

## ÜLLE SAKS

Arbuscular mycorrhizal fungal  
diversity patterns in boreonemoral  
forest ecosystems



DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

**250**

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forest ecosystems



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Dissertation was accepted for the commencement of the degree of *Doctor philosophiae* in plant ecology at the University of Tartu on September 23, 2013 by the Scientific Council of the Institute of Ecology and Earth Sciences, University of Tartu.

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Commencement: Room 218, 40 Lai Street, Tartu, on 19 December 2013 at  
12.15 a.m.

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences, University of Tartu and by the Doctoral School of Earth Sciences and Ecology created under the auspices of European Social Fund.



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ISSN 1024–6479  
ISBN 978–9949–32–445–3 (print)  
ISBN 978–9949–32–446–0 (pdf)

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University of Tartu Press  
[www.tyk.ee](http://www.tyk.ee)

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## LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following papers, which are referred to in the text by the relevant Roman numerals:

- I Öpik M, Saks Ü, Kennedy J, and Daniell T. 2008.** Global diversity patterns of arbuscular mycorrhizal fungi – community composition and links with functionality. In: Varma A (ed.) *Mycorrhiza: state of the art, genetics and molecular biology, eco-function, biotechnology, eco-physiology, structure and systematics*. pp. 89–112. Springer.
- II Öpik M, Moora M, Zobel M, Saks Ü, Wheatley R, Wright F, and Daniell T. 2008.** High diversity of arbuscular mycorrhizal fungi in a boreal herb-rich coniferous forest. *New Phytologist* **179**: 867–876.
- III Saks Ü, Davison J, Öpik M, Vasar M, Moora M, Zobel M. 2013.** Root-colonizing and soil-borne communities of arbuscular mycorrhizal fungi in a temperate forest understorey *Botany* doi: 10.1139/cjb-2013-0058.
- IV Koorem K, Gazol A, Öpik M, Moora M, Saks Ü, Uibopuu A, Söber V, Zobel M.** Soil nutrient content influences the abundance of soil microbes but not plant biomass at small-scale. Manuscript.

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The contribution of Ü. Saks to the respective papers is as follows:

	I	II	III	IV
Idea/Experimental design			*	*
Data collection	NA	*	*	*
Data analysis	NA	*	*	*
Manuscript preparation	*	*	*	*

# I. INTRODUCTION

Arbuscular mycorrhizas (AM) are formed between fungi in the phylum Glomeromycota (Schüßler et al., 2001) and majority of land plant species. It is the most common mycorrhizal type that occurs in 80% of all vascular plant families and in nearly all terrestrial ecosystems from tropical to boreal forests, deserts, grasslands, meadows and agroecosystems (Smith & Read, 2008).

AM fungi are obligate plant root symbionts. The carbon needed for AM fungal vital functions is received from plants in return to nutrients, such as phosphorus and nitrogen. Additional benefits to plants include provision of pathogen suppression and drought resistance and improvement of soil structure (Smith & Read, 2008).

Studies of plant-AM fungal interactions have shown that different AM fungal taxa (van der Heijden et al., 1998) and AM fungal communities (Corkidi et al., 2002; Moora et al., 2004) can have different effects on plant species growth and performance. These studies have mostly been conducted in experimental conditions and results depend on AM fungal community composition. For the understanding how plant-AM fungal interactions could function in natural conditions, there is increasing interest in describing the distribution of AM fungal diversity in natural ecosystems (van der Heijden & Scheublin, 2007; Fitter, 2005; Kivlin et al., 2011; Turrini & Giovannetti, 2012; Öpik et al., 2013).

Studies of mycorrhizas in boreal and temperate forests have targeted mainly ectomycorrhizal (ECM) associations due to the dominating ECM tree species (Smith & Read, 2008). Where environmental conditions enable growth of AM plant species in shrub and ground layer, the herbaceous communities may constitute high proportion of the plant and AM fungal diversity in these ecosystems. The focus of this study is boreo-nemoral forest ecosystem with species rich understorey vegetation.

## I.1. Diversity of AM fungi in roots and soil

The traditional method for describing AM fungal communities has been extraction of spores from natural soil or from so-called ‘trap-cultures’ and identification on the basis of morphological traits (I). The use of molecular markers for identifying AM fungal taxa has radically transformed the taxonomy and systematics of AM fungi during recent years (Stürmer, 2012). In addition, phylogenetically defined groups of rDNA sequences allow identifying of AM fungal taxa originating from environmental samples without having morphologically described equivalent taxa. These groups have been intended to correspond approximately to species level and are referred to as ‘virtual taxa’ (VT; Öpik et al., 2009, 2010).

Techniques for acquiring sequence data from natural samples have developed quickly during the last decades. Among the currently available

technologies, the cloning-Sanger sequencing approach has been prevailing in the AM fungal studies. Due to the constraint of this approach – the cloning step – new technologies such as 454-pyrosequencing have been tested. 454-pyrosequencing methodology has high throughput suitable for the assessment of the natural AM fungal diversity. It avoids the cloning step and also provides sequence data of sufficient length for robust phylogenetic analysis. In addition, with 454-sequencing the number of sequences obtained per sample is orders of magnitude higher, which results in increased probability to detect rare taxa as compared to the cloning-Sanger sequencing approach (Öpik et al., 2009).

With the expanding use of molecular methods numerous studies have focused mainly on intraradical AM fungal communities and extraradical (including extraradical hyphae and spore) communities in soil have often been not considered (Lumini et al., 2010). Although some studies have described molecular diversity of AM fungi in roots and of AM fungal spores extracted from soil at the same site (Liu et al., 2009; Guo et al., 2012), these studies have overlooked the non-spore AMF structures present in soil. As far as I know, the only detailed investigation of the AMF species composition of intraradical mycelia in roots, extraradical mycelia and spores in the soil has been conducted in a temperate meadow ecosystem by Hempel et al. (2007).

### **1.1.1 Richness**

Previous studies have shown that the AM fungal taxon richness may differ between ecosystems (Öpik et al., 2010). On the basis of plant root samples, different numbers of AM fungal taxa have been recorded in a natural temperate forest site (Öpik et al., 2009), tropical rainforest (Husband et al., 2002) and agricultural systems (Tian et al., 2013), although interpreting such data is complicated due to the uneven sampling intensity of studies. The number of AM fungal taxa per host plant species may also vary between habitat types with values ranging from 5 in arable fields and polluted sites to 18 in tropical forest (Öpik et al., 2006). In a temperate forest, 29 AM fungal taxa per host plant species, comparable to the respective values in tropical forests, has been recorded (Öpik et al., 2009). On the basis of soil samples, 28 taxa have been recorded from Mediterranean ecosystems (Lumini et al., 2010), 17 taxa from a managed vineyard site (Lumini et al., 2010), and 37 taxa from temperate forest site (Davison et al., 2012).

Species richness of spores around a single plant root system can differ between plant species. It can be affected by the identity of plant species or by sampling time during the season (Su et al., 2011).

It has been hypothesized that AM fungal spores in soil could serve as part of the propagules bank of AM fungi (I) and a pool for potential partners for plants (Davison et al., 2012). Identifying AM fungal taxa from soil and root samples may yield different taxon richness estimates, being higher in soil (Danielsen et al., 2012) or similar in roots and soil (Busby et al., 2013). Factors that trigger

sporulation and influence observed variation in spore numbers in natural environments are still not sufficiently clear (**I**), but include effects of host (Su et al., 2011), seasonal variation and soil nutrient content (Zangaro et al., 2013). Furthermore, it is known that Glomeromycota species show conserved functional traits at family level (Hart & Reader, 2002, Maherali & Klironomos, 2007), including sporulation time and the number of spores produced (Smith & Read, 2008). Thus, with respect to ecosystem functioning, the information about AM fungal species richness together with the abundances of different AM fungal taxa may be of great importance.

### **I.1.2. Community composition**

There is evidence that distinct AM fungal communities occur in different ecosystems (Öpik et al., 2006; Kivlin et al., 2011). In a global meta-analysis Kivlin et al. (2011) found that most of the AM fungal taxa were site-specific – two thirds of taxa had been detected from a single site and the most widespread taxon occurred in one fourth of the sites. At the local scale, the AM fungal taxon composition in plant roots may differ between host plant species (Vandenkoornhuysen et al., 2003; Torrecillas et al., 2012). When taking into account the abundance of AM fungal taxa, there is a trend that more abundant AM fungal taxa have broader host range and taxa unique to certain plant species are more often less abundant (Öpik et al., 2010). The composition of AM fungal community in plant roots can be affected by host identity (Helgason et al., 2002). In addition, environmental conditions have an effect on AM fungal community composition (Kivlin et al., 2011).

### **I.1.3. Host effect on AM fungal communities**

AM fungi have been considered as low-specificity mutualists that associate with a wide range of plant partners (Smith & Read, 2008). The root systems of individual plants are generally colonized by multiple fungal species, and likewise, individual fungal clones can colonize roots of multiple plant species across space and time (Fitter, 2005; Rosendahl, 2008; Helgason & Fitter, 2009). However, there are studies indicating that AM fungi have different levels of host preference or specificity (Helgason et al., 2002, Husband et al., 2002, Vandenkoornhuysen et al., 2003). There are AM fungal taxa recorded from all or from only few of studied plant species at a site. This may reflect specific interactions between AM fungi and host plants that are not significant at species level, but at the level of plant ecological groups such as shade tolerant forest specialists and generalist plant species that can grow in wide range of habitats (Öpik et al., 2009; Davison et al., 2011).

#### **1.1.4. Effect of environmental parameters on AM fungal communities**

Environmental factors, such as soil chemical properties – mineral nutrient content, soil organic matter content and pH have been shown to affect AM fungal communities (Fitzsimons et al., 2008; Liu et al., 2009; An et al., 2008), but the patterns described are contradictory. Yoshimura et al. (2013) found that the distribution of AM fungal taxa was related to the soil chemical properties (total C, total N, and available P content). On the other hand, it has been reported that soil C, N or P contents are not correlated with AM fungal community diversity (González-Cortés et al., 2012). Dumbrell et al. (2010) found that the main factors determining the composition of communities of AM fungi are soil pH, P and C/N ratio. Soil nutrient content can affect the biomass of AM fungi in soil (McNaughton & Oesterheld, 1990; Olsson et al., 1997). High P levels in the soil can reduce early AM colonization of the roots and growth of the extraradical mycelium (Miranda & Harris, 1994). In addition, soil nutrient contents can vary in time and space, including at small spatial scale (Farley & Fitter, 1999). Veresoglou et al. (2013) suggest that distinct environmental drivers shape the niches of AM fungal isolates.

#### **1.1.5. Effect of forest management on AM fungal communities**

Studies of management effect on species richness in boreal forests have mainly focused on plants and only few of them have also considered fungi (Paillet et al., 2010). Studies of plant communities have shown that various management practices can have significant impact on plant diversity and community composition (Reich et al., 2001; Ramovs & Roberts, 2003). Logging affects the vegetation directly by disturbing the forest floor and soil, by altering the habitat structure and microclimate and by removing nutrients (Roberts & Gilliam, 1995; Bergeron & Harvey, 1997; Closa & Goicoechea, 2011). Clearcutting can also alter the forest understory species composition via changing light conditions and thereby lead to differences in AM fungal community (Closa & Goicoechea, 2011). The effect of different land uses (plantation on former clearcuts versus natural stands) on the AM fungal spore diversity has been recorded in arid areas (Ndoye et al., 2012). Moderate management intensities in arable fields and ex-industrial site have shown to retain rather high numbers of AM fungal taxa (Hijri et al., 2006; Vallino et al., 2006). These results suggest that the relationship between management practices and AM fungal communities is complex and may vary depending not only on the type and intensity of management practices, but on other environmental conditions.

## **I.2. Phylogenetic structure of AM fungal communities**

There is increasing interest to understand the rules that govern the assembly of ecological communities. From plant community studies it has been suggested that communities are not random collections of species, although the processes that drive the community assembly are not fully understood (Götzenberger et al., 2012). The dispersion of functional traits among species within communities may provide clues to the processes influencing community composition. If resource-use traits are divergent, so that competition is reduced between these traits, species can more readily coexist (Götzenberger et al., 2012). In addition, if resource-use traits are phylogenetically conserved among closely related species, it may generate a community where species are less closely related than expected by chance (i.e., phylogenetic overdispersion) (Webb et al., 2002). The opposite pattern may arise, when traits are convergent and habitat filtering causes coexistence of species with shared ecological tolerance/niche. Species within such communities may be more closely related than expected by chance (i.e., phylogenetic clustering; see Götzenberger et al., 2012 for a review).

Among AM fungal taxa there are family level differences in their root and soil colonization strategies (Hart & Reader, 2002). For example, members of the families Glomeraceae and Acaulosporaceae allocate biomass into roots more extensively than to soil and Gigasporaceae, conversely, allocate more biomass into soil than roots. These functional differences may also influence the community assembly.

One of the few studies that have addressed the question of AM fungal phylogenetic community assembly is a global scale meta-analysis by Kivlin et al. (2011). AM fungal communities tended to be phylogenetically clustered within sites, suggesting that habitat filtering or possibly also dispersal limitation is a driver of AM fungal community assembly. Phylogenetic overdispersion was observed only in a few field AM fungal communities by Kivlin et al. (2011) and in an experimental system by Maherli & Klironomos (2007). The generality of these results remains to be investigated in ecosystems from where detailed data about the local AM fungal communities exist.

## **I.3. Aims of the thesis**

1. To give an overview about what is known about AM fungal natural diversity patterns and factors shaping AM fungal communities (**I**).
2. To describe the AM fungal taxon richness and community composition in a natural boreo-nemoral forest ecosystem (**II, III**).
3. To investigate the effect of host identity on AM fungal taxon richness and community composition in roots of forest understorey plant species (**II, III**).
4. To determine whether there are differences in AM fungal taxon richness and community composition between forest understorey plant roots and soil (**III**).

5. To determine the effects of environmental parameters and forest management on AM fungal communities **(II)**.
6. To assess the biomass of AM fungi in relation to soil nutrient content in boreo-nemoral forest ecosystem **(IV)**.
7. To analyse the phylogenetic structure of AM fungal communities in boreo-nemoral forest ecosystem **(III)**.

## 2. MATERIALS AND METHODS

### 2.1. Study sites

Study sites were located in two forests in different regions of Estonia. One study site (**II**, **IV**) was near Koeru in central Estonia (58°58'N; 26°03'E). It is a boreo-nemoral forest patch of 130 ha, representing the *Hepatica nobilis* site type (Lõhmus, 2004). The soil is a calcaric cambisol and soil conditions are relatively constant across the study area (Zobel et al., 2007). The predominant tree species was Norway spruce (*Picea abies* (L.) H. Karst.) with *Corylus avellana* L. prevailing in the shrub layer. *Oxalis acetosella* L., *Fragaria vesca* L. and *Hepatica nobilis* Mill. were the most abundant understorey plant species. Koeru forest contains stands of different age and management intensity. In our study mature spruce forests with a heterogeneous canopy represented old-growth stands, where the intensity of forest management has been low and the ecosystems are close to their natural state. Early successional stages were represented by young dense stands in areas that were clear-cut 20–25 years ago and then replanted with Norway spruce. Young stands have been thinned repeatedly since planting.

Second study site (**III**) was in Järvselja forest reserve, south-eastern Estonia (58°17.916'N, 27°15.744'E). The reserve area contains an old-growth mixed boreo-nemoral forest belonging to the *Aegopodium-Filipendula* site-type on a gleyic pseudopodzolic soil (Reintam 1987). An herb-rich arbuscular mycorrhizal plant understorey was dominated by *Calamagrostis arundinacea* (L.) Roth., *O. acetosella*, *H. nobilis*, *Galeobdolon luteum* Huds. The tree layer consisted of Norway spruce (*P. abies*) and deciduous tree species (most commonly *Acer platanoides* L., *Populus tremula* L., *Tilia cordata* Mill.) (see Zobel, 1989 and Zobel et al., 1993 for detailed descriptions of the area). The forest is believed to have received minimal anthropogenic impact throughout history since it has been under strict protection from 1924.

### 2.2. Plant root sampling

Plant roots (entire plant root systems) were collected from the above two study sites according to slightly different sampling designs, described below. In both studies all collected roots were carefully cleaned of soil and other adhering materials, dried with silica gel and stored at room temperature. A subsample (up to 80 mg of dry root) of a root system of a plant was used for DNA extraction.

In study **II**, plant roots were collected from plots with different forest stand ages and management intensities, but similar soil conditions. Both old and young forest stand types were replicated three times, resulting in six plots in total. Plots, 10x10 m in size, were divided to 1x1 m subplots. 1x1 m subplots were further divided into six equal parts for six sampling times (the beginning of June, end of July, and beginning of October 2003 and 2004), thus minimizing

the soil disturbance and breaking the fungal mycelium during each sampling. The plant species sampled were: *O. acetosella*, *H. nobilis* and *F. vesca*, which were the most frequent species in the field layer and present abundantly in all succession stages; *G. luteum*, which was patchily distributed and present only in two stands of old forest; and *Trifolium pratense* L., which was present only in young stands. Entire plants (several individuals if roots were very small) of each species were excavated from the 1/6-m<sup>2</sup> subplot if present. Two samples of each plant species per plot per sampling time were analysed and the samples from first three sampling times were used in study II (Table 1).

In study III plant roots were collected randomly from two plots of 30×30 m with the distance of 30 m in June 2009. Six plant species that were abundant in the plots were sampled: *H. nobilis* and *C. arundinacea* only from the first plot, *Pulmonaria obscura* Dumort. and *Mercurialis perennis* L. only from the second plot, *Convallaria majalis* L. and *Rubus saxatilis* L. from both plots. Four random individuals of each plant species per plot were excavated.

### **2.3. Vegetation analysis and environmental conditions**

In study II the per cent coverage of all vascular plant species was recorded in the field layer of 1x1 m subplots before root sampling. The total cover of all bryophytes was also recorded, but the shrub layer was not analysed. In each subplot, light availability was estimated using fish-eye photographs taken at the height of 30 cm at the centre of each subplot with a Nikon CoolPix 950 digital camera equipped with a hemispherical lens. An indirect site factor (ISF) and a direct site factor (DSF) were calculated with WinSCANOPY software (Regent Instruments Inc., Québec, Canada). ISF and DSF are defined as the proportion of diffuse and direct radiation received below the tree canopy as a fraction of that received above the canopy (Rich, 1990).

### **2.4. Soil sampling for chemical and fatty acid analysis**

In study II, while sampling plant roots, from the centre of each subplot soil samples were taken for the determination of pH and the content of mineral nitrogen (N), phosphorus (P) and dissolved organic material (DOC). Soil pH was measured in 0.01 M CaCl<sub>2</sub> (10 g of soil in a 50-ml solution). DOC and mineral N were extracted from 10 g of soil with 1 M KCl (soil:extractant ratio 1 : 4) and filtered through Whatman No. 1 filter paper (Wheatley et al., 1989). Available soil P was extracted using the sodium bicarbonate (Olsen) method (Olsen et al., 1954). N, P and DOC concentrations were determined colourimetrically on a segmented flow autoanalyser (Skalar Analytical, Breda, the Netherlands).

In study IV soil samples were collected from three plots, marked as A, B and C, – with 5 m distance in a relatively homogenous area. All three 105×105 cm

plots were divided into 49 (15×15 cm) quadrates corresponding to the average size of the root system of an adult plant and expected to harbour the majority of the biomass of herbaceous plant roots and microbes. Plot A was sampled twice, at the beginning (May 2008) and in the middle (July 2008) of the growing season to address temporal variation in soil nutrient content and AM fungal abundance at small scale. At the second sampling time (July 2008) remaining two plots (B and C) were sampled also and all three plots were used to address spatial variation in soil nutrient content and AM fungal abundance. 50 g and 10 g of soil were collected from the soil surface (depth 5 cm) at both sampling times for soil chemical and fatty acid analysis, respectively. During the first sampling the soil corer (2 cm diameter and 5 cm deep) was used to minimize the disturbance to plots at the beginning of the plant growing season. Soil samples collected in the middle of the growing season were collected during destructive harvesting. Soil cores of 15 cm diameter and 10 cm deep were cut from each quadrate and transported to the laboratory. Soil samples were collected from all of the soil cores while separating the roots and shoots of herbaceous plant species. Soil samples for chemical analyses were kept at –80°C until processing in order to prevent the loss of soil nutrients. Soil ammonium (NH<sub>4</sub>) and nitrate (NO<sub>3</sub>) content (mg/kg) was determined according to ISO 14256–2:2005 protocol. Organic carbon (C) and total nitrogen (N) content (%) were determined based on ISO 10694:1995 and ISO 13878:1998 protocols, respectively. Soil NH<sub>4</sub>, NO<sub>3</sub> and C content correlated highly with soil total N content, thus only the latter was used in further analysis. Soil phosphorus (P) and potassium (K) content (mg/kg) was determined according to the Mehlich III procedure: P was extracted by reaction with acetic acid and fluoride compounds; exchangeable K was extracted by the action of ammonium nitrate and nitric acid (Sen Tran & Simard, 1993).

For fatty acid analysis three grams of fresh soil was lyophilized immediately after separation and stored at room temperature. Phospholipids were converted to ELFAs and extracted from the soil following the protocol of Schutter & Dick (2000). Fatty acid 16:1 $\omega$ 5c was used as indicator for AM fungi (Graham et al., 1995; Hinojosa et al., 2005). Fatty acid 16:1 $\omega$ 5c is normally not found in other fungi (Müller et al., 1994), although it may be present in some Gram-negative bacteria (Olsson et al., 1995). In paper **IV**, extracted ELFAs contain whole-cell batch of fatty acid 16:1 $\omega$ 5c, including both the phospholipid fatty acid (PLFA; structural lipids in cell membranes) fraction of 16:1 $\omega$ 5c that can occur also in bacteria and the neutral lipid fatty acid (NLFA; storage lipids) fraction of 16:1 $\omega$ 5c that does not occur in bacteria.

## 2.5. Soil sampling for AM fungal identification

The soil AM fungal community data analysed in study **III** was previously published by Davison et al. (2012). In short, soil samples were collected from the same Järvelja study site as plant root samples of study **III**. Three 10×10 m plots located 30 m from one another in the forest between and adjacent to the plant sampling plots. Within each plot, 10 g of soil was collected from nine points on a regularly-spaced sampling grid in May, June, July and September 2008. Soil samples were dried with silica gel and stored air-tight at room temperature until DNA extraction.

## 2.6. Molecular analyses

Glomeromycota in plant root samples (**II**, **III**) were identified on the basis of sequence variation within central fragment of nuclear ribosomal small-subunit RNA gene (SSU rDNA). Dried roots of each plant individual were milled to powder, followed by DNA extraction. Also, there were differences in PCR primers and sequencing methods used in studies **II** and **III**, aiming to increase the amplification of AM fungal sequences from different Glomeromycota families and to increase the sequencing depth of environmental samples in **III**.

In study **II** Glomeromycota sequences were identified using the primers NS31 and AM1 (Simon et al., 1992; Helgason et al., 1998) for amplification of Glomeromycota DNA from total root DNA extracts. After cloning, 16–32 colonies were grown per sample and prepared for Sanger sequencing in an ABI Prism 3700 DNA Analyzer (Applied Biosystems, Warrington, UK).

In study **III** Glomeromycota sequences were amplified from root DNA extracts using the primers NS31 and AML2 (Simon et al., 1992; Lee et al., 2008) and identified using 454-sequencing as in Öpik et al. (2013). In order to identify sequences originating from different samples, a set of 8-base-pair bar-codes were designed following Parameswaran et al. (2007). A two-step PCR approach was used: in the first PCR reaction the PCR primers were linked to bar-codes and partial 454-sequencing adaptors A and B; the second reaction was performed with the full 454-adaptors A and B serving as PCR primers, thus completing the addition of the full 454-adaptor+bar-code+PCR primer construct to the amplicon. Resulting PCR products were sequenced on a Genome Sequencer FLX System, using Titanium Series reagents (Roche Applied Science) at GATC Biotech (Konstanz, Germany).

For the identification of Glomeromycota in soil samples Davison et al. (2012) used the NS31 and AML2 primer pair, the 454-sequencing approach and bioinformatics routine as in study **III**.

## 2.7. Bioinformatical analyses

### 2.7.1. AM fungal taxon identification

Differences between methods used for AM fungal sequence identification in study **II** and **III** reflect the state of the art in environmental sequence analysis at the respective times of publishing and were conducted as follows.

In study **II**, raw AM fungal SSU rDNA sequences from 911 clones were aligned using the freeware POA (Lee et al., 2002). Thereafter, all root-derived sequences were submitted to neighbor-joining analysis (F84 model with gamma substitution rates) implemented in TOPALi version 1 (Milne et al., 2004). From the apparent sequence groups second strands of representative clones were sequenced; the double-stranded sequences were submitted to a BLAST search. Retrieved sequences of closely related ‘known’ fungi and environmental samples, sequences of major clades of Glomeromycota, and double-stranded sequences obtained in this study were then aligned automatically using the MAFFT multiple sequence alignment web service in JalView version 2.3 (Clamp et al., 2004). A phylogenetic tree was constructed using MrBayes software (Ronquist & Huelsenbeck, 2003) with a general time-reversible model with gamma distribution of remaining sites (GTR + G).

In study **III**, 454-sequencing reads qualified for further analysis only if they carried the correct barcode and forward primer sequences, and were  $\geq 170$  bp long (excluding the bar-code and primer sequence) and passed the chimera check. After removing the barcode and primer sequences, BLAST search against the MaarjAM database (Öpik et al., 2010) was conducted for the taxonomic assignment of the obtained 454-sequences. The MaarjAM database contains representative sequences covering the NS31/AML2 amplicon from published environmental Glomeromycota sequence groups and morphologically described taxa. Samples yielding at least 10 sequences were analysed further.

AM fungal SSU rRNA gene sequence groups in study **II** were delimited according to the same principle as the sequence groups in MaarjAM database referred to as virtual taxa (VT). Thus, the latter term is used also for the sequence-based taxa of study **II**.

### 2.7.2. Phylogenetic dispersion analysis

In study **III**, the Bayesian AM fungal VT phylogenetic tree published by Öpik et al. (2013) was used to generate a phylogenetic tree containing all AM fungal VT type sequences from the MaarjAM database and several divergent sequence groups not yet assigned VT codes. The consequent tree was trimmed to contain only type sequences using the function `drop.tips` in R package `ape` (Paradis et al., 2004).

We asked whether AM fungi present in plant root and soil communities represent phylogenetically non-random sets of taxa (phylogenetically clustered or overdispersed) from globally or locally available AM fungal taxon pools. The

VT associating with different community types were defined in the following ways: a) all samples derived from plant roots were pooled to define a single community of VT found associating with plants, b) samples derived from the roots of individual plant species were pooled to define a single community of VT for each plant species, and c) samples derived from soil were pooled to define a single community of VT recorded from soil. The mean pairwise phylogenetic distance (mpd) was calculated between VT in each community type (using the function `ses.mpd` from R package `picante`; Kembel et al., 2010). For this analysis, phylogenetic distance was calculated between each pair of taxa as the sum of intervening branch lengths in the phylogenetic tree, and a mean of the pairwise distances was calculated. The observed mpd was compared with 999 mpd values calculated using randomisation of a reference phylogenetic tree representing the available taxon pool. Two reference trees were used: a) the full AM fungal phylogenetic tree (the full MaarjAM VT type sequence tree), representing a global taxon pool of AM fungi, and b) a further trimmed phylogenetic tree containing only VT type sequences of those taxa encountered at Järvelja in study III or Davison et al. (2012), representing a local taxon pool of AM fungi at the Järvelja site. For each step of the randomisation, a data matrix was generated by randomly shuffling the VT identities of tips in the phylogenetic tree. Thus, each randomised mpd value represented the mpd that might be encountered when drawing taxa randomly from an available taxon pool. A standardised effect size was calculated using the observed mpd value along with the mean and standard deviation of the 999 randomised mpd values. Mean pairwise phylogenetic distances may be strongly influenced by deep divergences between major clades in a phylogenetic tree. Since most taxa in this study were Glomeraceae, and occurrence of VT belonging to other families could have a strong influence on mpd values, we repeated the analysis using only Glomeraceae taxa and reduced phylogenetic trees representing the global and local pools of Glomeraceae VT. The mpd of the AM fungal community associating with all plants species pooled was not compared with a null model based on the trimmed Järvelja phylogeny because plant-associating VT constituted the great majority of all VT recorded at Järvelja.

## 2.8. Statistical data analyses

In study II the effect of sampling effort on fungal taxon accumulation was assessed by calculating the number of detected fungal taxa ( $S_{\text{obs}}$ ) as a function of the number of samples using EstimateS version 7.5.1 (Colwell, 2005) based on presence/absence of fungal taxa in individual samples of the five plant species. All following statistical analyses were implemented in GENSTAT version 10 using only samples from the three plant species (*F. vesca*, *H. nobilis* and *O. acetosella*) that occur in all study sites; site-specific *G. luteum* and *T. pratense* were not included in these analyses.

Effects of forest management intensity (stand type), host plant species identity and sampling time on the number of AM fungal taxa in root samples were estimated using linear mixed models with the residual maximum likelihood method (REML).

The variation in AM fungal community composition was analysed by principal coordinate analysis (PCoA, or metric multidimensional scaling). The experimental factors (forest management type, site, host plant species, and sampling time) were visualized on the plots of PCoA axis scores using different colours. As no clear patterns were observed, no further statistical analyses were applied.

The relations of the environmental variables (ISF, DSF, soil  $\text{NO}_3^-$ -N and  $\text{NO}_4^+$ -N, P, pH and DOC), cover of bryophytes and cover and richness of vascular plants in a 1×1 m subplot with the number of AM fungal taxa or the fungal community composition in root samples were assessed by plotting the values for the number of AM fungal taxa or scores of the first five PCoA axes against the above variables, again visualizing the experimental factors using colours. Again, no clear patterns were observed and no further statistical analyses were applied.

In study **III** all statistical analyses were implemented in R (R Development Core Team, 2011). Sampling efficacy was assessed with rarefaction analysis using the function `rarefy` from the R package `vegan` (Oksanen et al., 2012). PERMANOVA (using the function `adonis` from `vegan`) was used to partition variance in AM fungal community composition in relation to a) plant species identity and b) plant roots and soil. The strength of pairwise associations between plant species and AM fungal VT were investigated using indicator species analysis (function `indval` from the package `labdsv`; Roberts, 2012). The richness of AM fungal communities associating with different plant species was assessed using a negative binomial GLM.

In study **IV** the temporal difference in soil nutrient content (N, P, K) and soil fatty acid biomarkers for AM fungi was assessed with Linear Mixed-Effect Models (LMM; Pinheiro & Bates, 2000). A model using time (sampling time: May or July) as a fixed factor and quadrat identity as a random factor were fitted. The presence of spatial autocorrelation in the distribution was studied with the Moran's I statistic. A spatial correlogram was constructed for abundance of AM fungi in each plot. The Moran's I statistic was evaluated at different distance classes (0 to 50 cm) and its significance was assessed by performing 9999 unrestricted permutations.

Generalized least square models (GLS; Pinheiro & Bates, 2000) were used to determine which factors best explain the variation of soil AM fungal abundance in plots. The influence of plot identity (A, B and C) and soil nutrients (N, P, K) were considered as the predictor variables. In order to select the most parsimonious model for each variable, the protocol proposed by Zuur et al. (2009) was followed. The best set of predictor variables was selected using Akaike's Information Criterion (AIC). If several models showed similar

AIC values (difference lower than two), the most parsimonious one, i.e. the one with less fixed components, was chosen (Zuur et al., 2009).

LMM and GLS were performed in R (R Development Core Team, 2011) using the package nlme (Pinheiro et al., 2011) and SpatialPack (Osorio et al., 2012). Maps of the spatial patterns of AM fungal abundance and soil P content were created using ArcGIS 9.3 software (ESRI Redlands, NY, USA).

## 3. RESULTS

### 3.1. AM fungal taxa in plant roots

From Koeru forest site (II) 34 AM fungal VT were recorded in the roots of five host plant species (90 plant root samples; 911 clones sequenced with the Sanger method). These taxa comprised: five *Acaulospora*, two *Diversispora* and 23 *Glomeraceae* taxa (Fig. 1, Table 2 in II).

From Järvselja forest reserve (III) 76 AM fungal VT were recorded in the roots of six host plant species (26 plant root samples; 22 419 454-sequencing reads that equals to 56% of reads which met the quality criteria required for further analysis). Remaining qualifying reads were included in a BLAST search against the INSD nucleotide collection (similarity  $\geq 90\%$ ): these reads matched Viridiplantae (24%) and Fungi (12%). Among the latter were potential matches to Glomeromycota, but these constituted only 5% of qualifying reads.

#### 3.1.1. AM fungal taxon richness

In study II we identified 26 AM fungal taxa from the roots of *H. nobilis* (31 samples), 20 taxa from *F. vesca* (20), 21 taxa from *O. acetosella* (26), 11 taxa from *T. pratense* (7) and 11 taxa from *G. luteum* (6). A mean of 3.17 ( $\pm 0.24$ ; SE of the estimate) AM fungal taxa colonized a root sample of the three abundant plant species (*F. vesca*, *H. nobilis* and *O. acetosella*). The effect of plant species identity on the number of fungal taxa per sample was marginally nonsignificant. Forest management intensity (stand type), sampling time, and their interaction had no significant effect on the AM fungal taxon richness in samples. We could not detect any relations between the number of AM fungal taxa and explanatory environmental variables.

In study III, the average number of VT per sample ranged from 8.2 in *R. saxatilis* to 15.3 in *Convallaria majalis* (Table 1 in III), but the taxon richness did not differ significantly between plant species.

#### 3.1.2. AM fungal community composition

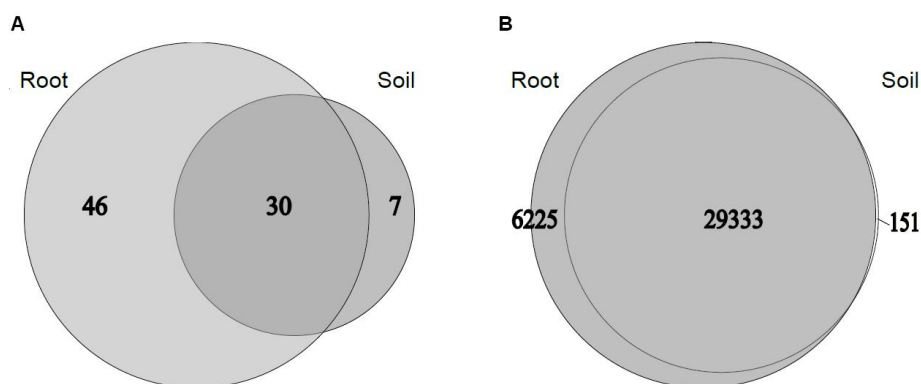
In study II, principal coordinate analysis (PCoA) of fungal community composition based on presence/absence and relative abundance data for AM fungi in root samples did not yield obvious groupings of samples; neither were there patterns relating to forest management type, site, plant species or sampling time. No relations were detected between the fungal community composition and explanatory environmental variables.

In study III PERMANOVA revealed that AM fungal community composition was not significantly different among studied host plant species

(Table 2 in **III**). Indicator species analysis revealed one significant indicator AM fungal taxon: *Glomus* VT229 (Glomeraceae) preferentially associated with *C. arundinacea*.

### 3.2. AM fungal diversity in plant roots vs soil

In study **III** the total number of AM fungal VT detected in roots was higher than that detected in soil (Fig. 1a, Table 1 in **III**). The total AM fungal richness at the study site was 83 VT (on the basis of 35 709 454-reads). Forty-six VT (55% of VT / 17% of reads) were found only in plant roots, 7 VT (8% / 0.4%) only from soil and 30 VT (36% / 82%) occurred in both types of sample (Fig. 1a, b). PERMANOVA showed that AM fungal community composition in roots was significantly different from that in soil (Table 2, Fig. 2 in **III**).



**Fig. 1.** Occurrence and characteristics of AMF VT in root and soil samples from Järvelja forest reserve. a) the numbers of VT unique to and shared between the different sample types; b) counts of reads derived from VT that occurred in (from the left) root samples only, both root and soil samples, and soil samples only.

### 3.3. AM fungal biomass in soil

In study **IV**, AM fungal biomass was significantly negatively affected by soil P and positively by soil N content (Table 3, Fig. 2 in **IV**).

### **3.4. AM fungal phylogenetic dispersion in plant roots and soil**

In study **III**, AM fungi associating with plant roots in Järvelja forest reserve were phylogenetically more closely related than would be expected from random sampling of taxa from the global Glomeromycota VT type sequence phylogeny (Table 3, Fig. 3 in **III**). However, the mean pairwise phylogenetic distance (mpd) of the soil AM fungal community did not differ from that of a random selection of global AM fungal taxa. Considering only those VT that belong to Glomeraceae, we still found that plant AM fungal community exhibited significantly lower mpd than expected by chance, but soil AM fungal community did not (Table 3 in **III**).

When the local taxon pool (i.e., all VT recorded at Järvelja by this study or Davison et al., 2012) was used as the basis for producing the null model, phylogenetic clustering was still recorded for two of six plant species. The same pattern was obtained when the local taxon pool was reduced to contain only Glomeraceae VT from the local taxon pool, though the identity of the two plant species was different. In both cases, the mpd of the soil AM fungal community did not differ from that of a random selection of Järvelja AM fungal taxa.

## 4. DISCUSSION

### 4.1. AM fungal taxa in plant roots

#### 4.1.1. Richness

AM fungal species richness in the studied boreo-nemoral forest ecosystem, represented by two sites, was high (**II**, **III**). As hypothesized in paper **I**, the number of AM fungal taxa detected in a location may be an indicator of ecosystem stability. The species richness recorded from Järvelja primeval forest (76 VT) may reflect the intact state of the forest, although there is limited number of studies from other forest ecosystems to make any conclusions.

Consecutive studies conducted at Koeru forest have gradually increased the initially recorded taxon richness from this forest site (34 VT), by analysing root samples of additional plant species (total 40 VT; Davison et al., 2011) or by applying 454-sequencing method (total 47 VT; Öpik et al., 2009). The information about the total number of Glomeromycotan taxa in different ecosystems has been accruing (Öpik et al., 2010; Kivlin et al., 2011). Among other factors, the recorded AM fungal richness may differ due to the sampling intensity (**I**). Analysing increased number of plant species from the same Koeru forest site/ecosystem revealed higher AM taxon richness in plant roots.

The high AM fungal taxon richness in Järvelja plant root samples can also be explained with the difference in sequencing methodology. The 454-sequencing method can detect orders of magnitude higher numbers of environmental sequences per sample than cloning-Sanger sequencing method at commonly applied sample-based sequencing intensities. The higher numbers of sequences per sample increases the likelihood of capturing more AM fungal sequences overall including those of rare taxa in the sample (Öpik et al., 2009). In the compared datasets the average sequence number (sequencing depth) per sample was 10 in the case of Sanger-sequencing (**II**) and 862 in the case of 454-sequencing (**III**). Such difference in sequencing depth is most probably the main reason behind the different VT richness values observed.

#### 4.1.2. Host plant effect

Host plant species identity had no effect on AM fungal taxon richness and community composition in root samples (**II**; **III**). Studies of AM fungal communities in roots of different plant species have provided contrasting data about the specificity of plant-AM fungal interactions at the species level. Vandenkoornhuyse et al. (2003) found significant host plant effect on AM fungal communities. In addition, Torrecillas et al. (2012) recorded different AM fungal taxa specific to host plant families. When the habitat preference of plant species was taken into account, Öpik et al. (2009) and Davison et al. (2011) showed significant difference between AM fungal communities in roots of forest specialist and generalist plants in the same Koeru forest as studied in

paper **II**. Plant species studied in paper **II** were included in the above-mentioned analysis and four of the five studied plant species were forest habitat specialists. All plant species studied at Järvelja site (**II**) were also forest specialists and the lack of any patterns between AM fungal communities in the roots of those plant species was therefore not unexpected. The latter result also supports the suggestion that partner specificity between plants and AM fungi may occur at the level of ecological groups, rather than species level (Öpik et al., 2009, Öpik & Moora, 2012).

#### **4.1.3. The effect of environmental parameters and forest management**

There was no relationship between the explanatory environmental variables and AM fungal taxon richness or community composition in study **II**. The effect of environmental parameters to AM fungal communities has been studied in respect to AM fungal root colonization, spore community in the rhizosphere soil (Li et al., 2010; González-Cortés et al., 2012), and intraradical taxon composition (Dumbrell et al., 2010). In the study of Li et al. (2010), spore density exhibited positive correlation with soil pH and available P and negative correlation with available N content. Thus, the effect of environmental variables to intraradical AM fungal community composition could be more indirect and related to other parameters, such as fungal biomass (**IV**).

In study **IV**, negative effect of soil P content on the abundance of AM fungi was recorded. It could be explained by the ability of plant roots to take up P directly from soil when P content is high, as opposed to mycorrhizal uptake in the case of low soil P availability. In the former case the cost-benefit ratio of supporting AM fungi in roots increases for plants and may cause the decrease in AM fungal abundances (Smith & Read, 2008).

It has been suggested that disturbance can decrease AM fungal taxon richness (Helgason et al., 1998; Schnoor et al., 2011). Indeed, different AM fungal community composition has been recorded in tree plantations compared to natural stands in arid ecosystems (Ndoye et al., 2012). On the other hand, studies conducted in arable fields and industrial sites indicate that if management intensity is low, the disturbed habitats may still have rather high numbers of AM fungal taxa (Hijri et al., 2006; Vallino et al., 2006). In the studied forest ecosystem (**II**) the forest management (stand type: young recently managed or old, unmanaged stands) had no significant effect on the AM fungal taxon richness or community composition in samples. The soil disturbance generated by clear-cut logging and planting tree saplings is less intense than recurrent ploughing. The lack of additional soil disturbance during subsequent years may aid to retain the fungal diversity.

Using the dataset of study **II** and six additional plant species from the Koeru site, Davison et al. (2011) reached quite the contrary result, detecting significant differences among AM fungal communities in the young and old stands of

Koeru forest. The AM fungal community present at the Koeru site did not differ between seasons, indicating that the same suite of taxa was consistently present. However, assessing assembly rules in AM fungal communities in successional stands it was tested if AM fungal communities in young and old stands are random subsets of the local AM pool. Since a constant set of host plants in young and old forest stand was studied by Davison et al. (2011) and there was no interaction between plant identity and successional stage, they suggested that the effect of successional stage was not a direct result of host plant identity.

## **4.2. AM fungal communities in roots vs soil**

Lower number of AM fungal taxa were detected in soil than in roots at Järvelja forest reserve (III). Furthermore, the intraradical AM fungal community composition was different from that in soil (III). It has been shown by Davison et al. (2012) that soil AM fungi represent a fairly constant species pool throughout the majority of the vegetation period, suggesting that from this pool the plant-AM fungal associations can form and disband during the growing season. Accordingly, one could expect the AM fungal richness in soil is higher (Hempel et al., 2007) or equal (Mirás-Avalos et al., 2011) to that in plant roots. However, the contrary was recorded in Järvelja forest – nearly twice as many VT were detected in total from root samples than from soil samples (III). Similar results have been recorded by Busby et al. (2013), who identified nearly equal numbers of AM fungal sequences from root and soil samples, with only two thirds of AM fungi found in roots also recorded in soil. Differences in AM fungal communities in roots and soil and the relatively low number of taxa detected in soil could be explained by the difference of AM fungal biomass. Olsson et al. (2010) recorded an order of magnitude lower density of AM fungal biomass in soil than in roots. It may result in lower quantities of AM fungal DNA and low DNA template quantity might be expected to result in underestimation of species richness (Lumini et al., 2010). Despite the AM fungal biomass and taxon richness difference in plant roots and soil, analyzing soil AM fungal community has the importance in assessing total AM fungal community composition at a site.

## **4.3. Phylogenetic dispersion**

The AM fungal community colonizing plant roots consisted of VT that were phylogenetically more closely related than expected from random sampling from global VT database MaarjAM. The same result was obtained also in the case of analyzing the most abundant family, Glomeraceae. It is in accordance with the results of Kivlin et al. (2011) who recorded phylogenetic clustering of

AM fungal taxa within sites. They explained this trend with habitat filtering or dispersal limitation affecting the AM fungal community composition.

Analysis of AM fungal phylogenetic dispersion in plant species separately showed that most of the six study plant species hosted more closely related AM fungal taxa than expected from random sampling from global VT pool and also from Glomeraceae. Dispersal limitation may be the force driving the phylogenetic clustering of AM fungi at Järvelja primeval forest when compared to the global taxon pool, but it is far less likely to be important at the local scale. Since the AM fungal communities detected in roots of two plant species remained more phylogenetically clustered than random communities drawn amongst the local AM fungal taxon pool (VT detected at Järvelja), there might be habitat filtering behind this pattern. Busby et al. (2013) found that more closely related AM fungi associated with a generalist (invasive) plant species than with a local habitat specialist plant in a sagebrush steppe ecosystem. Although our target plant species are all shade-tolerant forest specialists, it is possible that there is a degree of preference for symbionts with specific traits and that such AM fungal taxa may be phylogenetically closely related.

A theoretical work by Mayfield & Levine (2010) has proposed that competitive exclusion does not necessarily result in overdispersion. They have explained that species in communities can have traits contributing to both niche and competitive ability differences. If both, niche and competitive ability differences are important, but only the latter are positively correlated with phylogenetic distance, it can be expected that competition drives to the clustered pattern we observed in our data from plant roots. The AM fungal community colonizing soil consisted of VT that were not phylogenetically clustered compared to random sampling from global or local VT pool.

According to the obtained results the AM fungal communities in plant roots are non-randomly assembled and are phylogenetically and potentially functionally similar subsets from the local taxon pool, while the fungi coexisting in soil represent a randomly assembled community. This suggests that non-random assembly processes may have shaped fungal assemblages in host plant roots.

## 5. CONCLUSIONS

High intraradical AM fungal taxon richness was recorded in boreonemoral forest. From Järvelja forest reserve nearly twice as much AM fungal taxa were recorded than from Koeru forest. It may reflect the virgin state of Järvelja old growth forest ecosystem. In the other hand, different sequencing methods with different sequencing depths per sample used in these studies show the state of the art in AM fungal community research at the time of publishing the respective papers. Due to the rapid methodological development in recent years, the ability to detect and identify higher numbers and diversity of environmental sequences of AM fungi has been improved.

The AM fungal communities in the roots of forest understory plant species did not differ significantly from each other. Almost all plant species studied were forest specialists and the lack of any patterns between AM fungal communities in the roots of those plant species may support the suggestion that partner specificity between plants and AM fungi may occur at the level of ecological groups, rather than species level.

In the studied forest ecosystem the environmental parameters and management intensity had no significant effect on the AM fungal taxon richness or community composition in samples. The effect of environmental variables to intraradical AM fungal community composition could be more indirect and related to other fungal parameters and deserves further evaluation. The lack of soil disturbance on young replanted stands during subsequent years may have aided to retain the AM fungal diversity.

The abundance of AM fungi in forest soil was negatively affected by soil P content. It may be related to the ability of plant roots to take up P directly from soil without AM fungal partners when P content in soil is high (Smith & Read, 2008).

The composition of AM fungal communities in roots and soil differed significantly, with the richness of AM fungal communities being considerably higher in roots than in soil. Differences in AM fungal communities in roots and soil and the relatively low number of taxa detected in soil could be explained by the lower density of AM fungal biomass in soil than in roots. It may result in lower quantities of AM fungal DNA and low DNA template quantity might be expected to result in underestimation of species richness. This result also indicates that in order to assess total AM fungal diversity in an ecosystem it is important to consider determining the AM fungal community composition not only in plant root or soil fraction, but in both.

Significant phylogenetic clustering of coexisting fungal taxa was recorded in plant roots, but not in soil. It may suggest that non-random assembly processes, like environmental filtering may have shaped fungal assemblages in plant roots. Although our target plant species were all shade-tolerant forest specialists having similar intraradical AM fungal communities, it is possible that there is a degree of preference for symbionts with specific traits and that such AM fungal taxa may be phylogenetically closely related.

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## SUMMARY IN ESTONIAN

### Arbuskulaar-mükoriisete seente mitmekesisusemustrid salumetsas

Arbuskulaarset mükoriisat (AM) esineb ligi 80% maismaataimede sugukondadest ning see moodustub taimejuurte ja krohmseente (hõimkond *Glomeromycota*) vahel. Seda tüüpi mükoriisat esineb väga erinevates ökosüsteemides: troopilistest boreaalsete metsadeni, kõrbetes, niitudel ja ka agroökosüsteemides. AM seened on obligaatset sümboolid ning saavad kogu elutegevuseks vajaliku süsiniku taimedelt. Seensümboolid varustab taimi fosfori, lämmastiku jm. mineraalsete toitainetega, tõhustab patogeenidevastast resistentsust ja põuataluvust ning parendab mulla struktuuri. Katsetest taimede ja seente vaheliste interaktsioonide uurimisel on selgunud, et erinevate AM seeneliikide ja -koosluste mõju taimpartneritele on varieeruv. Et mõista taimede ja AM seente vahelisi suhteid looduslikes ökosüsteemides, on oluline kirjeldada AM seente levikut ja mitmekesisuse mustreid ning viimaste seoseid taimpartneritega.

Järjest enam kasutatakse AM seente määramisel molekulaarseid meetodeid, sealhulgas tuuma ribosomaalset RNAd kodeerivate geenide järjestamist. DNA järjestusi nende fülogeneetilise kuuluvuse alusel liikideks rühmitades on võimalik tuvastada ka keskkonnaproovidest pärinevaid AM seente liike, millel ei ole morfoloogiliste tunnuste põhjal kirjeldatud liigi sekveneritud vastet. Molekulaarseid meetodeid kasutades on lihtsustunud seenekoosluste uurimine taimejuurtes, kuid juureväliste (mulla) seenekoosluste uurimisele molekulaarsete meetodite abil on vähem tähelepanu pööratud.

Varasematest uurimustest on selgunud, et AM seente liigirikkus ja koosluste koosseis varieerub erinevates ökosüsteemides. Suurim liigirikkus on tuvastatud looduslikes parasvöötme ja troopilistes metsades ning väiksem majandatavates piirkondades. Koosluse koosseisu osas on leitud olulisi erinevusi nt. metsa-, niidu- ja majandatavate ökosüsteemide vahel. Lisaks on leitud, et valdav osa AM seeneliike esineb vaid teatud ökosüsteemides, kuid on ka liike, mis on globaalse levikuga. Võimalik, et need erinevused peegeldavad ökosüsteemide seisundit skaalal stabiilsest häirituni.

AM seente liigirikkus ja koosluse koosseis erineb taimeliigiti nii taimejuures kui juuri ümbritsevas mullas. Et AM seeneliikide arv on mitu suurusjärku väiksem kui võimalike peremeestaimede arv, on AM seeni peetud madala spetsiifilisusega sümboolideks. Uuringud on aga tuvastanud erinevusi AM seente ja peremeestaimede vaheliste interaktsioonide spetsiifilisuses. Hiljutiste uurimuste tulemused viitavad sellele, et sümbooli spetsiifilisus taime- ja AM seeneliikide vahel avaldub mitte taimeliikide, vaid taimede ökoloogiliste, nt. kasvukoha eelistuse alusel jaotatavate gruppide tasemel. On oletatud, et AM seente eosed ja seeneniidistik mullas võiks olla taimede seemnepangaga sarnane AM seente liikide kogum, kust taimed seenpartneri leiavad. Samas uurimusi, kus kasutatakse taime juuresise ja mullas leiduva AM seente koosluse kirjeldamiseks sama meetodit, on järelduste tegemiseks ebapiisavalt.

AM seenekoosluste liigirikkust ja koosseisu võivad mõjutada keskkonnamitingimused nagu mulla toitainete ja orgaaniliste ainete sisaldus, pH ning majandamine. Kõrgema fosforisisaldusega muldades (sh. väetamise tõttu) on tuvastatud vähem AM seeneliike kui madala fosforisisaldusega muldades. Toitainetesisaldus ja mehhaaniline häirimine (põllumajandustegevus, metsa lageraied) võivad lisaks mõjutada ka AM seente koosluse koosseisu ja biomassi mullas ning taimejuurtes. On näidatud, et keskkonnaparameetrid võivad varieeruda nii ajas kui ruumis ning arvatakse, et erinevused keskkonnatingimustes loovad nišid erinevate AM seente jaoks.

Järjest aktuaalsemaks teemaks AM seente koosluste uurimisel on tõusnud koosluste liigilist komplekti mõjutavad mehhanismid. Taimekoosluste kohta arvatakse, et need ei ole juhuslikult kokku sattunud liikide kogumid, kuigi seda mõjutavad tegurid pole üheselt teada. Looduslike AM seenekoosluste puhul on leitud, et ühes elupaigas koosinevad liigid on enamasti fülogeneetiliselt sarnased, kuid on kirjeldatud ka suure fülogeneetilise mitmekesisusega kooslusi. Üldisemate järeldute tegemiseks on vajalik koguda detailsemaid andmeid erinevatest AM seente kooslustest.

Käesolevas doktoritöös on kirjeldatud salumetsa AM seente koosluse mitmekesisuse mustreid ning neid mõjutavaid tegureid.

Töö eesmärgid olid järgmised:

1. Anda ülevaade AM seente looduslikust mitmekesisusest ning seenekooslusi mõjutavatest faktoritest (I).
2. Kirjeldada loodusliku salumetsa AM seente liigirikkust ja koosluse koosseisu (II, III).
3. Uurida peremeestaime liigi mõju juuresisese AM seenekoosluse liigirikkusele ja koosluse koosseisule metsa alustaimestik (II, III).
4. Uurida, kas esineb erinevusi taimejuurtest ja mullast tuvastatud AM seenekoosluste liigirikkuses ja koosseisus (III).
5. Uurida keskkonnaparameetrite ja metsa majandamise mõju AM seente kooslustele taimejuurtes.
6. Kirjeldada AM seente biomassi seoseid mulla toitainete sisaldusega salumetsa ökosüsteemis (IV).
7. Analüüsida AM seente koosluste fülogeneetilist struktuuri salumetsas (III).

Saadud tulemused näitasid, et AM seente mitmekesisus salumetsa alustaimestiku juurtes on suur. Järvelja ürgmetsa uurimiselalt tuvastatud AM seente liigirikkus oli liigi kaks korda suurem kui Koeru metsas. See võib viidata nende metsaökosüsteemide, aga eriti Järvelja metsa stabiilsusele. Samuti võib aga oma mõju olla viimastel aastatel toimunud arengul molekulaarsetes uurimismeetodites – võimalus tuvastada ja määrata suuremal arvul keskkonnaproovidest pärinevaid AM seente DNA järjestusi on pidevalt paranenud.

Juuresisesed AM seente kooslused ei erinenud oluliselt taimeliikide vahel. Kõik uuritud taimeliigid on nõ. metsaspetsialistid ja erinevate mustrite

puudumine AM seenekoosluste vahel nende taimeliikide juurtes võib tuleneda sellest, et spetsiifilisus peremeestaimel ja AM seente vahel avaldub mitte liikide tasemel, vaid nn. ökoloogilise grupi tasemel.

Keskkonnaparameetrid ja metsa majandamine ei omanud olulist mõju AM seente liigirikkusele ega koosluse koosseisule taimejuurtes. Keskkonnaparameetrite mõju AM seente koosluse koosseisule võib olla kaudne ja seotud AM seente muude (morfoloogiliste, füsioloogiliste) parameetritega ning väärib edasist uurimist. Samuti, mullakeskkonna suhteliselt minimaalne häirimine puuseemikute istutamisel pärast lageraiet võis aidata säilitada AM seente mitmekesisust.

AM seente koosluse koosseis mullas ja taimejuurtes oli erinev. AM seente liigirikkus oli tunduvalt suurem juureproovides võrreldes mullaproovidega. Erinevused taimejuurtest ja mullast tuvastatud AM seenekoosluste vahel ja suhteliselt väike mullast tuvastatud AM seente taksonite arv võivad tuleneda väiksemast AM seente biomassi madalamast tihedusest mullas võrreldes juurtega. Selle tulemuseks võib olla väiksem AM seente DNA hulk proovides ning sellest tulenev liigirikkuse alahindamine. Arvestades AM seente koosluste erinevusi mullas ja juurtes võiks AM seente koosluse koosseisu määramisel ökosüsteemis analüüsida paralleelselt nii taimejuure- kui mullaproove.

AM seente koosluse koosseisu ühe aspektina uuriti AM seenekooslusi moodustavate liikide fülogeneetilist dispersiooni ehk kas uuritud kooslus on moodustunud üksteisega fülogeneetiliselt sarnasematest/erinevamatest liikidest, kui juhuslikkuse alusel võiks oodata. Juhusliku koosluse moodustamiseks kasutati Maarj*AM* andmebaasi, mis koondab DNA järjestuste põhjal määratud AM seeneliike üle maailma. Samuti uuriti ka ainult Järvelja uurimisala mullaproovidest tuvastatud AM seente koosluse fülogeneetilist dispersiooni. Analüüsides selgus, et taimejuurtest tuvastatud AM seenetaksonite komplektid olid moodustunud fülogeneetiliselt sarnasematest seeneliikidest võrreldes Maarj*AM*is leiduvate AM seeneliikide hulgast juhuslikult valitud komplektidega. Mulla AM seenekoosluse liigiline komplekt aga ei erinenud Maarj*AM*is leiduvate AM seeneliikide või Järvelja ürgmetsast leitud liikide hulgast juhuslikult valitud komplektide omast. See viitab mitte-juhuslike protsesside mõjule AM seente koosluste moodustumisele taimejuurtes, kuid mitte mullas.

## AKNOWLEDGEMENTS

My sincerest gratitude goes to Dr. Maarja Õpik and Prof. Martin Zobel. Thank you for the comprehensive supervision, sharing the knowledge and expertise during the years of my doctoral studies and for understanding at times, when my family has been my only priority. I am thankful to all the co-authors, especially John Davison for statistical advice. I am most grateful to all the colleagues from plant ecology workgroup for generating always friendly working atmosphere in the office, in the lab and in the forest. Teele, Odile, Kadri, Inga, Virve, Annika, Tsipe, Eve, Pille, Ingmar and many more, my parents and my family – you have made hard times easier to go through and good times much more joyful!

\* \* \*

This research was supported by Estonian Science Foundation grants (6533, 7366, 9050, 9157) and targeted financing (SF0180098s08), EU FP6 integrated project ALARM (GOCECT-2003-506675) and EU Marie Curie Fellowship grant MEIF-CT-2005-024657, Scottish Government Rural and Environment Research and Analysis Directorate (RERAD) and the European Regional Development Fund (Centre of Excellence FIBIR).



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### **Research articles referenced in Thomson Reuters Web of Science:**

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- Öpik, M., Moora, M., Zobel, M., Saks, Ü., Wheatley, R., Wright, F., Daniell, T. (2008). High diversity of arbuscular mycorrhizal fungi in a boreal herb rich coniferous forest. *New Phytologist*, 179, 867–876.

#### **Book chapters:**

- Öpik M, Saks Ü, Kennedy J, and Daniell T. (2008). Global diversity patterns of arbuscular mycorrhizal fungi – community composition and links with functionality. In: Varma A (ed.) *Mycorrhiza: State of the Art, Genetics and Molecular Biology, Eco-Function, Biotechnology, Eco-Physiology, Structure and Systematics*. pp. 89–112. Springer.

#### **Conference abstracts:**

- Saks, Ü., Davison, J., Öpik, M., Vasar, M., Moora, M., Zobel, M. “Communities of arbuscular mycorrhizal fungi in plant roots: more diverse than those in soil?” 56<sup>th</sup> Symposium of the International Association for Vegetation Science (IAVS), 26–30 June, 2013. Tartu, Estonia.
- Saks, Ü. Öpik, M. “Diversity of arbuscular mycorrhizal fungi in boreo-nemoral forest” 8<sup>th</sup> clonal plant workshop – generality, specificity and diversity of clonal growth. June 27–30, 2006. Pärnu, Estonia.
- Saks, Ü., Daniell, T., Öpik, M. “Diversity of arbuscular mycorrhizal fungi in boreo-nemoral forest” 5<sup>th</sup> International Conference on Mycorrhiza (ICOM). July 23–27, 2006. Granada, Spain.

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- Öpik, M., Moora, M., Zobel, M., Saks, Ü., Wheatley, R., Wright, F., Daniell, T. (2008). High diversity of arbuscular mycorrhizal fungi in a boreal herb rich coniferous forest. *New Phytologist*, 179, 867–876.

#### **Raamatu peatükk:**

- Öpik, M., Saks, Ü., Kennedy, J., Daniell, T. 2008. Global diversity patterns of arbuscular mycorrhizal fungi – community composition and links with functionality. In: Varma A (ed.) *Mycorrhiza: State of the Art, Genetics and Molecular Biology, Eco-Function, Biotechnology, Eco-Physiology, Structure and Systematics*. pp. 89–112. Springer.

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- Saks, Ü., Daniell, T., Öpik, M. “Diversity of arbuscular mycorrhizal fungi in boreo-nemoral forest” 5<sup>th</sup> International Conference on Mycorrhiza (ICOM). 23.–27. juuli, 2006, Granada, Hispaania.

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