in petri dishes after 21 days of growth at 23°C.

conditions, practical applications in the field are needed to determine the agricultural effectiveness of these symbioses.

# **Plant Protection**

Annual agricultural losses caused by animal pests, pathogens, and weeds worldwide have been estimated at 26 to 30% for cash crops like soybean, cotton, etc., and at 35%, 39% and 40%, respectively for maize, potatoes and rice (Oerke and Dehne, 2004). To control these losses, global annual pesticide consumption had exceeded 5.0 billion pounds of active ingredient in 2000 and 2001 (EPA, 2007). This huge amount of pesticides could potentially be reduced if researchers can develop practical techniques for the application of fungal endophytes as biological control agents to suppress diseases and insect pests.

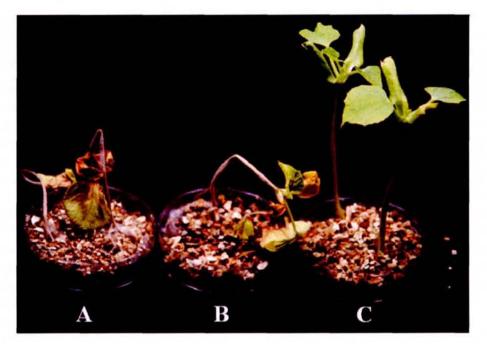
## 1. Suppression of Plant Diseases

Meliniomyces variabilis isolated from a natural forest in Japan was able to increase the tolerance of melon seedlings to Fusarium oxysporum f. sp. melonis compared to control plants and plants infected with another endophyte isolate; plants in both of the latter groups wilted after being challenged with the pathogen for 2 weeks (Fig. 3). Research also has shown that M. variabilis could inhibit by 84% the yellows disease of Chinese cabbage caused by *Verticillium longisporum* Karapapa Stark (Narisawa *et al.*, 2004). Several other examples of disease control by endophytes have been documented, including the highly effective control in non-sterile soil of the clubroot disease (*Plasmodiophora brassicae* Woronin) of Chinese cabbage by *H. chaetospira* (Narisawa *et al.*, 1998). Under greenhouse conditions, the same endophyte reduced the incidence of disease symptoms by 90 to 100% at spore concentrations of  $10^4$  to  $10^6 g^{-1}$  of soil (Narisawa *et al.*, 2005). This approach permitted effective control of the clubroot disease, potentially serving as a precursor for the future control of the disease in the field.

The control of club root disease and *Verticillium* yellows by endophytes is a significant achievement, since there are few effective control methods for these two diseases. Nevertheless, this approach is only at an experimental stage, and prior determination of the spore concentration is necessary because the symbiote is less effective at high spore concentrations.

#### 2. Suppression of Insect Pests

The effects of fungal endophytes on aphids have been investigated in the past few years and have shown interesting results. *Neotyphodium*-infected



**Fig. 3.** Effect of the endophyte *Meliniomyces variabilis* on the suppression of damage caused by *Fusarium oxysporum* f. sp. *melonis* in melon seedlings grown in petri dishes at  $23^{\circ}$ C and assessed 2 weeks after transplantation. Melon seedlings in (A) the control and (B) in the treatment with an ineffective endophyte, showing severe wilting after being challenged by *F. oxysporum*. (C) After treatment with *M. variabilis*, seedlings remain erect and healthy.

plants of tall and meadow fescue have deterred barley aphids (Sipha maydis Passerini) from feeding on these plants and have decreased the preference of the mealybug Phenococcus solani for feeding on these plants under greenhouse conditions (Sabzalian et al., 2004). Insecticidal activities on adult turnip aphids (Lipaphis erysimi) were reported by Hu et al. (2005) as a result of the production of secondary metabolites by Penicillium sp. endophytes. A double impact on the aphid Rhopalosiphum padi was observed in Neotyphodium coenophialuminfected plants (Züst et al., 2007). First, the presence of the endophyte decreased the colony size of the aphids on infected plants. Second, the endophyte inhibited the production of wings that would allow the aphids to escape their predators and disperse between plants.

Successful results have also been reported for other insect pests. For example, *Neotyphodium* endophytes have conferred resistance against the leaf bug *Trigonotylus caelestialium* that causes peaky rice (Shiba and Sugawara, 2005), and high mortality (up to 100%) was observed in both first-instar larvae and adults after 2.5 and 9 days, respectively. Insecticidal activity against *Plutella xylostella* was caused by secondary metabolites of *Penicillium* sp. (Hu *et al.*, 2005).

Such findings are important because they reveal the possibility of controlling aphids and other important insect pests without using synthetic pesticides. However, *Neotyphodium* endophytes are obligate asexual fungi, so efficient culture and inoculation methods must be developed before their usage can be extended to cultivated crops.

# Salt, Drought, and Heat Tolerance

Salt, drought, and heat represent serious limiting factors for agricultural production. Salt-affected soils are a global problem (Sparks, 1995), particularly in arid areas, and occupy an estimated 6% of the world's agricultural land (Mandal and Sharma, 2006). Drought is an even more serious problem worldwide and affects more than 30% of the total global land area (UN, 2008). Heat is a particular problem in many areas, and even where it is not currently a serious agricultural problem, it may soon become one as a result of global warming, which will challenge agriculture around the world in various ways (IPCC, 2007).

The management of salt stress is generally based on irrigation to flush the salt out of the soil, and the elimination of drought symptoms is also based on irrigation. Endophytes that are able to tolerate salt and drought stresses in agricultural crops have not yet been well documented; therefore, we report here the few recent cases that have been examined. Recently, tolerance of salt stress was conferred to several plant species, including dunegrass, panic grass, rice, and tomato, by the endophytic fungus Fusarium culmorum (Rodriguez et al., 2008). To our knowledge, this is the only reported case in which an endophyte induced tolerance to salt stress. More documented is the tolerance to aluminum and other heavy metals induced by fungal symbiotes to their host plants. Although heavy metals can affect critical life stages of some mycorrhizea, specially metal-sensitive ecotypes (Pawlowska and Charvat, 2004), studies have shown that the endophyte infection can contribute to aluminum tolerance with a positive or neutral effect on dry weight in fine fescues, but mycorrhization can protect from heavy metal-induced oxidative stress (Zaurov et al., 2001; Schützendübel and Polle, 2002). For drought tolerance, Neotyphodium endophytes have shown an ability to support the growth of Lolium perenne under water shortages (Hesse et al., 2003). Culturable fungal endophytes of Curvularia protuberate and F. culmorum have also conferred drought tolerance and supported the survival of their host plants under drought conditions for 7 to 14 days (Rodriguez et al., 2008). In addition to drought tolerance, C. protuberate endophytes conferred heat tolerance to panic grass and tomato plants.

The mechanism of tolerance of these stresses involves the maintenance (or lowering) of osmolyte concentrations, the consumption of less water, and the generation of reactive oxygen species for heat, drought, and salt tolerance, respectively (Rodriguez *et al.*, 2008).

Improved tolerance of these abiotic stresses represents a promising answer to the challenges that limit agriculture in many parts of the world. Nevertheless, only a few effective fungal isolates are currently available, and considerable additional research is required before we understand these symbioses sufficiently well to gain approval for their widespread use.

# Barriers to Practical Use of Fungal Endophytes

Among the factors limiting the practical use of fungal endophytes, three major are identified and include the host specificity, Need for efficient cultures and inoculation technique and Stability of the symbiosis

## Host specificity

If the symbiosis involving mycorrhizas and plants is a universal phenomenon, it may not the case with fungal endophytes and plants where host specificity continues to be found (Smith and Read, 2008). Unlike dark septate endophytes known to present little or no host specificity (Jumpponen and Trappe, 1998), Neotyphodium endophytes, for example, are known to be specific to cool season grasses only, which limits their application in other plants despite their useful traits (Hesse *et al.*, 2003; Shiba and Sugawara, 2005).

## Need for efficient cultures and inoculation technique

Despite all efforts accomplished in the search of endophytes and the diversity of endophytes already reported, serious issues such as methods of inoculation for their practical application remain unsolved. The spray method as used with pesticides is not practical for matter of time and plant height. Thus a seedling management technique with two times inoculation via roots and leaves & stems during the nursery stage appears easier and can be a sustainable solution to the inoculation problem.

#### Stability of the symbiosis

Fungal endophytes should not cause symptoms of disease or decay to their host plants and that is particularly important when producing any fungal biocontrol agent for commercial usage. However, studies have shown that environmental conditions can induce undesirable effects on hosts of endophytes such as *Phialocephala fortinii* and *Leptodontidium* orchidicola (Wang and Wilcox, 1985; Wilcox and Wang, 1987). This represents a limiting factor for the use of endophytes. In addition, examples have been documented where *Colletotrichum musae* and other *Fusarium* species strains were pathogenic while others were endophytic (Rodrigues Costa Pinto *et al.*, 2000; Kuldau and Yates, 2000), making it difficult for acceptance by users.

## **Conclusions and Recommendations**

Symbiotic fungal associations with crops offer benefits that range from the promotion of plant growth to improvements in the tolerance of abiotic and biotic stresses. The application of this symbiosis has shown promising results in the lab, with effective control of diseases and insect pests obtained under specific conditions. Plant growth promotion results from increased uptake of nitrogen and phosphorus, as well as from hormone production (auxins), in response to the fungal symbionts. Consequently, fungal endophytes offer the potential to significantly decrease the use of synthetic pesticides and fertilizers, which will only be applied to complement the use of the fungi, where necessary. Remarkably, challenges to agriculture such as salinization of soils and drought may be amenable to simple solutions in the future if the use of fungal endophytes allows farmers to convert lands affected by these problems into productive arable lands.

To achieve these ambitious objectives, researchers must assess the species richness of endophytes found in nature, because many symbioses have not yet been discovered and the ecological roles of the fungi are not fully understood. Most research on endophytes is still at an experimental level, and moving from the lab or greenhouse to the field should be encouraged to determine the effectiveness of the endophytes under real-world conditions, thereby permitting the practical use of these endophytes in agriculture. It will also be necessary to build awareness of this new field of research among farmers to improve interactions and collaboration with scientists working in different fields, thereby encouraging the adoption of endophytes in agriculture and maximizing their benefits. Although different endophytes seem to play different ecological roles, it should be possible to find or create endophytes that combine two or more roles, such as the simultaneous suppression of diseases and insect pests. If the agricultural use of endophytes becomes feasible, the practical aspects of this use will also have to be researched so farmers can learn how to integrate these species within pre-existing ecologically sound agricultural methods so as to ensure continuity in the approach to sustainability.

#### References

- Arnold, A.E., Mejia, L.C., Kyllo, D., Rojas, E.I., Maynard, Z., Robbins, N., and Herre, E.A., 2003. Fungal endophytes limit pathogen damage in a tropical tree. Proc. Natl. Acad. Sci. 100, 15649-15654.
- Brown, L.R., 2005. Outgrowing the earth: The food security challenge in an age of falling water tables and rising temperatures. Earth Policy Institute, NY.
- Druege, U., Baltruschat, H. and Franken, P., 2007. *Piriformospora indica* promotes adventitious root formation in cuttings. Sci. Horticult. 112, 422-426.
- EPA, 2007. 2000-2001 Pesticide market estimates: Usage. USA Environmental Protection Agency. http://www. epa.gov/oppbead1/pestsales/01pestsales/usage2001. htm (accessed January 2009.
- FAO, 1999. The multifunctional character of agriculture and land. United Nations, Food and Agriculture Organization, Rome.
- FAO, 2008. The state of food and agriculture 2008. United Nations, Food and Agriculture Organization, Rome.
- Gasoni, L. and De Gurfinkel, B.S., 1997. The endophyte Cladorrhinum forcundissimum in cotton roots: phosphorus uptake and host growth. Mycol. Res. 101, 867– 870.
- Heffer, P. and Prud'homme, M., 2007. World agriculture and fertilizer demand, global fertilizer supply and trade 2007-2008: Summary report. International Fertilizer Industry Association, Paris.
- Hesse, U., Schoberlein, W., Wittenmayer, L., Forster, K. Warnstorff, K., Diepenbrock, W. and Merbach, W., 2003. Effects of *Neotyphodium* endophytes on growth, reproduction and drought-stress tolerance of three *Lolium perenne* L. genotypes. Grass and Forage Sci. 58, 407-415.
- Hu, M.Y., Zhong, G.H., Sun, Z.T., Sh, G., Liu, H.M. and Liu, X.Q., 2005. Insecticidal activities of secondary metabolites of endophytic *Penicillium* sp. in *Derris elliptica* Benth. J. Appl. Entomol. 129, 413-417.
- IPCC, 2007. Climate change 2007: Synthesis report. Fourth assessment report. IPCC, Valencia.
- Jumpponen, A. and Trappe, J.M., 1998. Dark-septate root endophytes: a review with special reference to facultative biotrophic symbiosis. New Phytol 140, 295-310.
- Kirk, P.M., Cannon, P.F., Minter, D.W. and Stalpers, J.A., 2008. The dictionary of the fungi, 10<sup>th</sup> edition. CABI, Wallingford, UK.
- Krings, M., Taylor, T.N., Hass, H., Kerp, H., Dotzler, N. and Hermsen, E.J., 2007). Fungal endophytes in a 400million-yr-old land plant: infection pathways, spatial distribution, and host responses. New Phytol. 174: 648-657.
- Kuldau, G.A. and Yates, I.E., 2000. Evidence for Fusarium endophytes in cultivated and wild plants. In: Bacon, C. W., White, J.F. Jr. (Eds), Microbial endophytes. Marcel Dekker, New York, pp. 85-117.
- Mandal, A.K. and Sharma, R.C., 2006. Computerized database of salt affected soils for agro-climatic regions

in the Indo-Gangetic plain of India using GIS. Geocarto Intl. 21, 47-57.

- Narisawa, K., Tokumasu, S. and Hashiba, T., 1998. Suppression of clubroot formation in Chinese cabbage by the root endophytic fungus, *Heteroconium chaetospira*. Plant Pathol. 47, 206-210.
- Narisawa, K., Usuki, F., Fukuhara, S. and Hashiba, T., 2004. Control of *Verticillium* yellows in Chinese cabbage by the dark septed endophyte fungus LtVB3. Phytopathology 94, 412-418.
- Narisawa, K., Shimura, M., Usuki, F., Fukuhara, S. and Hashiba, T., 2005. Effects of pathogen density, soil moisture and soil pH on biological control of clubroot in Chinese cabbage by *Heteroconium chaetospira*. Plant Disease 89, 285-290.
- Nassar, A.H., EI-Tarabily, K.A. and Sivasithamparam, K., 2005. Promotion of plant growth by an auxin-producing isolate of the yeast *Williopsis saturnus* endophytic in maize (*Zea mays L.*) roots. Biol. Fertil. Soils 42, 97-108.
- Oerke, E.C. and Dehne, H.W., 2004. Safeguarding production-losses in major crops and the role of crop protection. Crop Protection 23, 275-285.
- Pawlowska, T.E. and Charvat, I., 2004. Heavy-metal stress and developmental patterns of arbuscular mycorrhizal fungi. Appl. Environ. Microbiol. 70, 6643–6649.
- Peterson, R.L., Wagg, C. and Pautler, M., 2008. Associations between microfungal endophytes and roots: do structural feathers indicate function? Botany 86, 445-456.
- Rodrigues Costa Pinto, L.S., J.L. Azevedo, J.O. Pereira, and Vieira, M.L.C., 2000. Symptomless infection of banana and maize by endophytic fungi impairs photosynthetic efficiency. New Phytol. 147, 609-615.
- Rodriguez, R.J, Henson, J., Volkenburgh, E.V., Hoy, M., Wright, L., Beckwith, F., Kim, Y.-O. and Redman, R. S., 2008. Stress tolerance in plants via habitat-adapted symbiosis. ISME J. 2, 404-416.
- Sabzalian, M.R., Hatami, B. and Mirlohi, A., 2004. Mealybug, *Phenococcus solani*, and barley aphid, *Sipha maydis*, response to endophyte-infected tall and meadow fescues. Entomol. Exp. Appl. 113, 205-209.
- Saikia1, S.P. and Jain, V., 2007. Biological nitrogen fixation with non-legumes: An achievable target or a dogma? Curr. Sci.92, 317-322.
- Schützendübel, A. and Polle, A., 2002.Plant responses to abiotic stresses: heavy metal-induced oxidative stress and protection by mycorrhization. J. Exper. Bot. 53, 1351-1365.
- Shiba, T. and Sugawara, K., 2005. Resistance to the rice leaf

bug, *Trigonotylus caelestialium*, is conferred by *Neo-typhodium* endophyte infection of perennial ryegrass, *Lolium perenne*. Entomol. Exp. Appl. 115, 387-392.

- Smith, S.E. and Read, D.J., 2008. Mycorrhizal symbiosis (Third edition). Elsevier, San Diego.
- Sparks, D.L., 1995. Sorption phenomena on soils, environmental soil chemistry. Academic Press, San Diego, CA, pp. 99-139.
- Suryanarayanan, T.S., Venkatesan, G. and Murali, T.S., 2003. Endophytic fungal communities in leaves of tropical forest trees: Diversity and distribution patterns. Curr. Sci. 85, 489-493.
- UN, 2007. World population prospects: The 2006 revision highlights. United Nations, department of economic and social affairs, population division, New York. Working paper No. ESA/P/WP.202.
- UN, 2008. Review of implementation of Agenda 21 and the Johannesburg Plan of Implementation (JPOI): Desertification - Report of the Secretary-General. Economic and Social Council E/CN.17/2008/7, New York.
- Usuki, F. and Narisawa, K., 2005. Formation of structures resembling to ericoid mycorrhizas by the root endophyte fungus *Heteroconium chaetospira* within roots of *Rhododendron obtusum* var. *kaempferi*. Mycorrhiza 15, 61-64.
- Usuki, F. and Narisawa, K., 2007. A mutualistic symbiosis between a dark, septate endophytic fungus, Heteroconium chaetospira, and a non-mycorrhizal plant, Chinese cabbage. Mycologia 99, 175-184.
- Varma, A., Verma, S., Suada, Sahay, N., Bütehorn, B. and Franken, P., 1999. *Piriformospora indica*, a cultivable plant-growth-promoting root endophyte. Appl. Environ. Microbiol. 65, 2741–2744.
- Wang, C.J.K. and Wilcox, H.E., 1985. New species of ectendomycorrhizal and pseudomycorrhizal fungi: *Phialophora findlandica, Chloridium paucisporum*, and *Phialocephala fortinii*. Mycologia 77, 951–958.
- Wilcox, H.E. and Wang, C.J.K., 1987. Ectomycorrhizal and ectendomycorrhizal associations of *Phialophora* findlandica with *Pinus resinosa*, *Picea rubens*, and *Betula alleghaensis*. Can. J. For. Res. 17, 976-990.
- Zaurov, D.E., Bonos, S., Murphy, J.A., Richardson, M. and Belanger, F.C., 2001. Endophyte infection can contribute to aluminum tolerance in fine fescues. Crop Sci. 41: 1981–1984.
- Züst, T., Härri, S.A. and Müller, C.B., 2007. Endophytic fungi decrease available resources for the aphid *Rhopalosiphum padi* and impair their ability to induce defenses against predators. Ecol. Entomol. 33, 80-85.