EUROPEAN SCIENCE FOUNDATION
SETTING SCIENCE AGENDAS FOR EUROPE

Exploratory Workshop Scheme

Standing Committee for Life, Earth and Environmental Sciences (LESC)

ESF Exploratory Workshop on

Diversity and Function in Ectomycorrhizal Communities

Nancy (France), 7-8 December 2009

Convened by:
Jean GARBAYE

SCIENTIFIC REPORT

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1. Executive summary

As shown by a previous ESF Exploratory Workshop on *Functional Biodiversity* held in Potsdam on June 2-4, 2008, there is a growing interest for this branch of ecological sciences, especially concerning two complementary challenges. The first one is about the structure-function relation in species communities; it aims at understanding how the functional traits contribute to the assemblage of species and determine the stability of the community structure, and how the activities of the different species combine in the community and result in processes at the ecosystem level. The second challenge, particularly relevant because of the present climate change concerns, is more answerable to applied ecology: how to control and manage the complex network of functional interactions in communities in a changing environment.

The objective of the 2009 project was to convene another, more specialized ESF Exploratory Workshop in order to apply the general concepts of community ecology and functional biodiversity to these two challenges in the precise case of the ecology and management of European forests, targeting the central compartment of any forest ecosystem: the community of the symbiotic fungi which inhabit the roots.

Besides its main sponsor the European Science Foundation, the workshop has been co-sponsored by the *Région de Lorraine,* the EU Network of Excellence EVOLTREE and INRA (*Institut National de la Recherche Agronomique).* The convenor, Dr. J. Garbaye, belongs to the Tree-Microbe Interactions laboratory of the INRA Forest Research Centre in Nancy.

The workshop was held in Nancy (France) over two full days. Participation numbered 18 people from nine countries, excluding the French convenor and the ESF representative. Besides 17 European researchers in the field, a speaker from the United States had been specially invited in order to put the present researches on ECM communities in the perspective of the general concepts of functional ecology. One invited speaker (Dr. Leho Tedersoo, from Estonia) failed to attend at the last moment because of health condition. Also due to health condition following an accident, Dr. Franck Richard from Montpellier has been replaced by co-worker Mélanie Roy.

The premises (the three-star hotel Park Inn in downtown Nancy), where all participants were accommodated, provided the ideal surrounding for such a small but intense meeting. In addition to the formal, moderated discussions in a comfortable meeting room, long coffee breaks and standing buffet lunches permitted plenty of informal interactions. The social evening of Dec. 7 also provided opportunities for participants to get acquainted with each other. Dr. François Le Tacon, mycorrhiza research scientist in INRA Nancy and renowned specialist of the Nancy's *Art Nouveau* school, led a private guided visit of the Daum's cristal work collection in Nancy's Museum of Fine Arts. Then, the whole party had dinner at the *Brasserie Excelsior,* a famous example of the A*rt Nouveau* architecture in Nancy around 1900.

The workshop has ended with a round table specially designed to translate the synthesis of the previous presentations and discussions into guidelines for further research and strategies to implement new collaborative projects (see section 3 for short-term research perspectives). The first practical result is a project of ESF network on the functional ecology of ectomycorrhizal communities proposed by a colleague from UK.

The full texts of selected communications from this exploratory workshop will be published in a special issue of *Annals of Forest Science.* The abstracts are in the Appendix at the end of this scientific report.

2. Scientific content of the event

European forests are presently suffering from increasing stresses from natural and man-made origins which affect not only the tree stands themselves but also the quality and quantity of ecosystem services such as wood production, soil protection, nutrient cycling, carbon sequestration or water quality.

These forests are dominated by social tree species that form mono-specific stands characterized by a particular type of root association with fungi: the ectomycorrhizal (ECM) symbiosis. The ectomycorrhizal communities play a major role in biogeochemical cycles, primary production and ecosystem sustainability. At the same time, they are shaped by sylviculture and environmental disturbances. The complexity of these interactions and the lack of appropriate investigation methods have so far prevented from deciphering the functional structure of ectomycorrhizal communities and its response to abiotic factors.

A range of new techniques has recently been developed to explore *in situ* the functional diversity of ectomycorrhizal communities. This makes possible for the first time to decipher the complex temporal and spatial activity patterns within them, as well as to determine to which extent they contribute to the resilience of the ecosystem when faced to environmental disturbances. This is the key to understand their contribution to ecological processes of interest for sylviculture, soil conservation and landscape management.

The present exploratory workshop aimed at bringing together the European scientists working in this rapidly developing field and discuss the most recent results of their research in the perspective of adapting the sylvicultural practices accordingly. It was organized with 18 invited speakers into four main sessions devoted to different categories of functions played by ECM communities in forest ecosystems. Each speaker delivered a 30-minute presentation followed by 10 minutes of question-answer exchange and general discussion the abstracts of the presentations are given in the Appendix). This time schedule proved to be adequate and provided enough time for the speakers to go deep in their subject and for the audience to contribute actively to the discussion.

- *Session 1 (four presentations)*: diversity of ECMs for non-nutritional functions (i.e. in how the symbiotic fungi contribute to protect roots against pathogens and chemical pollutants or control the hormonal status and development of the trees).
- *Session 2 (five presentations):* diversity of ECMs for nutritional functions (i.e. in how the symbiotic fungi contribute to mobilize water and inorganic nutrients and to their uptake by the trees).
- *Session 3 (four presentations)*: diversity of carbon status and translocation in the ectomycorrhizal symbiosis (fungus strictly dependant on photosynthates *vs* partly saprotrophic, tree strictly autotrophic for carbon *vs* partly myco-heterotrophic, time pattern of carbon fluxes, carbon 'cost' of the symbiosis for the plant host, tree phenology and seasonality, carbon transfers in mycelial network, etc.).

- *Session 4 (four presentations)*: structure-function relations in ectomycorrhizal communities (functions and assembling rules, functional groups, complementarity *vs* redundancy, etc.) and response to disturbance. A speaker from the US (Prof. Koide, Pennsylvania State University) had been specially invited to open this session and put the present researches on ECM communities in perspective with the general concepts of functional ecology.

An additional communication dealt with the broader subject of ECM fungi as a commercial component of managed forests through the production of edible fruiting bodies, in perspective with the global climate change.

Finally, the workshop ended with a general discussion in the form of a round table moderated by the convenor J. Garbaye and dedicated to defining research priorities and planning future collaborative projects (see next section of the scientific report).

3. Assessment of the results, contribution to the future direction of the field

The last session of the workshop (on Tuesday night) ended with a two-hour and a half round table on *"Plans for follow-up research activities and/or collaborative actions"*. The warm and lively intercourse, rooted in the previous presentations and discussions, resulted in the following guidelines for short-term research perspectives:

Carbon and nutrient cycling

- Carbon cost of ECM exploration types: do exploration types share energy cost?
- Carbon fluxes through ECM communities in forest ecosystems (allocation of photosynthates and SOM-derived C to trees, mycelium and fruiting bodies).
- Phosphorus at the plant-fungus interface (transport, fluxes, diversity of mechanisms).
- What soil nutrient sources are available to ECMF?

Structure-function in ECM communities

- How does community structure affect N and C cycles?
- Are there proxis to functions (e.g. tree growth, soil respiration, etc.)?
- What are the most relevant functional traits?
- Spatial distribution of functional traits.
- Phylogeny of functional traits.
- Linking traits and functional groups.
- Phenotypic plasticity of ECM fungi.
- How do species assemble and disassemble?
- Biotic interactions between species.
- Ascomycetes vs. Basidiomycetes: how functionally distinct are these two categories of ECMF?

ECM communities in forest ecosystems and at the global scale

- Position in the food web.
- Effect on tree stand nutrition and health.
- ECMF as indicators of ecosystem quality.
- Contribution to the global climate model.

Questions of research strategy

- How to quantify the functional diversity of ECMFs?
- Addressing 3-D space occupation by ECM communities.
- Metabiosis in ECM communities.
- Reduce the diversity of model systems.
- Length-biomass relation in ECM mycelium.
- Linking fruiting body production with ECM functional community structure.

A number of the participants to the present exploratory workshop are or have already been collaborating on the subject through European or national programmes such as the Network of Excellence EVOLTREE or the French ANR project FUNDIV, with French, Swiss and German partners. This meeting has clearly tightened these links further and triggered talks for new collaborative projects with extended consortia.

For instance, in the short term, the participant from UK (Dr. Andy Taylor), stimulated by the outputs of this exploratory workshop and by Mr. Avril's presentation of ESF, expressed his intention to apply for an ESF Research Network on the functional aspects of ectomycorrhizal communities as soon as he gets the authorization from his home institution (Macauley Land Use Research Institute, Aberdeen). The participants to the Nancy exploratory workshop will naturally be privileged partners in such a project.

Concerning the dissemination of the outputs of the workshop, seven (7) participants to date have positively answered to the invitation of the journal *Annals of Forest Science* to publish full papers of their communications in a special issue on ectomycorrhizal communities.

4. Final programme

Monday 7 December 2009

8:30-8:40	**Welcome by Convenor** **Jean Garbaye** (INRA, Nancy, France)
8:40-9:00	**Presentation of the European Science Foundation (ESF)** **Bernard Avril** (Standing Committee for Life, Earth and Environmental Sciences, ESF, Strasbourg, France)
9:00-12:00	**Morning Session: Diversity of ECMs for non-nutritional functions**
9:00-9:40	**Presentation 1 "Water uptake and resistance to desiccation"** **Sylvia HUTTER** (WSL, Zurich, Switzerland)
9:40-10:20	**Presentation 2 "Response of ECM communities to environmental pollution — Scots pine *vs* poplar"** **Maria RUDAWSKA, Tomasz LESKI and Leszek KARLINSKI** (Polish Academy of Science, Poznan, Poland)
10:20-10:40	*Coffee / Tea Break*
10:40-11:20	**Presentation 3 "Detoxification and protection of roots by ECM fungi"** **Jan COLPAERT** (University of Hasselt, Belgium)
11:20-12:00	**Presentation 4 "Growth regulators and control of plant development"** **Titty SARJALA, Haly HÄGMAN and Karoliina NIEMI** (Finnish Forestry Research Institute (METLA), Parkano, Finland)
12:00-14:00	*Buffet lunch*
14.00-17:40	**Afternoon Session: Diversity of ECMs for nutrient mobilization and uptake**
14:00-14:40	**Presentation 1 "Foraging and nutrient translocation in ectomycorrhizal communitiess"** **Reinhard AGERER** (Ludwig Maximilien University, Munich, Germany)
14:40-15:20	**Presentation 2 "Enzyme secretion by ectomycorrhizal fungi and exploitation of mineral nutrients from soil organic matter"** **Karin PRITSCH** (Helmoltz Center, Munich, Germany)
15:20-16:00	**Presentation 3 "Diversity in Nitrogen mobilisation and uptake"** **Andy TAYLOR** (Macaulay Land Use Resarch Institute, Aberdeen, UK)
16:00-16:20	*Coffee / tea break*
16:20-17:00	**Presentation 4 "Diversity for phosphorus mobilisation and uptake"** **Claude PLASSARD** (INRA, Montpellier, France)
17:00-17:40	**Presentation 5 "Weathering of minerals by ECM fungi"** **Anna ROSLING** (Swedish University of Agricultural Sciences, Uppsala, Sweden)
18:15	*Guided visit of the Daum glassware collection in the Museum of Fine Arts by François LE TACON, specialist of the Art Nouveau School of Nancy.*
20:30	*Dinner at the Brasserie Excelsior near the hotel*

Tuesday 8 December 2009

9:00-12:00	**Morning Session: Diversity in Carbon cycling**
9:00-9:40	**Presentation 1 "Meta-genomic approach of the diversity of ECMs for cellulolytic activity"** **Roland MARMEISSE** (CNRS, Lyon, France)
9:40-10:20	**Presentation 2 "Saprotrophy of ECM fungi and interactions with decomposers"** **Pierre-Emmanuel COURTY** (University of Basel, Switzerland)
10:20-10:40	*Coffee / Tea Break*
10:40-11:20	**Presentation 3 "Carbon cost of the ECM symbiosis and carbon allocation to external mycelium"** **Håkon WALLANDER** (University of LUND, Sweden)
11:20-12:00	**Presentation 4 "Sugar uptake and metabolism in ectomycorrhizas"** **Uwe NEHLS** (University of Bremen, Germany)
12:00-13:40	*Buffet lunch*
14:00-16:20	**Afternoon Session: Structure-function relations and response to disturbance**
13:40-14:20	**Presentation 1 "General concepts of functional ecology of ectomycorrhizal fungal communities"** **Roger KOIDE** (University of Pennsylvania, University Park, USA)
14:20-15:00	**Presentation 2 "Case study #1: the effect of liming on ECM community structure and functioning"** **François RINEAU** (University of LUND, Sweden)
15:00-15:40	**Presentation 3 "Case study #2 : effect of drought on structure and function of ECM communities in a *Quercus ilex* forest in the Mediterranean area"** **Mélanie ROY** (CNRS Montpellier, France)
15:40-16:20	**Presentation 4 "Functional and taxonomic diversity: example from ECM fungi in the FunDiv project"** **Alain FRANC, Myriam DUCHEMIN, Elvire LEGNAME, Mélanie ROY and Claude PLASSARD** (INRA, Bordeaux, France)
16:20-16:40	*Coffee / Tea Break*
16:40-22:00	**Evening Session: Implications in terms of ecosystem services and forest management**
16:40-17:20	**"Forest mushroom diversity and productivity: an indicator of forest health?"** **Simon EGLI** (WSL, Zurich, Switzerland)
17:20-18:00	**Presentation of the European Science Foundation** **Bernard Avril** (ESF headquarter, Strasbourg, France)
18:00-20:30	**Round table "Plans for follow-up research activities and/or collaborative actions"**
20:30	*Dinner*
22:30	*End of Workshop*

5. Statistical information on participants

- Eighteen (18) contributing participants (presenting oral contributions) + 1 convenor + 1 ESF representative. The invitee from Estonia (Dr. Leho Tedersoo) fell ill just before the workshop and had to cancel his travel.
- Proportion of "young" scientists: 5/18 (28 %)
- Proportion of female scientists: 7/18 (39 %)
- 9 countries: France, Germany, Belgium, USA, Poland, UK, Finland, Sweden, Switzerland.

6. Final list of participants

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Appendices: abstracts of the communications

Water uptake and resistance to desiccation

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The Intergovernmental Panel on Climate Change (IPCC) has published a report stating a realistic possibility of a significant climate change within this century. European forest ecosystems will most likely be confronted with higher temperatures and a temporal distribution of the precipitations from summer to winter months. ECMs reflect important functions in maintaining the balance in these forest ecosystems, by eg. improving the water uptake and increasing the drought resistance of the plants. Several thousand fungal species live in ectomycorrhizal symbiosis with trees. It becomes more and more evident, that these different ectomycorrhizal species differ in their functional abilities and, thus, exhibit differing benefits for the host plant. So a closer look will be made on single species in performing these functions. Moreover recent results on this topic from an irrigation experiment in one of the driest valleys in Switzerland will be discussed.

Response of ECM communities to environmental pollution - Scots pine vs. poplars

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So far it is unclear, how mycorrhizal root systems of different trees function under unfavorable site conditions influenced by environmental pollution. The aim of the present investigations was to compare the diversity and abundance of mycorrhizas of Scots pine and different clones of poplars subjected to environmental pollution originating from copper smelter or phosphate fertilizer plant. Ectomycorrhizal (ECM) communities of 22 years old Scots pine were assessed on a 5000 m^2 stands situated either in the vicinity of phosphate fertilizer plant (resulting in acidified soil and increased aluminum level) (Luboń) or active copper smelter with soil characterized by high metal contamination (Cu, Pb, Zn, Cd) (Głogów). Reference site was represented by stand situated in the forest free of acute industrial pollution and reflecting mycorrhiza diversity of the intact environment (Kórnik). Aboveground, sporocarp surveys revealed in total 31 species: 17 in reference site (Kórnik), 17 in Luboń considered as moderately polluted site and 10 in Głogów considered as heavily polluted site. In compare with the reference site the total number of sporocarps was stimulated by industrial pollution and was 10 times higher in Luboń (with the most abundant fruiting species of *Suillus luteus*, *Paxillus involutus*, *Lactarius rufus* and *Laccaria laccata*) and 6 times higher in Głogów (with the most abundant fruiting species *L. laccata*, *P. involutus* and *Scleroderma citrinum*). Belowground, ECM morphotypes were identified by morphological/anatomical analysis and comparing sequences of the internal transcribed spacer region from nuclear rDNA with sequences from the GenBank database. Colonization rate of tested pines at all stands was near 100 %, but the total number of mycorrhizas differed significantly between stands and was the lowest in heavily polluted site in Głogów and the highest in Luboń, considered as moderately polluted site. Twenty nine fungal species were identified by molecular analysis of their ectomycorrhizas. The species richness of tested sites was higher in stands with disturbed soil (17 in Luboń, 16 in Głogów) than with undisturbed soil in reference site (13 species). Each site showed site-specific ECM communities. In the most heavily polluted site near the copper smelter 56 % of the total number of identified species was site specific. The most abundant was fungi with masses of extramatrical mycelium identified as Atheliaceae. The total number of mycorrhizas decreased rapidly with soil depth for control and slightly polluted site. In contrast in the heavily polluted site the highest number of mycorrhizas was moved into the deeper (20-30 cm) part of the soil profile. The distribution of the fungal types did not show a vertical niche differentiation. We speculate that along with changes in soil condition the EMF community shifts into the taxa more specialized for acidified conditions and high availability of Al (e.g. *Phialophora finlandia*, *L. rufus*) or heavy metals (e.g. *Atheliaceae, Xerocomus subtomentosus, S. citrinum*).

Similar data set were also obtained on different poplar clones, and ECM communities of Scots pine and poplars were compared. Our data provide ecologically important information about the direction of changes of ECM community of forest ecosystem on disturbed sites in industrial areas compared with those on undisturbed soils of the area free of acute industrial pollution.

Detoxification and protection of roots by ECM fungi

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Organisms trying to survive in polluted ecosystems are subjected to selective pressures for increased resistance to the toxic pollutants. Evolutionary adaptation to heavy metal toxicity is a well-documented phenomenon in different groups of organisms including bacteria, higher plants, animals and fungi. However, such genetic modifications resulting in true tolerance occur in relatively few species. Surprisingly, on toxic soils some tree species can survive without acquiring additional heritable metal tolerance traits. The question arises whether these trees can colonize metal-polluted sites with the assistance of particular mycorrhizal fungi that have acquired increased metal tolerance.

Up to now, no highly adapted fungi with a distribution restricted to contaminated soils were detected. There is only some circumstantial evidence that mycorrhizal communities, both ECM and AM, are affected by heavy metal pollution. Species diversity seems to be lower on the most polluted areas, but in general, we have only a very incomplete view on the biodiversity of mycorrhizal fungi in metal-polluted environments.

The heavy metal tolerance in the ectomycorrhizal fungi from the Suilloid clade is now well documented and the importance of this tolerance for host plants exposed to toxic metal concentrations is evident. The specific zinc and cadmium tolerance mechanisms in *Suillus luteus* were investigated. Both zinc and cadmium tolerance is based on exclusion mechanisms. Zn-tolerant *Suillus* genotypes accumulate less Zn than their sensitive counterparts. Flux studies were performed to unravel the patterns of Zn accumulation in these fungi and two Zn-transporter genes of the CDF-family were studied. Identification of the molecular determinants of the zinc homeostasis network in *Suillus* is essential to better understand the mechanisms responsible for the adaptive zinc tolerance in *S. luteus*. The metal exclusion mechanisms in the fungi result in a lower transfer of these metals towards a host plant. Together with the better nutrient acquisition, metal-adapted ectomycorrhizal fungi assist their host plants in their survival on severely metal-polluted sites.

Growth regulators and control of plant development by ECMs

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Ectomycorrhizal (ECM) fungi have been reported to produce auxins, cytokinins, gibberellins, ethylene and polyamines (referred to here as a plant growth regulator, PGRs). However, ability to produce a certain plant growth regulator has been shown to be highly variable depending on the fungal strain and culture conditions. The role of fungal PGRs in plant development is complicated because, in addition to the production of the fungus, it depends on the plant's ability to take up PGRs and the balance between plant´s endogenous PGRs and those taken up. Both auxins and PGRs are known to be essential in primary processes of the plant cell. Auxins stimulate cell division and early phase of cell elongation by loosening cell walls but inhibit the later phases of elongation. It also participates in for example, phototropism, geotropism and hydrotropism. PGRs are involved in stimulation of cell division, response to environmental stresses and regulation of rhizogenesis, embryogenesis, senescence, floral development and fruit ripening.

Both auxin and PGRs play an important role in the development of root architecture and rooting process and putrescine (Put) has been suggested to interact with indole-3-acetic acid (IAA) during root formation. Slankis (1973) was the first to postulate the involvement of production of IAA by the ECM fungus to root morphology and mycorrhiza formation. Recently, it has also been shown that PGRs are tightly involved in the interaction between tree roots and ECM fungi.

We have studied production of IAA and PGRs by different ECM fungi and involvement of them in adventitious root formation, subsequent root growth as well as ECM formation of *P. sylvestris*. Production of IAA has varied significantly between fungal species and strains. Although exogenous auxins are well known to induce root formation, there has been no correlation between IAA production and root induction by the ECM fungus. When rooting fascicular shoots *in vivo*, the root induction was dependent on the interaction between fungus and plant genotypes. In the case of hypocotyl cuttings *in vitro*, the fungus *Paxillus involutus* with low IAA producing but high Put producing activity *in vitro* resulted in better rooting percentage and also subsequent root growth than *Pisolithus tintorius* with high IAA producing activity. However, the fungus did not form ECMs, which in several studies have been shown to be regulated by fungal IAA.

The presence of the ECM fungus induces significant changes in PGR concentrations both in the shoots and roots of the host plant *P. sylvestris*. Changes are dependent on the fungus strain and developmental phase of the host plant. The most significant change is a transient increase in Put concentrations in the shoots of *P. sylvestris* seedlings *in vitro* concomitantly with increased growth of the host plant in the pre-mycorrhizal phase. This change was caused, for example, by *P. involutus* with low IAA producing activity and no ability to form ECMs. On the other hand, *P. tintorius* with high IAA production and ability to form ECMs caused only a slight increase in Put concentration in the shoots and resulted in a slower root growth. Production of the PGRs of the fungus and its effects to root growth is variable and dependent on the fungus strain. For example, fungus with low IAA production may, however, induce good root growth. In addition, the increase in PGRs and improved growth in the early phase of interaction do not necessarily correlate with subsequent ECM formation

Foraging and nutrient translocation in ectomycorrhizal communities

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Ectomycorrhizae show a high diversity of functionally important features as indicated by functional anatomics. Most important is amount, organization and range of extramatrical mycelium. Of particular importance is the internal structure of rhizomorphs because of their function as tools for long-distance transport. The so-called exploration types represent categories of putative ecological importance of ectomycorrhizae. In addition, the relation to water plays an important role, whether ectomycorrhizae are hydrophilic, being easily in contact with water, or whether they reveal a hydrophobic nature.

Four aspects will be treated: Features important for foraging strategies, characteristics facilitating nutrient translocation, competition for nutrients, and investments of ectomycorrhizae for nutrient acquisition.

Enzyme secretion by ECM fungi and exploitation of mineral nutrients from soil organic matter

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Before nutrients can be taken up by ectomycorrhizal roots they have to be mobilised - unless they are already in solution. The nutrient source in soil can either be parent rock and minerals therein – a topic which is covered by Anna Rosling – or from organic material - usually litter. Plant roots which become mycorrhizal as well as hyphae of mycorrhizal fungi actively grow towards patches of nutrient enrichment. Several tracer studies showed allocation from these patches along ectomycorrhizal hyphae to the plant.

For the release of nutrients from complex organic materials such as leaves or dead roots enzymes are needed. For the break-down of organic material which entraps the nutrients different enzymes are involved for example those responsible for the breakdown of dead plant materials such as cell walls (oxidases such as laccase, and hydrolases such as cellulases, hemicellulases and others). By mineralising organic nitrogen (see Andy Taylor's presentation) or organic phosphorus forms (see Claude Plassard's presentation) nutrients are recycled and made available for plant uptake and growth. Nitrogen and/or phosphorus are contained in a broad range of natural polymeric compounds such as for example nucleic acids, proteins, chitin. For this variety of different natural sources correspondingly a range of different enzymes are involved in their biochemical break-down processes.

Only recently methods have been developed to allow biochemical studies addressing functional diversity of field sampled excised ectomycorrhizae on the basis of their enzyme activity profiles. In this approach potential enzymatic activities of up to eight different enzymes are determined by repeated enzyme activity measurements on individual mycorrhizal tips that can be identified if necessary on the basis of DNA analyses. This approach has been widely used by now as for example in a joint project (FUNDIV) that aims at analysing structural and functional diversity of ectomycorrhizal communities and their response to disturbances such as drought, fertilisation, or elevated ozone concentrations.

Another approach allows in situ measurements of enzyme activities on imprints of roots and mycelia on membranes that are subsequently stained for specific enzyme activities. Although restricted by a low number of suitable enzymes, this method allows for assaying location of enzyme activities even in mycelial structures that are difficult if impossible to asses by other methods.

Several open questions need to be addressed in future enzyme work on field sampled ectomycorrhizae:

How can we study enzyme activities of naturally grown mycelia? How can we separate enzyme activities derived from plant roots, mycorrhizal mycelia, bacteria and saprotrophic colonisers of ectomycorrhizae? What do enzyme activity measurements tell us? What other methodical approaches could we use as a supplement to enzyme activity measurements?

Diversity in Nitrogen mobilisation and uptake

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Taxonomic diversity within soil microbial communities has often dictated a simplified approach with the recognition of broad functional groups as a compromise to understanding the complexity. Inherent within the idea of functional groups is the concept of organism redundancy or functional equivalency, which implies that any organism within a functional group can take the place of any other. For the great majority of soil organisms; including ectomycorrhizal (ECM) fungi, these concepts are largely unexplored. There is however, a widespread assumption that is often put forward in the literature that there is great functional diversity and niche specialisation among ECM fungi. During this presentation I will examine this assumption using several avenues relating to the acquisition of N from various substrates by ECM fungi. In particular, the ideas of qualitative and quantitative differences in functional traits will be examined.

Early studies on potential differences in N acquisition abilities among ECM fungi resulted in the widespread use of the terms protein and non-protein fungi, which described ECM fungal isolates that could utilise protein as an N source and those that could not, respectively. More recent studies using methods independent of high biomass production have demonstrated that this ability may be more quantitative and potentially universal among the dominant taxa in the boreal forest. Similarly, detailed studies of growth on nitrate found large quantitative differences among isolates, but with all isolates showing some growth. These results were contradictory to field observations on the response of ECM species to N fertiliser additions but may be explained when considered in relation to the morphological diversity in the mycorrhizal structures by the ECM taxa. These and other studies will be used to suggest potential directions for exploring ECM functional diversity and to highlight the need for integrated approaches that incorporate physiology and morphology with organism ecology. In addition, although this contribution is entitled 'Diversity in Nitrogen mobilisation and uptake, it is important to remember that nutrient acquisition is only one part of the relative efficiency of the symbiotic association between an ECM fungus and its host plant. It is necessary to extend the concept of functional diversity among ECM fungi beyond the acquisition of N (and other nutrients) to include the relative cost of nutrient transfer to the host plant.

Diversity for phosphorus mobilisation and uptake

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Ectomycorrhizal (ECM) symbiosis improves markedly the P nutrition of the host plant, but the mechanisms sustaining this positive effect are not all understood. Several hypothesis have been proposed to explain this positive effect that are (1) a better soil exploration and a better Pi uptake from soil solution, (2) the ability of fungal partner to produce organic anions to mobilise insoluble mineral phosphorus and (3) the ability of the fungal partner to release acid phosphatases (Pases) to mobilise organic phosphorus.

Regarding the first mechanism, a better knowledge of transport systems able to mediate Pi uptake by the fungal partner should help us to understand how the fungus favours Pi accumulation by the host-plant. Here, the functional characterization and the patterns of expression of two phosphate (Pi) transporters identified in the ectomycorrhizal basidiomycete *Hebeloma cylindrosporum* will be presented. These two Pi transporters exhibited different affinities for Pi when expressed in yeast. Expression patterns of the two genes in ECM plants grown in a low-P or high-P soil indicate that the two transporters might be differentially involved in the uptake of Pi from the soil solution according to soil P availability. However, recent data suggest that the expression of these two genes may be dependent upon the soil type. Finally, the two genes from *H. cylindrosporum* will be compared with the data obtained so far in other fungi.

Regarding the second mechanism, data obtained so far with ectomycorrhizal species indicate that a huge variability to produce organic anions exists among the studied species. However, data obtained with a fungal species able to release high amounts of oxalate demonstrated its capacity to improve the P nutrition of the host plant, confirming that this fungal property is an important mechanism used by ectomycorrhizal fungi.

Finally, regarding the third mechanism, recent data obtained in the field indicate that a high variability to release acid phosphatase activity occurs among ectomycorrhizal fungi associated with *Pinus pinaster* trees planted in the region of “The Landes de Gascogne”, near Bordeaux. The results obtained so far showed that the regulation of phosphatase activity evaluated *in situ* is complex. This was confirmed when we used *H. cylindrosporum* to study how many isoforms displaying acid phosphatase activity could be released by this fungal species.

Weathering of minerals by ectomycorrhizal fungi

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Ectomycorrhizal fungi are mutualistic symbionts of many forest trees and play a mayor role in nutrient uptake. They form diverse communities in boreal forest soils but functional differences within this diverse group of fungi remain largely unknown. We study ectmycorrhzial fungi in mineral soil to determine how abiotic preferences and biotic interactions influence their spatial distribution in stratified soil profiles. This is achieved by correlative field studies of species distribution and soil characteristics at a spatial resolution relevant to soil heterogeneity and mycelial size.

Most studies of ectomycorrhizal fungi on roots focus on the organic and upper mineral soil, where root density is high. In a typical podzol profile, however, 65% of the short roots were found in the mineral soil. The composition of the ectomycorrhizal community was shown to vary depending on the soil horizon. As much as half of the ectomycorrhizal taxa were restricted to mineral soil horizons.

In Podzol soils the forms of phosphorus vary from complex organic forms in the litter layer, to simpler organic forms in the organic soil. Further down the profile complex forms accumulate and primary minerals, such as apatite (Ca10(PO4)6(OH,F,Cl)2) are found in the mineral soil (Figure 1a). To obtain phosphorus from this range of phosphorus forms, fungi need to adopt different strategies such as enzymes, acids and possibly siderophores (Figure 1b). We hypothesis that different strategies to release phosphorus is a determinant for the observed differential composition of ectomycorrhizal communites in vertically stratified soil profiles.

Species-specific substrate preferences are examined by studies of regulation of enzymatic and biogeochemical activity in response to relevant organic and inorganic sources of phosphorus. Studies of four species in the genus Piloderma have demonstrated that different strategies to obtain phosphorus are reflected by their spatial distribution in a podzol soil profile.

Ectomycorrhizal fungi have been demonstrated to induce weathering of primary minerals and this activity has been suggested to play a central role in forest nutrient availability. Production of LMMOAs is frequently addressed, as the main agent of biotic weathering in soil. Mechanisms by which ectomycorrhizal fungi may induce weathering in response to nutrient limiting growth conditions remains largely unresolved. Future studies of weathering by ectomycorrhzial fungi must be performed using fungal isolates and conditions relevant to the process and nutritional constrains of the studied system.

Meta-genomic approach of the diversity of ECMs for cellulolytic activity

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The extraradical mycelia of ectomycorrhizal fungi play an essential role in soil nutrient acquisition by being capable of exploiting complex molecules such as chitin or proteins as N sources. Significant degradation of plant-derived soil organic matter, in the form of lignocellulosic material, by ectomycorrhizal fungi remains however a controversial issue. Ectomycorrhizal fungi are nevertheless known to produce laccase, an enzyme susceptible to interact with lignin.

Recent developments in environmental genomics offer an opportunity to study *in situ*, directly in the soil the activities expressed by complex communities of microorganisms. Metatranscriptomics is an approach based on the direct extraction of RNA from soil, followed by their conversion into sDNAs which can be cloned to constitute soil cDNA libraries representative of the genes expressed by the soil microbial community. Since eukaryotic mRNA can be specifically isolated thanke to their polyA tail, metatranscriptomics can specifically target soil eukaryotic microorganisms, among which ectomycorrhizal fungi. Soil cDNA libraries can be specifically explored by systematic sequencing or by expression in heterologous microbial host cells such as *Saccharomyces cerevisiae.*

This strategy was followed to compare two forest soil communities, one under beech and the other under spruce trees, two plant species which differ with respect to the quality, chemistry and degradability of the litter they produce.

The diversity of eukaryotes, and more specifically of the fungi present in the studied soils, was explored by cloning and sequencing different portions of the nuclear rRNA cluster and also of the mitochondrial cox1 gene. The content of the cDNA libraries made from each of the soil was explored by focussing on genes encoding enzymes acting on plant-derived organic molecules. In this respect, we identified carbohydrate active enzymes, different fungal enzymes potentially involved in lignin breakdown as well as members of different families of P450 monooxygenases. Exploration of the libraries by expression in yeast focussed on membrane transporters involved in the assimilation of N-rich organic molecules.

In the context of functional diversity of ectomycorrhizal fungi, and of their potential role in biomass degradation, a future challenge of metatranscriptomics will be to identify among the different environmental sequences those coming from symbiotic fungi. This challenge could be met with the increasing number of fungal genome sequences that should be produced in the coming years.

Saprotrophy of ECM fungi and interactions with decomposers

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In temperate forests, fungi play a central role in the circulation of carbon and nutrients through the ecosystem. Saprotrophic fungi are the main decomposers of wood and litter and obtain energy by degrading dead organic matter. However, even if ectomycorrhizal (ECM) fungi obtain energy mainly as photoassimilates provided by symbiotically associated plants, they are also able, as saprotrophic fungi, to mobilize nutrients from organic matter. For many years, studies have clearly demonstrated that ECM fungi possess many of the genes (i.e. laccases, class II peroxidases) shared with their most recent saprophytic common ancestors.

ECM fungi can shift between their biotrophic or their saprotrophic behaviour depending on their carbon demand and on the host carbon availability. This discovery is interesting and can potentially change paradigms in our understanding of mycorrhizal interactions. The former distinction between ECM and saprotrophic fungi is artificial and we should should consider that ECM fungi occur along a biotrophy-saprotrophy continuum.

This capability is of interest in microbial ecology to understand the role and the contribution of ECM communities in re-circulating carbon, nitrogen and phosphorus from organic matter in forest soils. In this respect, I present here (i) recent advances in our knowledge on the saprotrophic capabilities of ECM fungi, (ii) some strategies which could be applied to address these features in ECM communities in field experiments, and (iii) how ECM and saprotrophic fungi could interact in the recycling of nutrients from organic matter.

Carbon cost of the ECM symbiosis and carbon allocation to external mycelium

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Ectomycorrhizal fungi are essential for the nutrient uptake of forest trees. In exchange for mineral nutrients, the trees supply the fungus with carbohydrates. It has been reported that up to 20% of the total photosynthetic assimilation is allocated to the fungal symbionts. The symbiosis may thereby constitute a major carbon cost for the trees and growth depressions induced by ectomycorrhizal colonization has been reported in young trees seedlings grown under laboratory conditions with optimal nutrient conditions. However, growth depressions are unlikely to occur under field conditions. In natural forests the carbon allocation belowground varies over the season. A minimum occurs in the early summer when carbon is needed aboveground to sustain shoot elongation. In contrast, massive amounts of carbon are allocated belowground in the fall when the demand from the trees declines. This carbon is used to sustain rapid growth of external ECM mycelium and fruitbodies. This separation of carbon use over time reduces competition between the symbiotic partners.

Carbon allocation to fungal symbionts belowground is also variable over the rotatation period of the forest stand. The mycorrhizal network is destroyed when forests are harvested and large amounts of carbon are needed to re-establish it in newly planted forests. We have found a maximum carbon allocation to the ectomycorrhizal community when the trees are between 10 and 20 years old. After this period it drops by over 50% during the rest of the rotation period (up to 130 years). This suggests that a major part of the mycorrhizal network is perennial and only need minor amounts of carbon to be sustained after it has been firmly established. Furthermore, we found that the ECM fungus *Tylospora fibrillosa* totally dominated the production of new ECM mycelia in young forests. This fungus can be described as a C strategist, being adapted to high population densities. C strategists are characterized by efficient conversion of resources to biomass, leading to rapid growth and ecosystem dominance when resources are abundant. Species diversity increased significantly in older forests apart from forests over 100 years old, when production dropped to very low amounts, making estimates of species diversity unreliable.

We have also studied how carbon is distributed within the ECM network when poorly soluble nutrients are added in patches. We found that more carbon is allocated to patches with mineral P sources such as apatite, especially when the trees were P deficient. Carbon allocation within the ECM network seemed thus to be controlled by the nutrient status of the trees.

Sugar uptake and metabolism in ectomycorrhizas

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Due to nutrient exchange and modified metabolism both the fungal and the plant partner have increased carbohydrate demands in ectomycorrhizal symbiosis. As a consequence, mycorrhized fine roots attract carbohydrates much more efficiently than non-infected roots. To elucidate this strong carbon sink, generated by plant cells and fungal hyphae during mycorrhizal interaction, carbohydrate uptake and metabolism was investigated for both partners.

Em fungi strongly increase their carbohydrate uptake capacity at the plant fungus interface as reflected by a genome wide analysis of hexose importers in *Laccaria bicolor*. Out of fifteen potential hexose transporter proteins four are induced in a mycorrhiza-dependent manner. All of them were proven as functional hexose importers by heterologous expression in yeast. Next to fast carbohydrate uptake and metabolization, storage carbohydrates are of special interest. In functional *Amanita muscaria* ectomycorrhizas, expression, and enzyme activity of proteins involved in trehalose biosynthesis was mainly localized in hyphae at the symbiotic interface, indicating trehalose as an important fungal carbon sink in mycorrhizal interaction.

Compared to our knowledge about the fungal partner, relative little is known about the response of infected host fine roots at the molecular level. As the poplar genome is available, we have analyzed the impact of ectomycorrhiza formation on the expression profiles of gene families involved in the hydrolysis of apoplastic sucrose and hexose import. Interestingly, both invertase activity and hexose importer expression was highest at the root tip but not at the symbiotic interface. Kinetic properties and gene expression studies defined one plant transporter that can be involved in hexose uptake at the symbiotic interface. In contrast to the fungal proteins this hexose transporter can import glucose and fructose efficiently.

General concepts of functional ecology of ectomycorrhizal fungal communities

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Knowledge of the factors that determine ectomycorrhizal fungal community structure is essential in many areas of practical significance including conservation, habitat restoration, prevention or amelioration of species invasions, and the prediction of responses to climate change. The field of community ecology in general, however, has a rather twisted and controversial history. One need only review the many concepts of "community" to discover that we define communities in multiple ways and study them at multiple spatial scales. Challenges also exist that are specific to the study of soil fungal communities. Subterranean organisms are largely invisible. Moreover, it is difficult to define fungal individuals and it is not even clear that the concept of individuals is at all relevant to fungi. These have all contributed to the perception by many that fungal community ecology is, at best, an esoteric discipline and, at worst, an inane one. But there is hope. Ectomycorrhizal fungal community ecologists have had several goals. For the goal of predicting diversity, island biogeography has been a useful approach. For the goal of predicting species composition, filter models have proven to be, at least theoretically, useful. For the goal of explaining high diversity, several studies demonstrating niche partitioning have been illuminating. But for the goal of discerning general rules of community assembly, there has been less progress. Here, we can learn much from plant community studies that relate organism function to environment. For example, physiological differences between C_3 and C_4 plant species allow one to predict their distributions across a range of latitudes. Two pioneering studies of ectomycorrhizal fungi have used a similar approach. In those studies, the ability to utilize N from protein by the fungi isolated along N deposition gradients allows one to predict distributions along the gradient. I believe more progress will be made in understanding distributions of fungi if we use this approach and focus on the relationships between important environmental gradients and relevant functional traits rather than on the simple distribution of taxa.

Case study #1: The effect of liming on ECM community structure and functioning

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Liming is a forestry practice consisting in Ca and Mg amendment used to correct tree cation deficiency induced by soil acidity. Ectomycorrhizae (ECM) provides the tree with nutrients derived both from mineral and organic sources. The ECM community structure and functioning are closely linked to soil nutrient availability, which is considerably modified by liming. The aims of this study were to assess, in declining beech and spruce stands, the long-term impact of liming on ECM community structure and functioning.

Results showed that liming decreased the abundance of ECM tips of some acidophilic morphotypes, especially *Russula ochroleuca*, and induced the dominance of those with a broader pH spectrum tolerance (*Clavulina cristata* for spruce, *Lactarius subdulcis* for beech). These morphotypes were more abundant in the organo-mineral layer.

Potential enzymatic activities were affected by liming in a complex and inconsistent way among different sampling seasons. However, liming significantly influenced only very few enzymatic activities for each of the dominant morphotypes (*Cenococcum geophilum*, *Xerocomus pruinatus*, *Lactarius subdulcis*, *Clavulina cristata*). A large part of rare species showed high enzymatic activities, putting in evidence the weight of these species in the community functioning.

The potential oxalate secretion by beech ECM community was higher in the limed plots, and depended mostly on the activity of one morphotype, *Lactarius subdulcis*. Analysis with Scanning Electron Microscopy X-ray spectroscopy showed that this morphotype stored also significantly more elements as Ca and Mg in its mantle in the limed plots.

Functional diversity was not affected by liming, whereas taxonomic diversity was significantly lower in the limed plots, whatever the season and the tree host.

Case study #2: effect of drought on structure and function of ECM communities in a *Quercus ilex* forest in the Mediterranean area

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In the hot and droughty environment of the Mediterranean basin, climatic models predict marked changes that will include an increased duration of the dry season and a decrease of the annual rainfall. In this region, more than 6.5 Mha are occupied by *Quercus ilex* (the holm oak), an evergreen sclerophyllous oak species that dominates the landscape at low elevation. Because of millenaries of anthropogenic pressure (fire, grazing, clearcuts), monospecific *Q. ilex* coppices have replaced natural forests in the major part of the region.

Previous studies showed that ectomycorrhizal (ECM) fungal communities in old-growth *Q. ilex* stands are particularly rich and diverse. Contrastingly, the composition of ECM assemblages in *Q. ilex* coppices is still undocumented from a below-ground point of view. In this study, we used a two-year long *in situ* experiment to address the following questions: (i) What are the structure and the composition of ECM fungal communities in *Q. ilex* coppices? (ii) Based on two successive spring and fall sampling, what are the temporal variations in these communities? Using an *in situ* rainfall exclusion simulation (-27%), we finally investigate the response of ECM communities to the predicted climate change in the region.

Based on the molecular analysis (ITS sequencing) of 1138 ECM tips, we found a rich community (H'=5.03; D=0.93) made of 94 ECM fungal taxa, mainly belonging to the Basidiomycota phylum (83,9% of the total number of tips). Two families, *i.e.* Thelephoraceae (35,3%) and Russulaceae (20,7%) strongly dominated the community, accounting for more than 55% of ECM tips, and the most abundant taxa were a *Tomentella* unnamed species, *Cenococcum geophilum* and *Inocybe tigrina*. These three taxa accounted for more than one third of the total number of mycorrhizae. Rank abundance curves showed a logseries distribution, typically dominated by ra re species with very few abundant ones.

Comparisons between spring and fall ECM communities showed marked changes at the family level: while Thelephoraceae were less represented on roots in fall as compared to spring (from 41.9 to 30% of the total number of root tips), relative abundance of Russulaceae significantly increased (from 15 to 25.2%) concomitantly. At the species level, phenologically "sensitive" species included *Lactarius acerrimus*, *Russula faustiana*, *Russula solaris* and *Thelephora caryophyllea*.

The rainfall exclusion experiment showed that species richness (number of taxa, 94 taxa in both control and treated plots) and community equitability (Shannon index, 5.01 and 5.05 in control and in treated plots) were not significantly affected by an increased water stress. Similarly, there was no effect of water exclusion on distribution of ECM families, excepted for Cortinariaceae that were significantly favored by a water reduction (accounting for 16.7 and 21.4 in controls and treated plots, respectively). Contrastingly, at the species level, the experiment showed contrasted responses of ECM taxa to the water reduction: while Cortinariaceae species responded positively (*Cortinarius aurilicis*, *Hebeloma sp*), Russulaceae species were either favored (*Russula globispora*) or affected (*Lactarius acerrimus*, *Russula faustiana*, *Russula solaris*) by the water stress.

Altogether, these results show (i) an unexpected and interesting conservation potential of *Q. ilex* coppices as reservoirs of ECM fungal diversity, (ii) evidences of a temporal dynamics of vegetative ECM communities under Mediterranean climatic conditions and (ii) contrasted responses of ECM communities to an increased drought that will be discussed in relation to functional diversity (enzymatic activities) within ECM communities.

Functional and taxonomic diversity: example from ECM fungi in the FunDiv project

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Diversity has been studied under different guises in ecology, e.g. functional, genetic and taxonomic. FunDiv project (J. Garbaye, 2006-2009) has assembled measurements from several experiments with control and treatments (fertilization, irrigation, earthworms, needle leaves / broadleaves, soil compaction, ozone deposition, etc.) in several locations (NE France, Munich, Switzerland, Breuil, Puechabon, Pierroton) from several teams. Sample unit is a soil core. Cores are sampled within plots, during campaigns, on each site. In each soil core, mycorhized root tips are sampled, of which ITS is sequenced, and eight enzymatic activities are measured. Several thousands of such tips have been sampled and measured. Although main results of this work still are under study, it seems clear that a definite hierarchy exists for determining enzymatic profiles: main determinant seems by far to be taxonomy, probably most important at genus level (several species from same genus may have similar enzymatic profiles) ; second determinant seems to be the campaign (four campaigns have been implemented), and treatments (mainly irrigation and fertilization) seem to be of third order only.

An open question in ecology is to decipher whether communities are better understood as assembly of traits or of taxa. There exist few general principles in ecology, and one of them, sometimes controversial, is competitive exclusion. We study here on data from Pierroton field trial whether competitive exclusion is more likely between enzymatic expressions among existing mycorhizae, or between taxa. We study whether more generally as well whether niche profiles are structured and organized more likely between enzymatic activities or between taxa.

This difficult question for a better understanding of community assembly has irrigated current research in community ecology for years, simultaneously in vegetation ecology and more recently in fungal ecology. Progresses are needed. We suggest that better progress is possible through cross fertilization between vegetation ecology and fungal ecology, as taxa are well known in plants, whereas functional traits still are empirical and integrated surrogates of functional processes, whereas in Fungi, e.g. ECM communities, taxa are difficult to assess with security (we will discuss some aspects of molecular taxonomy through ITS), whereas functional activity can be measured with higher accuracy, as in enzymatic activity.

We will conclude with a plea for a better connection between vegetation and fungal ecology.

Forest mushroom diversity and productivity - an indicator of forest health?

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Forest mushrooms play important ecological roles in forest ecosystems as mycorrhizal symbionts, decomposers, and pathogens. In addition, picking their fruitbodies is a popular pastime and recreational activity for a high proportion of the population in many countries of the world. Fruit body production considerably fluctuates from year to year and it is common knowledge that good or poor mushroom years are highly determined by weather conditions. But climatic factors alone do not completely explain mushroom occurrence and productivity. Other factors must be also involved. In this context mycorrhizal fungi are of special interest, because they mostly depend on photosynthetically fixed carbon produced by the associated host trees to extend their vegetative mycelium in the soil and to form mycorrhizas as well as fruit bodies for sexual reproduction. Considering this mutual interdependency a relationship between the physiological status of trees and the growth of the associated mycorrhizal fungi might be expected, and questions come up like: Do strongly growing trees with a high photosynthetic capacity produce more ectomycorrhizal fruit bodies than poorly growing trees? Can forest mushrooms be used as indicators for tree health? Does the presence or absence of certain fungal species tell us something about the health status of the associated tree? Such questions scientists asked in the context of the forest dieback phenomenon in the 80's, without having found concrete answers. However, in the same period as the forest dieback in Europe was observed, a decline in species richness and abundance of forest mushrooms has been reported in Europe, and ectomycorrhizal species were particularly affected. Increasing atmospheric input of nitrogen and enhanced soil nitrogen availability was hypothesized to be the main reason for these changes. Such effects were confirmed by numerous fertilization experiments.

On the basis of a mycological long term data set we want to pick up these questions again. The results of a long-term study over 32 years in the fungus reserve La Chanéaz, Switzerland, reveal striking changes in the species composition of the fungal flora: the mycorrhizal species considerably decreased in relation to the other species. We raise the question about a possible causal relationship between the decrease of the mycorrhizal fungi and the health of the associated forest trees.

In addition, we discuss the results of a thinning experiment, which reveals a clear temporal relationship between the thinning, the growth reaction of the remaining trees and the reaction of the fungal community.