# Ectendomycorrhiza of conifers

Peitsa Mikola

*SELOSTE: HAVUPUIDEN EKTENDOMYKORRITSA*

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The fungal symbiont of ectendomycorrhizae is an ascomycete *Wilcoxina* (*Tricharina*)) *mikolae* Yang & Korf. It forms ectendomycorrhizae with *Pinus* and *Larix* and ectomycorrhizae with *Abies*, *Picea*, *Pseudotsuga* and *Tsuga*. It is common in forest nurseries around the world. After transplanting the seedlings into natural forest soil, indigenous fungi rapidly replace *Wilcoxina*. Inoculation of nursery soil with *Wilcoxina* is recommended if soil has been sterilized or for other reason mycorrhizal fungi are absent.

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Ektendomykorritsan sienisymbiontti on kotelosieni *Wilcoxina* (*Tricharina*) *mikolae* Yang & Korf. Se muodostaa ektendomykorritsoja *Pinus*- ja *Larix*-lajien kanssa, mutta *Abies*-, *Picea*-, *Pseudotsuga*- ja *Tsuga*-lajien kanssa ektomykorritsoja. Se on hyvin yleinen taimitarhoissa kaikkialla maapallolla. Taimitarhasta metsämaahan siirron jälkeen paikalliset ektomykorritsa-sienet nopeasti syrjäyttävät *Wilcoxinan*. Taimitarhan ymppäystä *Wilcoxinalla* suositellaan, jos maa on steriloitu tai mykorrit-sasienet muusta syystä puuttuvat maasta.

## 1. Ecto-, ectendo- and pseudomycorrhiza

Since the beginning of mycorrhiza research 100 years ago, two main types of mycorrhizae have been distinguished, viz. the ectotrophic and endotrophic ones or, according to modern terminology, ecto- and endomycorrhiza. Melin (1917), when stydying plant colonization on drained peatbogs, adopted the term pseudomycorrhiza or "false mycorrhiza" for pine short roots which were infected by fungi but lacked a mantle and Hartig net, essential features of a true ectomycorrhiza. In pseudomycorrhiza the fungus grew both on the root surface and intracellularly in the cortex; even rudimentary intercellular network could be present. Pseudomycorrhizae were thinner than true mycorrhizae and usually unforked. Melin believed that the fungus was a weak parasite and that no symbiotic

relationship existed between the root and the fungus; therefore the name pseudomycorrhiza.

Later Melin (1923) observed that in some ectomycorrhizae fungal hyphae also were growing intracellularly in cortical cells and called this type of mycorrhizae ectendotrophic, i.e. having characteristics of both ecto- and endomycorrhizae. Although intracellular infection in ectotrophic mycorrhizae had been described earlier by some workers, Melin (1923) first used the term "ectendotrophic".

Since then there have been somewhat divergent uses of the above terms. Pseudomycorrhiza, in particular, is a confusing term. Under this name have been put non-mycorrhizal short roots, both fungus-free and infected by saprophytes or weak parasites, old and dead mycorrhizae, and sometimes even typical ectendomycorrhizae. A distinguishing characteristic should be that in mycorrhizae the relationship between the host and the fungus is symbiotic, while in pseudomycorrhizae the fungus is either a weak parasite or a harmless saprophyte and the host obtains no benefit from the association. The physiological relationship, however, can not always be discovered solely by macroscopic or microscopic examination. A whole spectrum of intermediate stages of infection can be found between typical ectomycorrhiza (well-developed mantle and Hartig net, no intracellular hyphae) and pseudomycorrhiza (intracellular infection only, non-symbiotic). Therefore the term "pseudomycorrhiza" should be used critically or preferably not at all.

The term ectendotrophic mycorrhiza or ectendomycorrhiza also has been used for various root/fungus associations. Melin observed that some fungal hyphae grew inside cortical cells in typical ectomycorrhizae, e.g. in the tuberous "C mycorrhiza" of pine with thick mantle and profuse dichotomous branching. Intracellular infection usually increases along with aging of mycorrhizae and therefore has been considered as a symptom of senescence and decreasing symbiotic activity. In mature ectomycorrhizae, four zones usually can be distinguished, viz. (1) the youngest part with a mantle only surrounding the root tip and no fungal hyphae inside the root, (2) the ectomycorrhizal part with

mantle and Hartig net, (3) the senescent part, perhaps one year old, with hyphae penetrating into cortical cells, and (4) the oldest basal section where cortical cells have collapsed and even disappeared with only remnants of the fungal mantle and Hartig net still visible. The hyphae that penetrate into cortical cells at senescence may belong to the fungal partner of ectomycorrhiza or to secondary saprophytes. The root tip and ectomycorrhizal part usually are light-colored or even white, depending on the color of the fungal mantle, whereas the oldest section is dark-brown or black. Many reports in literature on ectendomycorrhizae may refer to senescent or moribund ectomycorrhizae.

There is, however, a distinct type of ectendomycorrhiza in which intracellular infection proceeds immediately behind the Hartig net development. In other words, inter- and intracellular infection develop almost simultaneously in the youngest and most active part of the mycorrhiza. Mikola (1965) found this "true ectendomycorrhiza" to be common on pine seedlings in Finnish forest nurseries, and Laiho (1965) confirmed its wide distribution in forest nurseries both in North America and Western Europe.

Wilcox (1971) who noticed this type of mycorrhiza common on red pine (*Pinus resinosa*) seedlings in North American nurseries, describes its external appearance as follows: "They are generally smooth, without a visible mantle and appear white for the first 2−3 mm after their emergence. They gradually turn amber and retain this color for the first 2−3 months of their development. Subsequently they either uniformly darken, become inactive, and are lost by attrition, or they undergo alternating cycles of activity and dormancy, gradually forming clusters of repeatedly bifurcate mycorrhizae". The inner structure is described by Wilcox (1971): "The fungal mantle is relatively inconspicuous, a Hartig net of thick hyphae surrounds the cortical cells, and coarse intracellular hyphae occupy the cortical cells. These features are seldom uniform throughout the axis of a mycorrhiza. The intercellular hyphae extend acropetally in advance of the intracellular hyphae, and both tend to disappear in the basal portion of older mycorrhizae along with the senescence of the cortex."

Similar mycorrhizae (thin or no mantle,

very coarse hyphae both in the Hartig net and intracellularly in cortical cells) have been described by Björkman (1942) in forest soil on poor sites and, as a predominant type, by Bergemann (1955) and Goss (1960) in pot experiments in greenhouses. Likewise the descriptions, e.g. the microphotographs, by Rayner (1934) and Levisohn (1963) correspond well with the above ectendomycorrhizae, although these authors believed that the fungus was more parasitic than beneficial and called those roots "haustorial mycorrhizae" or pseudomycorrhizae.

Other types of ectendotrophic mycorrhizae occur in the families of Arbutoideae, Pyrolaceae and Monotropaceae. They are usually considered in connection with other Ericales as varieties of the ericoid mycorrhiza. However, they differ greatly from the typical ericoid mycorrhizae of *Calluna* and *Vaccinium*. The mycorrhiza of *Arbutus*, the arbutoid mycorrhiza, is essentially ectendotrophic with a mantle, a Hartig net and intracellular hyphae (Harley & Smith 1983). The ericoid mycorrhiza is endotrophic, without a mantle or intercellular network. The

root systems of Arbutoideae resemble those of Pinaceae and other ectomycorrhizal tree families by distinct differentiation into long roots and short roots; the short roots are infected by fungi and converted to ecto- or ectendomycorrhizae. In contrast to typical ectendomycorrhizae of pines, the arbutoid mycorrhizae have a thick mantle. Externally and internally similar ectendomycorrhizae are found in the Pyrolaceae and Monotropaceae, although the physiological function of the association in these plants may be somewhat different. In the Pyrolaceae the fungus seems to exert some effect on the seed germination and early growth, as in orchids. The achlorophyllous *Monotropa* depends on the fungal associate in carbon nutrition throughout its entire life.

This article is mainly restricted to the ectendomycorrhiza of forest trees, such as has been described by Mikola (1965) and Wilcox (1971). Penetration of hyphae into cortical cells as a symptom of senescence and death of normal ectomycorrhizae is omitted in this review.

## 2. Fungi of ectendomycorrhizae

Mikola (1965) and Laiho (1965) isolated some 150 fungal strains from ectendomycorrhizae of pine seedlings from several Finnish nurseries. One morphologically identical strain was isolated from an ectomycorrhiza of a *Picea abies* seedling. On grounds of morphological similarity, Mikola (1965) concluded that all the 150 isolates belonged to the same fungal species, and called it provisionally the "E-strain" fungus. The same conclusion was reached by Wilcox et al. (1974) who isolated a similar fungus from nursery-grown red pine seedlings in the United States. On Hagem agar the colony is light brown and aerial hyphae are coarse, of variable thickness ($4-9\ \mu$) and septate. Submerged hyphae in the agar are hyaline, septate, winding and branching, and bear chlamydospores up to $30\ \mu$ in diameter (Wilcox 1971).

The ectendomycorrhizal "E-strain" fungus seems to be common on pine seedlings in

forest nurseries around the world. Laiho (1965) isolated eight identical strains from ponderosa and white pine seedlings in a nursery of north-western United States and found typical ectendomycorrhizae in five nurseries in the United States and four Western European nurseries. Mikola (1980), when surveying mycorrhizal relations in tropical pine nurseries, found the same type in Tanzania, Zambia, Swaziland, Australia and New Zealand, as well as in Mediterranean and Central European nations. Since mycorrhizal inoculum has been brought rather haphazardly into the tropics, the ectendotrophic type is present in some nurseries and absent in others.

Wilcox et al. (1974) found the "E-strain" fungus to produce characteristic chlamydospores in an axenic synthesis experiment with red pine. The chlamydospores are spherical, $45-100\ \mu$ in diameter, mostly terminal, sometimes intercalar, occasionally in chains.

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They occur both in external mycelium and in inter- and intracellular hyphae.

Later on Wilcox et al. (1983) extracted the same kind of chlamydospores from seedbeds of 17 nurseries in the United States. Their great similarity spurred interest in the taxonomy of the fungi involved. Yang and Wilcox (1984) showed that this widely spread ectendomycorrhizal fungus is an ascomycete and named it *Tricharina mikolae* Yang & Wilcox. In a more recent revision, Yang and Korf (1985) have separated a new genus *Wilcoxina* (Yang & Korf, gen.nov.) from *Tricharina*. All the four *Wilcoxina* species are ectendomycorrhizal with pines. In addition to *Wilcoxina mikolae*, Wilcox has isolated two other ectendomycorrhizal fungi from pine roots. They have been designated *Phialophora finlandia* and *Chloridium paucisporum* (Wang & Wilcox 1985). Separation of these dark-colored ectendomycorrhizal fungi from numerous *Mycelium radicis atrovirens* type pseudomycorrhizal fungi which are extremely common in forest soils, is difficult. The dominant species in nurseries around the world, however, most probably is *Wilcoxina mikolae*.

Basidiomycetes are known as associates in the arbutoid and related types of ectendomycorrhizae of Ericales. Zak (1974, 1976) has shown that the same species can form ectomycorrhizae with conifers and ectendomycorrhizae with *Arctostaphylos* and *Arbutus*. Eventual occurrence of the "E-strain" fungus or *Wilcoxina mikolae* in Ericales is not known.

Two different types of fungi can be causative organisms of arbutoid mycorrhizae (Harley & Smith 1983). In addition to the thick septate hyphae of the mantle and Hartig net, coils of thin hyphae have been found intracellularly in cortical cells, similar to those of the endotrophic ericoid mycorrhiza.

# 3. Occurrence of the ectendomycorrhiza

As previously mentioned, a strain of *Wilcoxina mikolae* (E-57) was isolated from an ectomycorrhiza of *Picea abies*. Laiho (1965) inoculated several tree species with this strain in semiaxenic cultures and found it forming ectendomycorrhizae with six *Pinus* species and *Larix occidentalis*. Ectomycorrhizae resulted from inoculating *Abies*, *Picea*, *Pseudotsuga* and *Tsuga*, as well as with *Betula verrucosa* and *Populus trichocarpa*. The structure of these ectomycorrhizae was externally similar to the pine ectendomycorrhizae but intracellular infection was lacking. Laiho concluded that the ectendotrophic structure is restricted to the genera of *Pinus* and *Larix* whereas the same fungus forms ectomycorrhizae with other trees. Furthermore, different pine species differed in the tendency to ectendotrophism; the intensity of intracellular infection also depended on soil conditions. Wilcox et al. (1983) observed that the tendency to intracellular infection varied between both pine species and fungal strains. Some of the strains could produce only ectomycorrhizae with a given pine species while other strains produced ectendomycorrhizae under the same conditions. One strain produced ectendomycorrhizae with all the other pine species but ectomycorrhizae with *Pinus elliottii*.

Ectendomycorrhizae are characteristic of forest nurseries, particularly in former agricultural soils. If *Wilcoxina mikolae* is present in the nursery soil, it is normally the first colonizer of young seedlings. In the first 1—2 years, often 70—100 % of pine short roots are ectendomycorrhizae, and ectendomycorrhizal infection also is widely spread in the long roots. Apparently the same fungus is also the first colonizer of other conifers, although the mycorrhizae are ectotrophic but otherwise similar with the pine ectendomycorrhizae. In the second or third season in the nursery, sheathed ectomycorrhizae may also appear and their proportion gradually increase. However, pine seedlings are often still completely ectendomycorrhizal at the time of transplanting into the field. After planting to forest soil, a rapid change usually takes place; ectendomycorrhizae disappear in 1—2 years and are replaced by ectomycorrhizae of different color and external appearance. An abrupt change from the nursery-borne ectendomycorrhiza to the ectotrophic structure is often easily detectable microscopically in longitudinal section and sometimes even macroscopically with naked eye (Mikola 1965).

Ectendomycorrhizae have also been found in seedlings of natural regeneration of pine forests and occasionally even in root systems of old trees. Laiho (1965) sampled many natural stands and plantations of various age and discovered "E-strain" ectendomycorrhizae in four stands only, viz. in seedlings of natural regrowth of *Pinus contorta*, *P. ponderosa*, and *P. strobus*. Björkman (1942) likewise found ectendomycorrhizae in stunted young *Pinus sylvestris* seedlings in the shade of old trees on most barren sites. Mikola et al. (1964) found the "E-strain" fungus as the first mycorrhizal colonizer of pine seedlings resulting from direct seeding after prescribed burning. All these findings indicate that *Wilcoxina mikolae* may be commonly present in forest soils although its competitive capacity with other mycorrhizal fungi seems to be weak.

Very little is known about the occurrence of other ectendomycorrhizae of conifers. *Chloridium paucisporum* was isolated from a nursery and *Phialophora finlandia* from a natural forest. Since *atrovirens* type fungi and pseudomycorrhizae are very common in forest soils, at least in raw humus, probably similar type of mycorrhizae are not so restricted to nurseries as are the common "E-strain" mycorrhizae.

# 4. Ecology of ectendomycorrhizae

The most striking features of the "E-strain" fungus *Wilcoxina mikolae* are its high infectiveness and rapid colonization of root systems and, on the other hand, its weak competive capacity with the indigenous ectomycorrhizal fungi of forest soils.

According to extensive experiments done under axenic and semiaxenic conditions, *Wilcoxina mikolae* has a wide ecological range which accounts for its extensive geographic distribution. There are, however, differences between different strains. In the pure culture experiments of Wilcox et al. (1983), for instance, northern strains (isolated from Finland, Canada, and New York) had optimum growth at +20°C and they still grew at +4°C, whereas optimum temperature for southern strains from Mississippi, North Carolina and West Virginia grew best at +24°C and failed to grow at +4°C.

In general, physiological requirements of *Wilcoxina mikolae* correspond well with those of typical ectomycorrhizal fungi which have been studied (Melin 1923, 1925; Norkrans 1950; Hacskaylo 1973; etc.). In the experiments of Mikola (1965), no strain was able to decompose cellulose. Glucose and sucrose were the best carbon sources for all the six strains studied, and all made some growth on starch. Ammonium salts were the best sources of nitrogen, nitrates were also good sources, and all strains utilized peptone and some amino acids to some extent. The optimum pH was 5.0—5.5 and the pH range over which the fungus grew in pure culture was from 3.0 to 7.8. The growth rate of different strains varied considerably.

Under more natural conditions the ecological amplitude of the fungus is much wider than as pure culture in liquid media. In semiaxenic pot experiments by Mikola (1965), two "E-strains" produced typical ectendomycorrhizae on pine over the whole pH range from 2.2 to 12.6 (initial pH; at the termination of the experiment the pH range varied from 3.6 to 11.9). Thus, the ectendomycorrhiza can exist in both very acid and alkaline soils. Typical ectendomycorrhizae were found, for instance, by Mikola (unpublished) on *Pinus halepensis* in the alkaline soil of several nurseries in Israel.

The development of ectomycorrhiza is closely dependent on the availability of soluble carbohydrates in the roots which, in turn, depends upon the intensity of photosynthesis and, consequently, by light availability to the host (Björkman 1949). However, the ectomycorrhizal fungi are not all equally dependent

on the photosynthesis by the host. *Wilcoxina mikolae* appears to have lower light requirements than typical ectomycorrhizal species. Thus, Mikola (1965) demonstrated that normal ectendomycorrhizae developed at the light intensity of 20 % of the full day light and that both inter- and intracellular penetration of the cortex still took place at 2 % of the full light. In natural forests, ectendomycorrhizae mainly have been found in seedlings under heavily shaded conditions (e.g. Björkman 1942).

The relative independence on light intensity may explain the early colonization of seedlings by the "E-strain" fungi and the dominance of ectendomycorrhizae in forest nurseries. The first ectendomycorrhizae usually develop at the cotyledon stage of the seedlings, when their photosynthetic efficiency still is low. Thus Goss (1960) observed that 2-month-old pine seedlings already had numerous ectendomycorrhizae whereas first ectomycorrhizae were detected three months later. Along with advancing age of the seedlings and increasing photosynthetic capacity, ectomycorrhizae gain more dominance and gradually may completely replace ectendomycorrhizae. In competition between fungi, light and increasing photosynthetic capacity seem to favor typical ectomycorrhizal fungi.

Little is known about the relative symbiotic efficiency of different ecto- and ectendomycorrhizal fungi. Some authors considered ectendomycorrhizal fungi less benefical or even harmful to the host (Rayner 1934; Levisohn 1963). In controlled experiments under more or less artificial conditions (e.g. Mikola 1965) no appreciable differences in growth of ectendomycorrhizal and non-mycorrhizal seedlings have been observed. Laiho (1965), however, when studying the effect of "E-strains" on the seedling growth of several conifers, noticed a remarkable effect of inoculation, inoculated seedlings being even two to three times bigger than the non-mycorrhizal control seedlings (Table 1). The inoculated seedlings also were green and healthy, whereas the control seedlings often appeared yellowish.

The influence of the fungus on the host also depends on environmental conditions, particularly on soil fertility. This clearly appears from a field experiment of Mikola (1967); the

Table 1. Shoot weight of 5 1/2-month-old seedlings, when inoculated (2–3 months after seeding) with "E-strain" fungi (Laiho 1965).

| Species | Shoot weight | Relative weight |
|---|---|---|
| | mg | (control=100) |
| *Abies procera* | 160 | 193 |
| *Picea abies* | 50 | 250 |
| *P. pungens* | 50 | 200 |
| *P. sitchensis* | 68 | 283 |
| *Pinus edulis* | 210 | 138 |
| *P. ponderosa* | 180 | 122 |
| *P. radiata* | 193 | 101 |
| *P. silvestris* | 86 | 307 |
| *P. strobus* | 118 | 171 |
| *Pseudotsuga menziesii* | 150 | 158 |
| *Tsuga heterophylla* | 88 | 463 |

Table 2. Average length (cm) of the top shoot of 3-year-old Scots pine seedling, when grown on peat substrate and inoculated with an ectendotrophic fungus (E-57) and a mixed ectotrophic population (forest humus) (Mikola 1967).

| Inoculation | Not fertilized | Fertilized |
|---|---|---|
| None | 7.59 | 12.20 |
| E-57 | 5.51 | 14.05 |
| Forest humus | 10.12 | 12.86 |

effect of an "E-strain" (E-57) was compared with that of a mixed forest soil population, with and without fertilization (Table 2). On the poor substrate (peat without fertilization) E-57 was definitely harmful to the host, whereas on the more fertile substrate it was beneficial. The natural ectomycorrhizal population, in turn, exerted a strong beneficial influence on the poor substrate but almost no effect on the fertilized peat.

Rather similar results were obtained in two other Finnish studies. Anttila and Lähde (1977) recorded the effects of different fertilizers and levels of fertilization on mycorrhizae of Scots pine seedlings in a forest nursery. In unfertilized seedlings only ectomycorrhizae were found, whereas moderate nitrogen and

Table 3. Mycorrhizal development and shoot weight of 2-year-old Scots pine seedlings, when inoculated with E-57 and planted in four different sites (C = uninoculated controls) (Laiho 1967).

| | | A Industrial peat field | B Forest land, clear-cut | C Forest land, burned | D Agricultural land |
|---|---|---|---|---|---|
| Mycorrhizae % of short roots | E-57 | 80 | 90 | 90 | 90 |
| | C | 70 | 90 | 90 | 90 |
| Ectendomycorrhizae, % of mycorrhizae | E-57 | 80 | 30 | 90 | 100 |
| | C | 0 | 0 | 0 | 0 |
| Av. length of top shoot, cm | E-57 | 16 | 22 | 24 | 39 |
| | C | 18 | 20 | 15 | 18 |
| Shoot dry weight, mg | E-57 | 290 | 410 | 1930 | 1560 |
| | C | 300 | 300 | 550 | 460 |

phosphorus fertilization greatly increased the proportion of ectendomycorrhizae.

Laiho (1967) planted inoculated (E-57) and uninoculated Scots pine seedlings to four different sites and recorded the growth and mycorrhizal relations after two growing seasons (Table 3). At that time the control seedlings also were mycorrhizal. No ectendomycorrhizae, however, were found in the control seedlings. Regarding the inoculated seedlings, after two years in natural forest soil (clear-cut area, site B) ectomycorrhizal fungi already had largely replaced E-57, whereas on the other sites, where the density of indigenous ectomycorrhizal fungi probably was low, ectendomycorrhizae still dominated two years after transplanting. The effect of the ectendomycorrhizal fungus E-57, in comparison with the indigenous ectomycorrhizal population, was different on different sites. On relatively poor sites, i.e. industrial peat field and clear-cut area (sites A and B) there were no considerable difference, whereas in more fertile sites C and D the E-57 was much superior to the indigenous fungi. On site C burning probably had released soluble nutrients to the soil, and site D had been fertilized during the agricultural use. Higher soil pH of sites C and D may also have favored ectendomycorrhizae.

Likewise in another study (Mikola et al. 1964) ectendomycorrhizae appeared on a heavily burned areas, whereas on unburned and slightly burned areas ectomycorrhizae only were found.

## 5. Applications

*Wilcoxina mikolae* is easy to inoculate, it infects seedlings rapidly at early stages, prefers relatively high level of soil fertility and tolerates even basic soil conditions. These properties make it a suitable symbiont for young seedlings in nurseries.

Conditions for ectomycorrhizal establishment are often not as favorable in nurseries as in natural forests because of heavy fertilization, high soil pH and initially low photosynthetic capacity of seedlings. If seedlings are kept in the nursery for a short time, as is

customary in the tropics and even in temperate climate where seedlings are nowadays often raised in greenhouses, *Wilcoxina mikolae* may be the only fungus that is able to establish mycorrhizal association before transplanting the seedlings to the field. For good survival of seedlings in the field, however, presence of mycorrhizal association at the time of planting is essential. Therefore inoculation of nursery soil with *Wilcoxina mikolae* might be recommended if it does not occur there naturally.

A successional process in which the ectendomycorrhizae are replaced with ectomycorrhizae after the transplanting, seems to take place with no disturbance to the healthy growth of seedlings.

# References

Anttila, T. & Lähde, E. 1977. Effect of fertilization on the development of containerized pine seedlings in a nursery. Folia Forestalia 314.

Bergemann, I. 1955. Die Mykorrhiza-Ausbildung einiger Koniferen-Arten in verschiedenen Böden. Zeitschrift für Weltforstwirtschaft 18: 184—202.

Björkman, E. 1942. Über die Bedingungen der Mykorrhizabildung bei Kiefer und Fichte. Symbolae Botanici Upsalienses VI.2.

— 1949. The ecological significance of the ectotrophic mycorrhizal association in forest trees. Svensk Botanisk Tidskrift 43: 223—262.

Goss, R. W. 1960. Mycorrhizae of ponderosa pine in Nebraska grassland soils. Univ. Nebraska, Agric. Exp. Station, Research Bulletin 192.

Hacskaylo, E. 1973. Carbohydrate metabolism of ectomycorrhiza. In: G. C. Marks & T. T. Kozlowski (eds.). Ectomycorrhizae. Academic Press Inc. New York. pp. 207—230.

Harley, J. L. & Smith, S. E. 1983. Mycorrhizal symbiosis. Academic Press Ltd. London.

Laiho, O. 1965. Further studies on the ectendotrophic mycorrhiza. Acta Forestalia Fennica 79 (3).

— 1967. Field experiments with ectendotrophic Scotch pine seedlings. IUFRO 14 Congress. Papers 5: 149—157.

Levisohn, I. 1963. Über Mykorrhizen und Pseudomykorrhizen. In: Mykorrhiza. Intern. Mykorrhizasymposium, Weimar 1960. VEB G. Fischer, Jena. pp. 27—34.

Melin, E. 1917. Studier över de norrländska myrmarkernas vegetation med särskild hänsyn till deras skogsvegetation efter torrläggning. Norrlands Handbibliotek VII. Uppsala.

— 1923. Experimentelle Untersuchungen über die Konstitution und Ökologie der Mykorrhizen von *Pinus silvestris* L. und *Picea Abies* (L.) Karst. Mykologische Untersuchungen und Berichte 2: 73—331.

— 1925. Untersuchungen über die Bedeutung der Baummykorrhiza. G. Fischer, Jena.

Mikola, P. 1965. Studies on the ectendotrophic mycorrhiza of pine. Acta Forestalia Fennica 79 (2).

— 1967. The effect of mycorrhizal inoculation on the growth and root respiration of Scotch pine seedlings. IUFRO 14 Congress. Papers 5: 100—111.

— 1980. Mycorrhizae across the frontiers. In: P. Mikola (ed.). Tropical mycorrhiza research. Clarendon Press, Oxford. pp. 1—10.

—, Laiho, O., Eräkäinen, J. & Kuvaja, K. 1964. The effect of slash burning on the commencement of mycorrhizal association. Acta Forestalia Fennica 77 (3).

Norkrans, B. 1950. Studies in the growth and cellulolytic enzymes of *Tricholoma*. Symbolae Botanici Upsalienses XI. 1.

Rayner, M. C. 1934. Mycorrhiza in relation to forestry. I. Researches on the genus *Pinus*, with an account of experimental work in a selected area. Forestry 8: 96—125.

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.

Wilcox, H. E. 1971. Morphology of ectendomycorrhizae in *Pinus resinosa*. In: E. Hacskaylo (ed.). Mycorrhizae. Misc. Publ. 1189, U.S. Dept. Agriculture. pp. 54—68.

—, Ganmore-Neumann, R. & Wang, C. J. K. 1974. Characteristics of two fungi producing ectendomycorrhizae in *Pinus resinosa*. Canadian Journal of Botany 52: 2279—2282.

—, Yang, C. S. & LoBuglio, K. F. 1983. Responses of pine roots to E-strain ectendomycorrhizal fungi. Plant & Soil 71: 293—297.

Yang, C. S. & Korf, R. P. 1985. A monograph of the genus *Tricharina* and a new segregate genus, *Wilcoxina* (Pezizales). Mycotaxon 24: 467—531.

— & Wilcox, H. E. 1984. An E-strain ectendomycorrhiza formed by a new species, *Tricharina mikolae*. Mycologia 76: 675—684.

Zak, B. 1974. Ectendomycorrhiza of Pacific madrone (*Arbutus menziesii*). Transactions of British Mycological Society 62: 201—204.

— 1976. Pure culture synthesis of Pacific madrone ectendomycorrhizae. Mycologia 63: 362—369.

*Total of 27 references*

# Seloste

## *Havupuiden ektendomykorritsa*

Männyn ektendomykorritsan tunnusomaisia piirteitä ovat vaipan lähes täydellinen puuttuminen, voimakas ja suurisoluinen Hartigin verkko sekä juuren kuorisoluja täyttävä suurisoluinen sienisolukko. Tällainen mykorritsa on tavattu hyvin samanlaisena monilla mäntylajeilla eri puolilla maapalloa kuten Suomessa, Keski-Euroopassa, Välimerenmaissa, Pohjois-Amerikassa, Australiassa ja Uudessa Seelannissa sekä eri puolilla trooppista vyöhykettä. Tästä on päätelty, että männyn ektendomykorritsan symbionttina olisi kaikkialla sama sienilaji. Tämä laji, josta on käytetty väliaikaista työnimeä "E-kanta", on hiljakkoin todettu kotelosieneksi ja sille on annettu nimi *Wilcoxina mikolae* (Yang & Wilcox) Yang & Korf (Yang & Korf 1985) (syn: *Tricharina mikolae*). Muutamia muitakin sille lähisukuisia lajeja on kuvattu ja todettu männyn ektendomykorritsan muodostajiksi.

*Wilcoxina mikolae* muodostaa edellä kuvattuja ektendomykorritsoja suvuissa *Pinus* ja *Larix*, mutta muiden havupuusukujen (*Abies*, *Picea*, *Pseudotsuga* ja *Tsuga*) juuristoihin ympättynä se on muodostanut ektomykorritsoja, samoin koivulla ja poppelilla (Laiho 1965). Intrasellulaarin infektion voimakkuus vaihtelee jonkin verran eri mäntylajeilla, samoin eri sienikantojen välillä on tässä suhteessa todettu eroja.

*Wilcoxina*-ektendomykorritsat ovat erityisen yleisiä taimitarhoissa, varsinkin peltomaalle perustetuissa taimitarhoissa taimien ensimmäisenä kasvuvuotena. Seuraavina vuosina ektomykorritsain osuus tavallisesti lisääntyy, mutta monasti männyntaimissa on vielä taimitarhasta lähtiessään pelkästään ektendomykorritsoja. Metsämaahan istuttamisen jälkeen ektendomykorritsat tavallisesti korvautuvat ektomykorritsoilla 1—2 vuodessa. Ektendomykorritsoja on kuitenkin tavattu, joskin harvinaisina, myös luonnon taimikoissa, mm. varjossa kasvavissa kituliaissa männyntaimissa (Björkman 1942).

*Wilcoxina mikolaella* on sangen laaja ekologinen amplitudi ja maantieteellinen levinneisyys. Se tavataan sekä kylmän ilmaston alueilla että tropiikissa ja sekä happamassa että emäksisessä maassa. Erilaisissa ympäristöissä lienee kuitenkin olemassa toisistaan poikkeavia rotuja tai kantoja.

Puhdasviljelykokeissa *Wilcoxina mikolae* on käyttäytynyt jokseenkin samalla tavalla kuin ne ektomykorritsasienet, joiden fysiologisia ja ekologisia ominaisuuksia on puhdasviljelykokein tutkittu, esim. *Boletus*-, *Amanita*- ja *Tricholoma*-lajit.

Todennäköisesti *Wilcoxina mikolae* ei ole niin riippuvainen isäntäkasvin valon saannista kuin muut ektomykorritsasienet. Tämä selittänee taimien nopean infektoitumisen *Wilcoxinalla* taimitarhassa jo sirkkalehtiasteella, jolloin fotosynteesi vielä on suhteellisen heikkoa, samoin kuin ektendomykorritsan esiintymisen päällysmetsän varjossa kasvavissa taimissa. Toisaalta *Wilcoxinan* kilpailukyky luonnollisessa metsämaassa monien ektomykorritsasienten kanssa on heikko.

Vaikutuksessaan isäntäkasviinsa *Wilcoxina* ei olennaisesti poikkea muista ektomykorritsasienistä. Kokeissa se on selvästi edistänyt isäntäkasvin kasvua, mutta vaikutus eri puulajeihin on vaihdellut melkoisesti (taulukko 1). Vaikutuksen voimakkuus riippuu myös ulkoisista olosuhteista, kuten maan viljavuudesta (taulukko 3) jopa niin, että joissakin olosuhteissa vaikutus on ollut haitallinen, toisissa taas edullinen (taulukko 2).

Puuntaimien ymppäystä taimitarhoissa *Wilcoxinalla* – joko puhdasviljelmällä tai *Wilcoxinaa* sisältävällä maalla – voidaan suositella useillakin perusteilla. Onhan mykorritsain läsnäolo juuristossa taimia tarhasta metsään siirrettäessä tarpeen, koska se edistää taimien eloon jäämistä ja alkukehitystä. Luonnollinen infektio taimitarhassa taas voi viivästyä, koska kasvualustana yleisesti käytetään maata, josta mykorritsasienet normaalisti puuttuvat, kuten kasvuturvetta, tai maa tuholaisten ja kasvitautien torjumiseksi steriloidaan. *Wilcoxinan* korvautuminen muilla sienillä maastoon siirron jälkeen näyttää tapahtuvan häiriöttömästi.