Ectomycorrhizal fungi

Ponge Jean-Franççois, Muséum national d’Histoire naturelle, CNRS UMR 5176, 4 avenue du Petit-Château, 91800 Brunoy

Mycorrhizal symbiosis has been studied for a long time given its interest for the nutrition of plants (Masui 1927) and later on for their resistance to pathogens (Marx & Davey 1967) and survival in deleterious or harsh conditions (Clément et al. 1977, Marx & Artman 1979). Fungal partners may be found in the three most common groups of soil fungi, i.e. zygomycetes, ascomycetes and basidiomycetes. Each of these groups is responsible for a given type of mycorrhiza, vs. vesicular-arbuscular- (VA), ericoid and ectomycorrhizae, respectively. Some genera of ascomycetes, such as *Tuber*, *Elaphomyces*, and *Cenococcum*, are ectomycorrhizal. Roughly speaking, VA-mycorrhizae are commonly found in most herbs and nutrient-rich deciduous trees (ash, maple, etc...), ericoid mycorrhizae in Ericaceae and allies, and ectomycorrhizae in nutrient-poor deciduous trees (oak, beech, etc...), and most coniferous trees (Moore 1987). The association between mycorrhizal types and botanical classification of host plants was used by Read (1991) to stress the importance of the mycorrhizal symbiosis at the ecosystem level and moreover at the biome level. Grassland, forest and heath ecosystems are each characterized by the dominance of one or the other of these three groups of fungi according to the abovementioned relationships. Differences in the ability of mycorrhizal fungi to use different nitrogen and phosphorus sources contribute to explain this association, beside host-fungus compatibility. In vitro the ericoid endophyte *Pezizella ericae* (ascomycete) has been found able to use the most recalcitrant forms of nitrogen, such as tanned chitin, at an optimum pH less than 4 (Leake & Read 1990a, b). Since most ecological studies on VA-mycorrhizae and ericoid mycorrhizae were done in grassland and heath ecosystems, respectively, with only a few exceptions, we will speak only of ectomycorrhizal fungi.

Ectomycorrhizae are characterized by the presence of a fungal sheath around the root cortex, together with a network of transformed fungal hyphae growing in intercellular spaces of the cortex after digestion of the middle lamella (Hartig net). Specificity of host-fungus relationships is quite poor, with well-known exceptions, such as *Suillus grevillei*, which is mycorrhizal on larch trees only. Despite strong anatomical and physiological relationships with the root system of trees, mycelia of ectomycorrhizal fungi permeate noticeable parts of the forest floor (Ponge 1990) and underlying horizons (Ogawa 1985). Thus the sphere of influence of the mycorrhizal root is not confined to its immediate environment. Translocation of water (Brownlee et al. 1983) and nutrients (Bending & Read 1995) has been demonstrated between tree seedlings interconnected by ectomycorrhizal mycelial systems, but conflicting views have been expressed concerning the direct role of ectomycorrhizal fungi in major nutrient providing processes such as litter decomposition and mineral weathering. Despite repeated evidence of degrading enzymes produced in vitro by ectomycorrhizal fungi (Norkrans 1950, Giltrap 1982, Trojanowski et al. 1984, Botton et al. 1986), the application of these laboratory results to field conditions may be highly questionable. Nevertheless some field studies can be considered as highly demonstrative. The presence of an eluvial (E or A2) horizon has been observed by Hintikka & Näykki (1967) in zones occupied by fungal mats of *Hydnellum ferrugineum*, which were characterized by a strong decrease in their content in iron, phosphorus and organic matter when compared with surrounding soil unaffected by this fungus. A possible mechanism for cation release could be the prodution of high quantities of oxalic acid, with strong chelating properties, by ectomycorrhizal fungi, as demonstrated by Cromack et al. (1979) in fungal mats of *Hysterangium crassum*, and in laboratory cultures of *Paxillus involutus* by Lapeyrie et al. (1987). Similar increase in nutrient release (N, P, K, Mg, and B) has been demonstrated in litter bags colonized by *Hysterangium setchellii* (Entry et al. 1991). This may help to explain why the growth of tree seedlings might be stimulated by ectomycorrhizal fungi even in the absence of infection (Levisohn 1956). The improvement in litter decomposition rate following trenching of the soil, which was attributed by Gadgil & Gadgil (1971) to disappearance of ectomycorrhizal fungi, remains unexplained, even after similar results were obtained in Sweden by Berg (1980) and in vitro experiments were conducted by Gadgil & Gadgil (1975) themselves and later on by Dighton et al. (1987) and Durall et al. (1994), which gave contradictory results. Examination of abovementioned studies points to the importance of the true fungal species and even to the true strain, no general landscape being perceptible at the present state of our knowledge.

During the last decade research on the ecology of ectomycorrhizal fungi was stimulated to a great extent by the discovery of successional trends in ectomycorrhizal fungal communities occurring in the course of forest stand development. These findings were based on collections of fruit bodies (Dighton et al. 1981), but they were later on confirmed by the direct observation of mycorrhizae (Dighton & Mason 1985, Ogawa 1985). These successions were interestingly demonstrated as well by comparing stands of varying age than by mapping the distribution of mycorrhizal fungi at varying distances of tree bases (Frankland 1992). Early-stage ectomycorrhizal fungi, belonging to genera such as *Thelephora*, *Hebeloma*, *Inocybe*, and *Laccaria*, are mainly living in hemorganicl horizons (typically in nursery soils), while late-stage fungi, such as *Russula*, *Suillus*, *Amanita*, *Leccinum*, rather live in ectorganic horizons (typically in mature forest soils). Several processes have been advocated for explaining this successional pattern. They probably occur together, reinforcing themselves in a strong interaction network involving both fungal communities, humus profiles and trees, from establishment to death. Late-stage species have more energy (glucose) requirements but are better able to use macromolecular substrates for their growth than early-stage species (Dighton & Mason 1985, Dighton et al. 1987, Dahm et al. 1987, Gibson & Deacon 1990, Durall et al. 1994, Bending & Read 1995, Turnbull et al. 1995), although this has been recently suspected for nitrogen by Baar et al. (1997). This shift from low to high energy requirements of ectomycorrhizal flora could be compared to changes in resource allocation between roots and shoots as trees are growing. Given our present knowledge on nutrient cycles and redistribution of photosynthates to subterranean parts of forest trees (Ågren et al. 1980, Miller 1984, Meier et al. 1985, Norton et al. 1990) the following scheme can be considered as most realistic. There are two phases during which the tree spends more energy in the development of its root system than in that of its aerial parts: the seedling/sapling stage and the mature stage. These steps are characterized by lower rates of growth of aerial parts compared to subterranean parts, according to the well-known hump-shaped curve (Miller 1981). Between them there is a phase of intense growth culminating during the pole stage. Accumulation of organic matter in thick ectorganic horizons is associated with the pole phase during which more nutrients are exported from the soil system per unit time than they could be returned through litter decomposition and mineral weathering (Page 1968, Turner & Long 1975, Ulrich 1986, Bernier & Ponge 1994, Ponge & Delhaye 1995, Bernier 1996). This phase can be followed by an increase in the litter decomposition rate under adult trees, depending on the nature of ground vegetation and possible recolonization by decomposer communities (Bernier & Ponge 1994, Ponge & Delhaye 1995). The question whether the shift from early- to late-stage ectomycorrhizal species is controlled by tree physiology, environmental factors such as humus type (which can be itself influenced by tree physiology, among others) or life history of ectomycorrhizal fungi themselves remains open, since all these features vary together along time sequences. Field observations on the distribution of macrofungi according to acidity and nutrient richness (Tyler 1985) and experiments on sporocarp occurrence and ectomycorrhizal development in varying soil conditions (Baar & Elferink 1996, Baar & Ter

Braak 1996) point to differences in the sensitivity of these two groups of basidiomycetous fungi to soil acidity, richness in organic matter and in main nutrients. The removal of ectorganic horizons, despite impoverishment of the soil in nutrients, has been observed to increase biodiversity and restore the development of early-stage fungi (De Vries et al. 1995, Baar & Ter Braak 1996). Other differences between early-stage and late-stage ectomycorrhizal fungi were observed in their dissemination pathways. Mycorrhization occurs mainly through spore germination in early-stage species, but rather through mycelial development of already established individuals in late-stage species (Fox 1986). Thus early-stage ectomycorrhizal fungi are better adapted to rapid colonization of new sites open to the establishment of a new tree cohort. This should be compared to the fact that natural regeneration occurs mainly in restricted sites both in time and space, the regeneration niche (Grubb 1977), and often after pronounced disturbance (Kuuluvainen 1994). The presence of early-stage ectomycorrhizal fungi such as *Thelephora terrestris* in decaying stumps and logs (Lanier et al. 1978), a well-known niche for the regeneration of spruce and fir species (Ponge et al. 1994), can be explained only by spore dispersal. On the contrary, late-stage species have to colonize ectorganic horizons as far as leaf or needle litter is progressively shed. They remain on the same place for a long-time, the number of genets (genetically different individuals) decreasing with time while the size of mycelia increases accordingly (Dahlberg & Stenlid 1994, 1995). Thus the observed pattern of increase in biodiversity (arrival of genets in the regeneration niche) followed by a decrease (competition between established mycelia) which has been observed in developing forest stands in the absence of perturbation (Last et al. 1987), can be explained by dissemination processes, antagonisms and differences in growth rates between genetically different species or strains. The functional classification of ectomycorrhizal fungi into early- and late-stage species has been criticized by Newton (1992) on the basis of abovementioned differences in dispersion mechanisms. This criticism, together with what we know about fungal successions in small ecosystems such as decaying wood (Coates & Rayner 1985, Niemelä et al. 1995, Renvall 1995), points to the importance of dispersion abilities, growth rates and interactions between mycelia in these successional patterns. In no case the observed physiological, ecological, and populational patterns of succeeding ectomycorrhizal fungi should challenge. As this is quite common in most ecological processes, they probably self-reinforce themselves, which could explain why, despite apparent complexity and incertitude, some common trends have been repeatedly observed in various forest ecosystems.

Interactions between ectomycorrhizal fungi and their environment concern also, among others, their role in the production of humic substances which, in turn, may influence their development and select them. The production of humic acid like substances by ectomycorrhizal fungi has been documented (Tan et al. 1978), but this phenomenon occurs with other fungi as well, as far as they produce melanins. This is the case in dematiaceous fungi, i.e. fungi with dark hyphal or spore walls (Valmaseda et al. 1989, Paim et al. 1990). Among dematiaceous fungi, the ectomycorrhizal ascomycete *Cenococcum geophilum* deserves attention. Given its wide host range and ecological tolerance it can be considered as the most widespread ectomycorrhizal fungus over the world (Trappe 1964). Its resistance to adverse conditions, such as high salt concentration, drought, acidity, shading, as well as water-logging, has been long time widely documented (Ferdinandsen & Winge 1925, Mikola 1948, Saleh-Rastin 1976, Meyer 1987). It has been demonstrated that allelopathic substances, when used at concentrations which prove inhibitory to other ectomycorrhizal fungi, may stimulate the growth of *C. geophilum* (Brown & Mikola 1974, Rose et al. 1983). Thus this fungus is directly or indirectly favoured by environmental conditions which preclude the development of most other ectomycorrhizal fungi. Its abundance in raw humus (mor) has been reported for a long time (Müller 1886) and even it has been considered by Meyer (1964) as responsible for the formation of this humus form. Its presence as a mycorrhizal symbiont of ericaceous species has been reported, too (Largent et al. 1980). The following sequence into which *C. geophilum* could be involved (rather than considered as responsible for the observed changes) can be considered in observed shifts towards mor humus when the forest ecosystem turns to an ericaceous heath (Bernier et al. 1993). Any process by which *C. geophilum* is favoured and other ectomycorrhizal fungi are disfavoured (for instance drought, water-logging, short rotations, or sylvicultural practices favouring growth of an ericaceous or fern understory) will start an excess development of this fungus in the humus profile, together with a decrease in the activity of most decomposer organisms. Its mycelium is known for the thickness of its wall (Ponge 1988, 1990), and its content in pigments (melanins) which reaches 11% (Mangin et al. 1986). This fungus seems to be a food resource for a lot of litter-dwelling animals, mostly enchytraeids, but these animals are unable to digest its hyphal wall, the transformation of which into a black amorphous mass having been observed only in old faeces of some oribatid mites (Ponge 1985, 1991). Thus the recycling of nutrients which have been immobilized in the walls of this fungus, such as nitrogen and phosphorus (Mangin et al. 1986), can be delayed a long time after death of the fungus occurs actually. Beside local impoverishment of the upper part of the soil in nutrients such as nitrogen and phosphorus, a quantity of organic matter is slowly humified, creating highly stable acid micro-sites within ectorganic horizons (Nilsson et al. 1982, Hänninen et al. 1987). In the absence of any mixing with mineral matter, which is the case at a low level of earthworm activity (Bernier & Ponge 1994), this process will contribute to the development of a strictly epigeic faunal activity (moder humus form), with a superficial and dense root system of trees (Meyer & Göttsche 1971, Babel 1977), associated with a dense mycorrhizal mycelial weft (Read 1987, Ponge 1990). At this stage of development of the observed shift, i.e. dominance of *C. geophilum* and enchytraeid-dominated faunal activity, with a strong acidity in ectorganic horizons, the biodiversity of both faunal and microbial communities is strongly reduced (Rastin et al. 1990, Ponge et al. 1997). Any further reduction in the nutritional status of the ecosystem and further increase in the production of toxic compounds such as phenolics or free aluminum, for instance following acid rain (Esher et al. 1992), deforestation (Zackrisson 1985) or badly adapted sylvicultural practices (Bernier & Ponge 1993), will cause the disappearance or strong reduction of some important functions such as litter comminution by fauna (Handley 1954) and ectomycorrhizal symbiosis (Blaschke 1986), by lack of suitable partners. This is associated with the collapse of the forest ecosystem (Oldeman 1990) and its replacement by the ericaceous heath with mor humus (Bernier & Ponge 1993), the features of which may still subsist after reafforestation (Scotto La Massese et al. 1980, Baar 1996).

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