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Communities of arbuscular mycorrhizal fungi in spruce forest ecosystem and their effect on performance of forest understorey plant species

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Department of Botany, Institute of Ecology and Earth Sciences,
Faculty of Science and Technology, University of Tartu, Estonia

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Supervisors: Professor Martin Zobel,
University of Tartu, Estonia

Senior Researcher Maarja Öpik,
University of Tartu, Estonia

Opponent: Dr. Miroslav Vosátka,
Institute of Botany,
Academy of Sciences of Czech Republic,
Czech Republic

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

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

I. **Uibopuu A, Moora M, Saks Ü, Daniell T, Zobel M, Öpik M. 2009.** Differential effect of arbuscular mycorrhizal fungal communities from ecosystems along management gradient on the growth of forest understorey plant species. *Soil Biology and Biochemistry* **41:** 2141–2146.

II. **Uibopuu A, Moora M, Öpik M, Zobel M. 2012.** Temperate forest understorey species performance is altered by local arbuscular mycorrhizal fungal communities from stands of different successional stages. *Plant and Soil* **356:** 331–339.

III. **Koorem K, Saks Ü, Sõber V, Uibopuu A, Öpik M, Zobel M, Moora M. 2012.** Effects of arbuscular mycorrhiza on community composition and seedling recruitment in temperate forest understorey. *Basic and Applied Ecology* **13:** 663–672.

IV. **Uibopuu A, Öpik M, Moora M, Saks Ü, Jairus T, Zobel M.** Effect of competition between arbuscular mycorrhizal and ectomycorrhizal fungi on host plant performance. Manuscript.

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Author's contribution to each paper (%)

	I	II	III	IV
Designing the experiments	80	90	30	90
Collecting the data	100	100	30	100
Analysing the results	90	90	10	100
Preparing the text	80	80	10	90

LIST OF ABBREVIATIONS

AM	Arbuscular mycorrhiza
ANOVA	Analisis of variance
DNA	Deoxyribonucleic acid
ECM	Ectomycorrhiza
GLM	Generalized linear model
NMS (NMDS)	Non-metric multidimensional scaling analysis
PCR	Polymerase chain reaction
T-RF	Terminal restriction fragment
T-RFLP	Terminal restriction fragment length polymorphism
Tukey HSD	Tukeys honestly significant difference

I. INTRODUCTION

Arbuscular mycorrhiza (AM) is a mutualistic symbiosis between land plants and fungi of the phylum Glomeromycota. The vast majority of plant species depend on this association because of mineral nutrient uptake (especially phosphorous and nitrogen) (Smith and Read 2008). AM fungi improve soil structure (Rothwell 1984; Piotrowski et al. 2004) and protect plants against pathogens and pollutants (Gange et al. 2002; Gonzalez-Chavez et al. 2002; Marulanda et al. 2003). AM fungi are obligatory symbionts and therefore depend on their plant partner to obtain carbohydrates for vegetative growth and sporulation (Smith and Read 2008). The Ordovician fossils reveal that AM fungi have existed on Earth for more than 460 million years (Redecker et al. 2000). They have been included into the earth biodiversity formation, to the creation of plant and soil microbial communities and consequently to stabilisation of ecosystems (Smith and Read 2008). AM symbiosis has influenced plant invasions (Marler et al. 1999; Callaway et al. 2004) and has played crucial role in the colonization of the land by plants (Brundrett 2002).

AM fungi establish symbiotic association mostly with herbaceous plant species, including agriculturally important crop species like wheat, corn and rice (Smith and Read 2008). These fungi can associate with tropical trees, but also trees from temperate forest such as *Acer platanoides*, *Fraxinus excelsior* and *Populus tremuloides* (Smith and Read 2008), and can co-colonize with ectomycorrhizal fungi in the same root system of particular tree species (e.g. *Populus* and *Salix* spp.; Dhillion 1994). Plant-AM fungus combinations seem to be not host specific, but rather host preferential (Vandenkoornhuyse et al. 2003; Smith and Read 2008), because low number of AM fungal species (over 250 morphospecies; Schüßler 2013) is associated with large number of potential host species (80–90% of terrestrial plants). Some studies have shown high selectivity between host plants and AM fungi (Bever 2002; Helgason et al. 2002), which can be related to the AM fungal benefits to host species.

In order to understand the importance of AM fungi for plant performance it is important to pay attention to the diversity and dynamics of these soil symbionts in particular ecosystems. It is evident that the diversity and composition of natural AM fungal communities varies in space (Öpik et al. 2006, 2010) and time (Dumbrell et al. 2011). Some AM fungal species appear to be more active in summer and other fungi more abundant in autumn (Merryweather and Fitter 1998). Also, seedlings and adult plants can be colonized by different AM fungal communities (Husband et al. 2002) and received benefits from fungal communities can be different for juvenile and adult plants (van der Heijden et al. 2006). Many studies have shown that anthropogenic activities affect the local AM fungal communities in plant roots (Helgason et al. 1998; Daniell et al. 2001; Alguacil et al. 2008; König et al. 2010; Schnoor et al. 2011) and in soil (Xavier and Germida 1999; Oehl et al. 2003, 2005; Schalamuk et al. 2006). In a forest ecosystem, Davison et al. (2011) showed that AM fungal

communities differ between successionally young and old forest stands. The mean AM fungal richness was also higher among forest specialist plant species (18.8 fungal taxa) than generalist (15.2) plants (Davison et al. 2011). Schalamuk et al. (2006) reported that agricultural practices like tillage and fertilization may affect the structure of AM fungal communities. For instance, the percentage of *Glomeraceae* species in soil samples was higher in no-tillage (65.55%) than in conventional tillage (56.87%) (Schalamuk et al. 2006). Also mowing in grassland decreased the abundance of AM fungi in forb roots (Šmilauer 2001). The agricultural soil cultivation, deforestation, pollution or fire etc. can drastically depress spore production and can break up the AM fungal mycelial networks in soil which leads to the decrease of mycorrhizal activity and AM fungal diversity (reviewed by Xavier and Germida 1999).

Differences in the diversity and community composition of AM fungi may result different growth responses in host plants (van der Heijden and Scheublin 2007) and changes in the structure of plant communities and ecosystem functioning (van der Heijden et al. 2006; Vogelsang et al. 2006; Scheublin et al. 2007). In most experiments, easily cultivated fungal taxa, functionally different isolates or artificial fungal communities have been used, which do not function as real natural fungal communities in the field. Sýkorová et al. (2007) have shown that in greenhouse trap culture experiments it is difficult to establish a root-colonizing AM fungal community reflecting the diversity of fungi in the field roots because fungal succession in such artificial systems may bias the results. Many AM fungal taxa that are common in natural ecosystems are not cultivable in trap cultures (Sýkorová et al. 2007). AM fungal inoculum from the field can support plant growth even better than fungal inoculum from culture (Estrada et al. 2013). For instance, in the high salinity soil conditions, only 30% of plants survived when inoculated with AM fungi from culture, while inoculated with the native AM fungi, the rate of survival were 100% (Estrada et al. 2013). There are only few studies where host plants have been inoculated with natural AM fungal communities. For instance, Moora et al. (2004) used natural AM fungal communities from grassland and mature boreal forest to address the effect of AM fungal inocula on the growth of *Pulsatilla* species. *P. pratensis* and *P. patens* showed better growth with AM fungal community from grassland than forest ecosystem. Moreover, an experiment with AM fungal inoculum from arable field showed that agricultural management practises influenced the abundance of AM fungi in the soil and its potential to support crop growth (Martinez and Johnson 2010). Some studies have reported the effect of nitrogen fertilization on local AM fungal communities and hence the differential effect of those communities on plant growth in particular conditions (Corkidi et al. 2002; Sigüenza et al. 2006; Johnson et al. 2008). As much as we are aware, no studies have demonstrated the effect of natural AM fungal communities from differently managed forest ecosystems on plant performance.

The species richness of plant communities depends on the recruitment of new seedlings in the vegetation (van der Heijden 2004; Smith and Read 2008).

Information of the effect of AM fungi on seedling establishment is very sparse. There have been suggestions that success of seedling establishment may depend on the interaction between mycorrhizal adults and emerged seedlings, because seedlings are exposed to severe competition for the resources (van der Heijden and Horton 2009). Adult plants facilitate the integration of seedlings into the extensive hyphal networks, acting as carbon sources for AM fungi and promoting inoculation of seedling via growth of a common mycelia network (Moora and Zobel 2010). Indeed, van der Heijden (2004) provided direct evidence that AM fungi enhance seedling recruitment in grassland communities. The seedlings grew larger and obtained more phosphorus when inoculated with AM fungi. For instance, the biomass of *Bromus erectus*, *Brachypodium pinnatum*, *Prunella vulgaris* and *Trifolium pratense* increased respectively with 55, 73, 17 and 100% in microcosms inoculated with AM fungi compared with non-mycorrhizal microcosms (van der Heijden 2004). At the same time, AM fungal benefits for seedling establishment can be species-specific and obviously more positive when nutrient availability for plants is low (Smith and Read 2008; Kiers and van der Heijden 2006; van der Heijden and Horton 2009). For instance, AM fungi may be important in unfertile conditions and detrimental in fertile conditions. However, there is still little information about the role of AM fungi on seedling establishment and especially their effect on seedling growth in natural ecosystems.

Competition for nutrients is crucial factor influencing plant performance and the structure of plant communities (Aerts 1999; Scheublin et al. 2007; Smith and Read 2008). Many tree species live in symbiosis with different types of mycorrhizal fungi like ectomycorrhizal (ECM) and AM fungi (Smith and Read 2008). Different species of mycorrhizal fungi (both AM and ECM) have different effects on the growth of particular plant species (van der Heijden et al. 1998; Wiseman and Wells 2005; Kipfer et al. 2012), variation in mycorrhizal fungus species composition can change competition patterns among plants (Hoeksema 2005; Scheublin et al. 2007). Competition can also occur among AM fungi or ECM fungi, whereby fungi are competing for root space of the same seedling (Kennedy et al. 2007; Bennett and Bever 2009). Information about the effect of AM symbiosis on plant competition is accumulating (Moora and Zobel 2010). In general, AM tends to amplify intraspecific and balance interspecific plant competition. Much less, however, is known about the effect of ECM on plant competition. As much as we are aware, no studies have examined the competition between AM and ECM plants, as well as competition between AM and ECM fungi and its effect on plant performance. There is only one study – Booth (2004) – which provides closer understanding of the possibility of competition between these two different types of fungi.

This thesis aims to study the effect of natural mycorrhizal fungal community variation on plant establishment and growth. The main emphasis is put on AM fungal communities, as well as AM plant species. However, as different types of mycorrhiza coexist in temperate ecosystems, interactions between AM and

ECM plants are also addressed. In particular, the aims of this doctoral thesis were the following:

- to assess the effect of AM fungal communities from differently managed ecosystems on plant performance **(I, II)**.
- to describe the communities of AM fungi in the roots of forest understorey plants and its relation to the forest management intensity **(I)**.
- to study the effect of AM fungi on seedling recruitment structuring plant communities and its dependence on soil fertility **(III)**.
- to examine the competition between two different types of mycorrhizal fungi (AM and ECM fungi) and its effect on host plant performance **(IV)**.

2. MATERIALS AND METHODS

2.1. Study sites

In papers **I, II, III**, the study site was located in Koeru, central Estonia (58°58′N; 26°03′E), which is flat area with a mosaic landscape of cultivated arable areas and forests. The climate is transitional between a maritime and continental climate. The mean annual precipitation is 700–750 mm. Mean annual air temperature in the region is 4.3–6.5 °C, ranging between −7 °C in January and 17.4 °C in July (Jaagus 1999). For greenhouse experiments, soil inoculum was collected from a boreo-nemoral forest old and young stands (**I, II**) and an adjacent arable field (**I**) at Koeru. In paper **III**, the field experiment was performed in the old forest of Koeru as well.

In the study area, the forest is a 130 ha patch of *Hepatica nobilis* Mill. site type spruce forest on a calcaric cambisol with uniform soil conditions throughout the study area (Zobel et al. 2007). According to the current information, Koeru forest has not been tilled in earlier times; it is classified as forest on the oldest map available (from 1828). The forest has been managed with clear-cutting in patches of approximately 1–2 ha, but still part of the forest can be classified as old growth, with different age classes present. In these patches the oldest spruce trees are 130–140 years old. Due to the low intensity management, those stands represent ecosystems with old growth spruce forests with heterogeneous canopy where only scattered selective felling of individual old trees has been practiced. The dominant tree species is *Picea abies* (L.) Karst. with individuals of *Fraxinus excelsior* L. and *Acer platanoides* L.; *Corylus avellana* L. prevails in the shrub layer (Moora et al. 2007). High intensity management in young stands present early successional stages of the forest, where young dense stands have been clear-cut 20–25 years ago and thereafter planted with *P. abies*. *Betula pendula* L. and *Tilia cordata* Mill. trees are other more common species in the young forest (Moora et al. 2007). Sixty nine herbaceous vascular plants species are recorded in the field layer in the Koeru study area with most abundant species like *Oxalis acetosella* L., *Fragaria vesca* L., *Viola mirabilis* L. and *H. nobilis* (Zobel et al. 2007). Arable field near the forests was cropped with winter oil-seed rape at the time of soil collection for paper **I**. In the study area, 53 AM fungal taxa have been recorded in roots of forest understorey plant species (Öpik et al. 2008, 2009; Davison et al. 2011). The AM fungal community composition varies between old and young forest stands (Davison et al. 2011).

In paper **IV**, the site, where the soil inoculum was collected, was located in Vapramägi, southern Estonia (58°16'N; 26°31'E). It is a boreo-nemoral forest patch of about 98.5 ha and is mostly covered by over 100 years old trees. Forest understorey is herb rich; the forest represents either *H. nobilis* or *O. acetosella* site type mixed pine forest. Dominant tree species is *Pinus sylvestris* L. with

scarce *P. abies*, *B. pendula* and *T. cordata* trees. *C. avellana*, *Padus avium* Mill. and *Alnus incana* L. are subdominants in the shrub layer.

2.2. Greenhouse experiments

To address the effect of soil inocula of different origin on the plant growth (**I, II**), the topsoil samples (3–10 cm) were collected from ten randomly chosen locations in old and young forest (**I, II**) and arable field (**I**) and stored in darkness at 10 ^{o}C until use. Soil from each ecosystem was sieved to remove roots, pooled and mixed before use. Seeds of *Trifolium pratense* L.*, Hypericum maculatum* L. and *Geum rivale* L. plants in paper **I** and seeds of *Geranium pratense* L.*, Prunella vulgaris* L.*, H. maculatum, Veronica chamaedrys* L.*, Fragaria vesca, Plantago lanceolata* L.*, Primula veris* L. and *Solidago virgaurea* L. plants in paper **II** were collected from the study forest or other natural ecosystems in Tartu County. In both papers, seeds were germinated on Petri dishes on moist filter paper. Three seedlings were sown into plastic pots (13×15 cm, depth × diameter) and one seedling was retained per pot after 4 weeks of growth. In paper **I**, the growth substrate was a mixture of sand and the three natural soils from old forest, young forest and arable field in equal parts. Two soils and sand were autoclaved (1 h at 1 atm) and third soil served as the AM fungal inoculum. A 1:1:1:1 mixture of autoclaved three soils and sand served as a non-mycorrhizal control. In paper **II**, we used growth substrate with a 1:1:1 mixture of sand and the two natural soils in equal parts, where one soil and sand were sterilized by gamma irradiation (20 h at 1 kGy) and the other soil served as the AM fungal inoculum. For a non-mycorrhizal control the whole growth substrate was irradiated. In paper **I** and **II**, all growth pots received 40 ml filtered washing of mixed soil inocula to correct for possible differences in the soil bacterial and non-AM fungal communities (pore size 50 μm; Koide and Li 1989). The mycorrhizal treatments (inoculum from old forest, young forest and arable field) were replicated 12 times (**I**) and 10 times (except inoculum from arable field) (**II**) and non-mycorrhizal control 6 times (**I**) and 10 times (**II**) for each host species giving 126 and 240 pots in total for paper **I** and **II**, respectively. Plants were grown in greenhouse with a day length of 16 h with continuous light and were watered every third day with tap water. After the growing period, plants shoot and roots were harvested separately, dried at 70 ^{o}C for 48 h, and weighed (**I, II**).

Subsamples of harvested roots were stained with trypan blue (Koske and Gemma 1989) and the percentage of root mycorrhizal colonization was estimated using the magnified grid-line intersection method (McGonigle et al. 1990) (**I, II**). Assessment was performed using the Olympus CH20 microscope at 400x magnification. Intersection in root sample was considered mycorrhizal when the vertical crosshair in microscope crossed the AM fungal structure (120 intersections in total per subsample).

The AM fungal community composition in experimental plant roots was assessed by terminal restriction fragment length polymorphism (T-RFLP) in paper **I**. Detailed information about DNA extraction from root samples and PCR is described in Öpik et al. (2008). In short, Glomeromycota specific primers NS31 and AM1 labelled with fluorescent dyes TET and FAM, respectively, were used in PCR. 3 ml of the fluorescent PCR product was digested with 1 unit HinfI and Hin1II (isoschizomer of Hsp92II; Fermentas UAB, Vilnius, Lithuania) in the manufacturer's buffer for 2 h at 37 ^{o}C in the reaction volume of 5 ml. Digested samples were diluted 1:10 in sterile distilled water. 1 ml of this diluted sample was then mixed with 9 ml formamide and 0.05 ml GeneScan 500 LIZ size standard (Applied Biosystems, CA, USA). The samples were run on ABI Prism 3730 DNA Analyzer (Applied Biosystems, CA, USA) and the resultant peaks analysed using GeneMapper version 4.0 (Applied Biosystems, CA, USA).

In order to compare biomass data from greenhouse experiment to natural stands, ten randomly-selected individuals of six experimental plant species (*G. pratense, P. vulgaris, H. maculatum, V. chamaedrys, F. vesca* and *S. virgaurea*; smaller number was used when there were not enough plant individuals) were excavated from the study forest (**II**). We collected no biomass samples of *P. veris*, owing to its rarity at the field site, nor of *P. lanceolata* because it occurred only along forest paths and not in the understorey (**II**). Plants were dried at 70 ^{o}C for 48 h and weighed.

2.3. Field experiment

Field experiment was performed to study the role of AM fungi on seedling recruitment of *O. acetosella* and *P. vulgaris* plants in forest ecosystem and its dependence on soil fertility (**III**). Experiment extended over two years in which soil fertility (using fertilizer Osmocote or sucrose) and AM fungal activity (using fungicide Benomyl) were manipulated. Within a 50 m × 50 m area, treatments were randomly assigned to 240 experimental units – 40 units per treatment. One unit was a round plot with 15 cm diameter. Plant seeds were collected from study area and sown in 60 randomly chosen experimental units (ten replicates per treatment combination). In forest floor, the species composition, the number of plant shoots and the number of emerged seedlings were recorded and the growth of three most distant seedlings of two target species were estimated in each experimental unit with fixed time intervals. At the end of the experiment, whole soil core with plants in experimental unit was harvested and collected using a special soil corer (diameter 15 cm). Samples were transported to laboratory where the shoot and root biomass of herbaceous plants and target plants were separated, dried at 70 ^{o}C (for shoots) and 50 ^{o}C (for target species roots) and weighed. Soil samples were collected from the soil cores for chemical analysis. To estimate the percentage of AM fungal

colonization in target plant roots were used staining method and the magnified grid-line intersection method as in paper **I** and **II**.

2.4. Competition experiment with AM and ECM fungi

Two tree species, *Acer platanoides* L. and *Betula pendula* (hereafter *Acer* and *Betula*), accordingly inoculated with AM fungus *Glomus irregulare* (isolate DAOM197198) and ECM fungus *Paxillus involutus* (isolate TFC200426), were used in greenhouse experiment to test the competition between two different types of mycorrhizal fungi and its effect on plant performance (**IV**). Plant seeds were collected from different forest stands in Tartu County and were disinfected with 2.5% sodium hypochlorite solution before germination. Seedlings were pre-infected with fungus in sand cups, one seedling per cup. *Glomus* spores in sterile distilled water (200 spores per plant) were pipetted directly onto the *Acer* roots; *Paxillus* mycelium on 2 × 2 cm agar medium block was placed near the *Betula* roots. Inoculation process was performed under aseptic conditions using laminar flow cabinet. Sand cups were watered with sterile distilled water. After three months of inoculation treatment in growth chamber, inoculated and non-inoculated seedling combinations were transferred to the 2 L soil pots (one *Acer* and one *Betula* seedling into one pot). We had altogether four experimental treatments: inoculation of only *Acer* with AM fungi, inoculation of only *Betula* with ECM fungi, inoculation of both plant species with respective fungi, and both plant species non-inoculated. All plants were placed in mesh bags (pore size 41 μm) to avoid competition between two plants in the same pot, but allow fungal hyphae to grow across the mesh. After one week, microbial wash was added to each pot following the process described by Koide and Li (1989). All treatments were replicated 7 times, thus there were 28 pots in total. Experiment was conducted in growth chamber and lasted about four months. At the end of the experiment, plant above- and belowground biomass harvested separately, dried at 50 ^{o}C and weighed. AM fungal colonization in *Acer* roots was recorded using root staining and microscopy by the magnified grid-line intersection method as in paper **I**–**III**. *Betula* roots were stained with the same method and ECM fungal colonization was estimated with the scoring the presence-absence of *Paxillus* fungal structures at each intersection of root and the vertical crosshair for 120 intersections per subsample. An intersection was ecto-mycorrhizal if the vertical crosshair crossed the following internal and external fungal structures: the fungal sheath, Hartig net, a hypha in the root, a hypha and/or fungal strand on the root. All these parameters (fungal structures) were summarised for the total ECM fungal colonization in *Betula* roots.

2.5. Data analysis

To analyze the effect of soil inoculum and its interaction with plant species on plant shoot and root biomasses, root AM fungal colonization (**I, II**) and root AM fungal community composition (**I**) two-way ANOVAs were used. The effects of AM fungal activity manipulation and soil fertility manipulation and their interaction on seedlings shoot (for *Oxalis* and *Prunella*) and root dry weight (for *Prunella*), seedling root AM fungal colonization and soil nutrient content were also analyzed by two-way ANOVA (**III**). The effect of experimental treatments on cumulative number of seedlings was tested by Generalized Linear Models (GLM) (using Poisson distribution and log link function), all with soil fertility and AM fungal activity serving as fixed factors (**III**). In paper **II**, in order to address the plant species growth response to live soil inoculum (as the difference in growth between plants with and without mycorrhiza (Janos 2007)), log response ratio for shoot, root and total biomass was calculated. To address the competition between mycorrhizal fungi, one-way ANOVA was performed to estimate the response of fungal colonization in *Acer* and *Betula* roots on inoculation of neighbor plant (**IV**). The effect of fungal competition on plant biomass measures and calculated *Acer:Betula* biomass ratio was analyzed using two-way ANOVA (**IV**). Tukey HSD post hoc multiple comparison test (**I**) and Fischer post hoc multiple comparison test (**II, III, IV**) was applied to estimate the differences between treatments. Biomass data were log-transformed and percentages of AM fungal colonization were arcsine-transformed prior to statistical analysis (**I, II, III, IV**).

In paper **I**, the variation of AM fungal community composition based on the relative peak areas of terminal restriction fragments (T-RFs) in samples was analyzed by non-metric multidimensional scaling analysis (NMS). NMS was performed with PC-ORD for Windows version 5 (MjM Software, Gleneden Beach, Oregon, USA).

Pearson correlation was used to test the relationships between the plant biomass and AM fungal root colonization rate and AM fungal richness in paper **I**. Linear regressions was used in paper **II** and **IV** to test the relationships between plant species growth response and AM fungal root colonization rate.

3. RESULTS

3.1. The effect of AM fungal communities from differently managed ecosystems on plant growth

The effect of natural AM fungal communities from the old and young forest and an arable field was differential on the growth of studied plant species (**I, II**). The AM fungal community from the arable field increased *H. maculatum* shoot and root biomass compared with forest inocula and *T. pratense* root biomass compared to sterile control (Fig. 1a, b in **I**). *G. pratense* and *P. vulgaris* showed higher growth response to old forest than young forest inoculum (Fig. 1). *H. maculatum* had higher growth response to the old forest stand in the case of shoot biomass and *V. chamaedrys* in case of root biomass (**II**). *T. pratense, H. maculatum* and *G. rivale* from paper **I** (Fig. 1a-c) and *F. vesca, P. lanceolata and P. veris* from paper **II** (Fig. 1) showed no difference in response to inocula from old and young forest stands. *S. virgaurea* growth response was more positive to young forest inoculum (Fig. 1). The biomass of three plant species from natural stands (*G. pratense, P.vulgaris* and *S. virgaurea*) was also larger in old than in young stands (Fig. 2).

AM fungal root colonization differed between host plant species, but not between the type of soil inoculum (**I, II**).

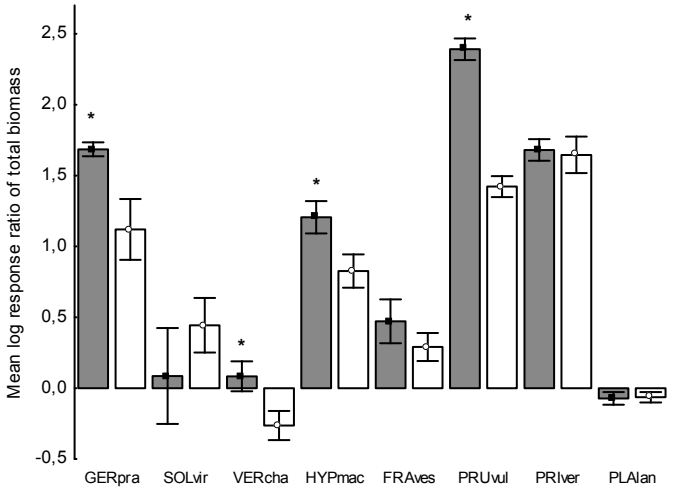

Fig. 1. Log response ratio of total biomass (calculated as a log-ratio of total biomass of inoculated and non-mycorrhizal plants; MR=ln(biomass inoculated/average biomass non-inoculated) of plant species to old (grey bars) and young (open bars) forest AM fungal inoculum in pot experiment. GERpra – *Geranium pratense,* SOLvir – *Solidago virgaurea*, VERcha – *Veronica chamaedrys*, HYPmac – *Hypericum maculatum*, FRAves – *Fragaria vesca,* PRUvul – *Prunella vulgaris,* PRIver – *Primula veris,* PLAlan – *Plantago lanceolata.* Asterisks (*) above bars indicate significant difference ($P < 0.05$) between plant species response to old and young forest inocula according to the Fischer LSD test. Values presented are means ± SE. Results from paper **II**.

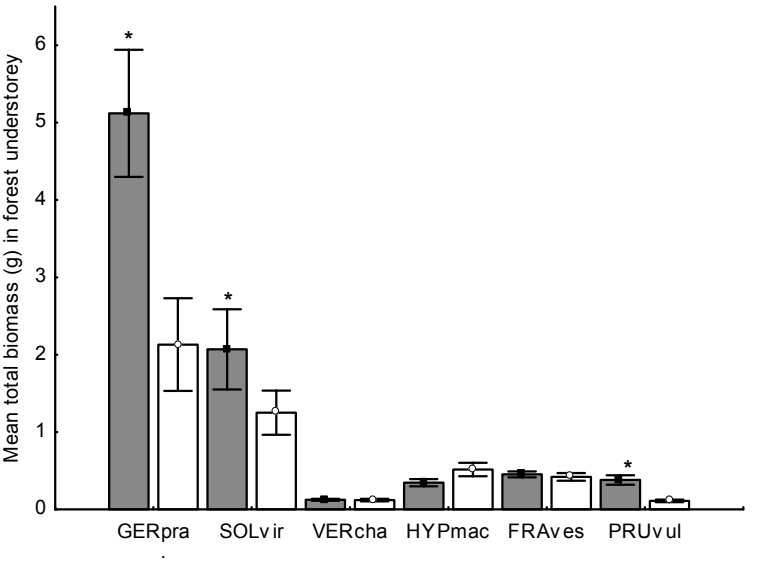

Fig. 2. Total biomass (g) of plant individuals growing naturally in the understorey of old (grey bars) or young (open bars) forest. Plant species codes are as in Fig. 1. Note that *P. veris* and *P. lanceolata* were not measured in vegetation due to either no sufficient number or absence in forest understorey. Asterisks (*) above bars indicates significant difference ($P < 0.05$) between forest stands in plant species biomass according to the Fischer LSD test. Values presented are means ± SE. Results from paper **II**.

3.2. AM fungal community composition in plant roots and its relation to the forest management intensity

Although the AM fungal communities in root samples (based on relative abundances of T-RFs in samples) showed overlapping composition in treatments (Fig. 3), there was the effect of soil inoculum and host plant species on the composition of fungal communities (**I**). *G. rivale* hosted a significantly different AM fungal community than *T. pratense* and *H. maculatum* (Fig. 3d-f; **I**). When inoculated with same soil, the three plant species were eventually colonized by different AM fungal communities. Such difference was most evident in the case of arable field inoculum (Fig. 3c). *G. rivale* and *T. pratense*, but not *H. maculatum*, displayed differing fungal communities in their roots when inoculated with the three inocula (Fig. 3d-f; **I**). AM fungal taxon richness was significantly higher in *T. pratense* roots than in *H. maculatum* and *G. rivale* roots (**I**). AM fungal inocula from old and young forest resulted in similar AM fungal communities in plant roots whilst plants grown with arable field inoculum hosted a different AM fungal community from those grown with old forest inocula (Fig. 3a-c; **I**).

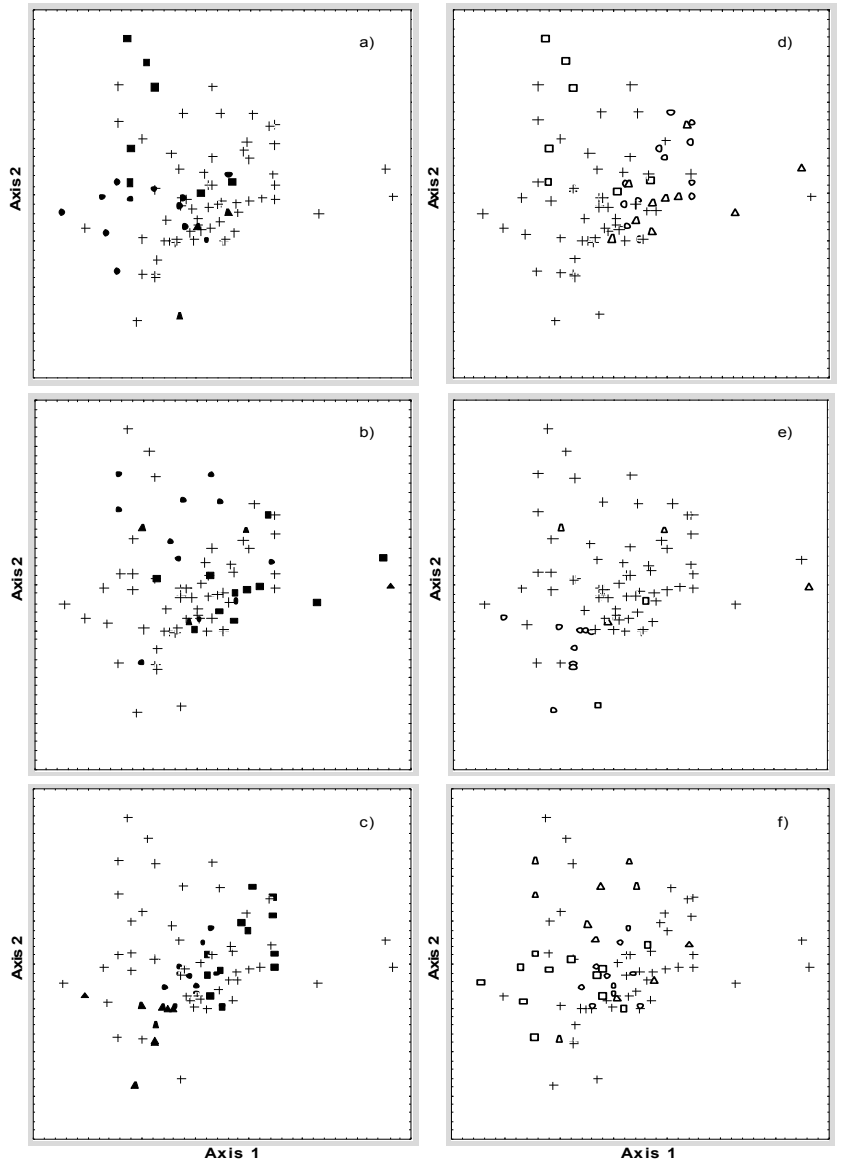

Fig. 3. NMS analysis of AM fungal community composition in plant roots based on T-RF data. Fungal community composition in individual plant roots is shown by labeling plant species inoculated with soils from young forest (a), old forest (b) and arable field (c): *G. rivale* (closed squares), *H. maculatum* (closed triangles) and *T. pratense* (closed circles), or labeling the origin of soil inocula for *G. rivale* (d), *H. maculatum* (e) and *T. pratense* (f) plants: soil inoculum from young forest (open squares), old forest (open triangles) and arable field (open circles). The first axis describes 32% and second axis, 21% of total variance. All panels are identical, except for the labeling of the treatments. Crosses denote samples of inoculation treatments (a–c) or plant species (d–f) not differentially labelled at the particular panel. Results from paper **I**.

3.3. The effect of AM fungi on seedling recruitment in the field and its dependence on soil fertility

Manipulation with AM fungal activity and soil fertility in the field had no effect on the number of naturally occurring *O. acetosella* seedlings (Appendix A: Table 3 in **III**). Suppression of AM fungal activity decreased the number of *P. vulgaris* seedlings whereas manipulation of soil fertility had no effect (Appendix A: Table 3 in **III**).

Aboveground biomass of *O. acetosella* seedlings was higher with natural AM fungal activity when soil fertility was decreased compared to conditions where soil fertility was decreased and AM fungal abundance was suppressed (Table 1, Fig. 2E in **III**). Aboveground biomass of *P. vulgaris* showed no significant difference between treatments (Table 1, Fig. 2F in **III**).

3.4. The effect of competition between AM and ECM fungi on plant growth in a pot experiment

A. platanoides biomass was not affected by its AM inoculation, as well as by ECM fungal inoculation of the neighbour *B. pendula* plant (Table 1 in **IV**). The biomass of ECM-inoculated *B. pendula* plants was three times higher than that of non-inoculated plants (Fig. 4a-c; Table 1 in **IV**). *B. pendula* shoot and total biomass was marginally positively affected by AM fungal inoculation of neighbour *A. platanoides* plants (Fig. 4d, f; Table 1 in **IV**).

AM and ECM fungal inoculation had no effect on the *Acer:Betula* biomass ratio, except that their interaction influenced *Acer:Betula* total biomass ratio (Table 1 in **IV**). *Acer:Betula* total biomass ratio was higher in the treatment with AM-inoculated *A. platanoides* and non-inoculated *B. pendula* than when both plants were not inoculated (Fig. 5).

AM fungal colonization in *A. platanoides* roots and ECM fungal colonization in *B. pendula* roots was not affected by the inoculation of the neighbour plant (Table 2 in **IV**).

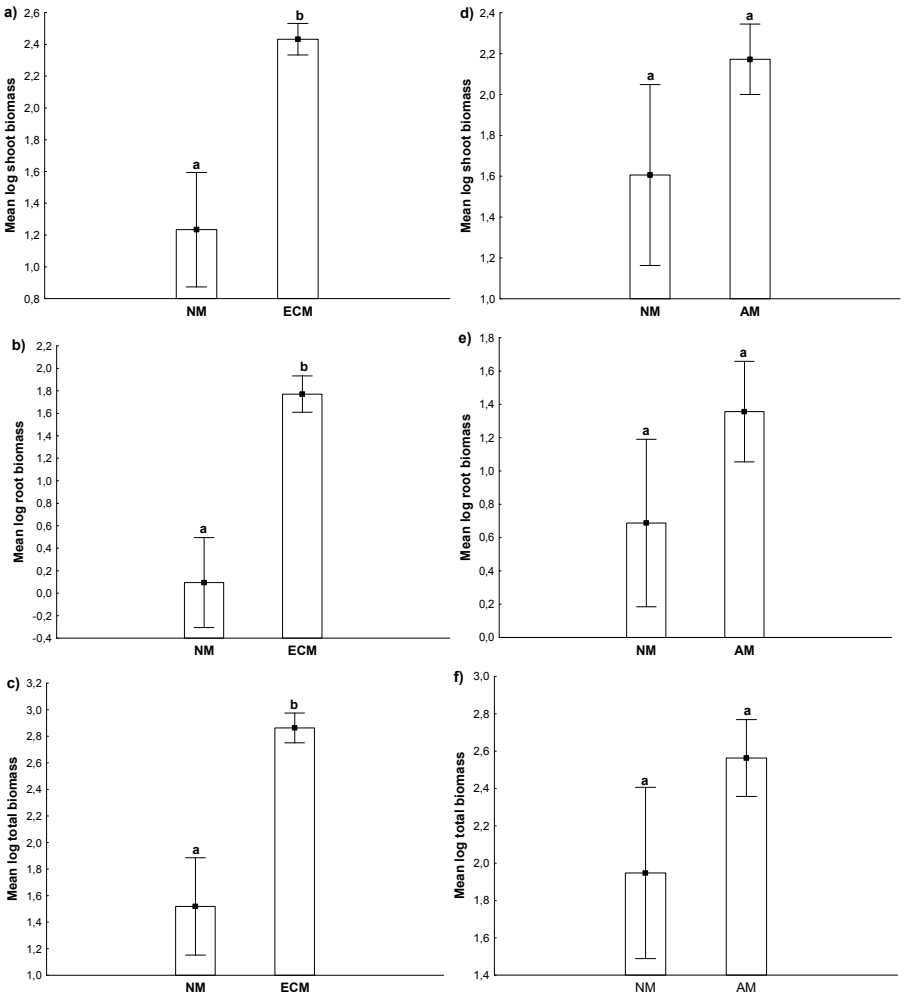

Fig. 4. *Betula pendula* shoot, root and total biomass response to ECM fungal inoculation (a, b, c) and AM fungal inoculation (of the neighbour *Acer platanoides* plant) (d, e, f). Biomass data are log-transformed. AM: arbuscular mycorrhizal fungal inoculation of *A. platanoides*; ECM: ectomycorrhizal fungal inoculation of *B. pendula*; NM: non-mycorrhizal control. Bars with different letters are significantly different ($P < 0.05$) according to the Fischer LSD test. Presented values are means ± SE. Results from paper **IV** Experiment 1.

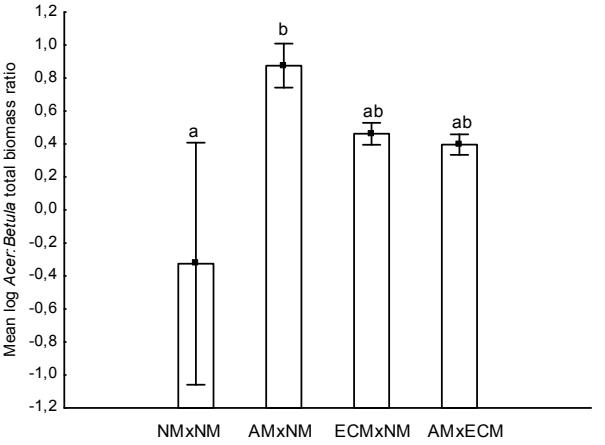

Fig. 5. The *Acer:Betula* total biomass ratio in response to inoculation with AM and ECM fungi. Biomass data are log-transformed. One *Acer platanoides* and one *Betula pendula* plant separately in mesh bags were grown together in a pot where *A. platanoides* was inoculated or not with AM fungus *Glomus irregulare* and *B. pendula* was inoculated or not with ECM fungus *Paxillus involutus.* The mesh allowed fungal growth across the bags but excluded root growth. AM: arbuscular mycorrhizal fungal inoculation of *A. platanoides*; ECM: ectomycorrhizal fungal inoculation of *B. pendula*; NM: non-mycorrhizal control. Bars with different letters are significantly different ($P < 0.05$) according to the Fischer LSD test. Presented values are means ± SE. Results from paper **IV** Experiment 1.

4. DISCUSSION

4.1. A differential effect of AM fungal communities on plant growth

The results of this study demonstrated that the AM fungal communities from differently managed ecosystems can have different effect on the growth of forest understorey plant species (**I, II**). AM fungal community from arable field caused better growth of *H. maculatum* plants than that from forest stands (**I**). *T. pratense* grew poorly without mycorrhizal fungi, but did not show different growth response to mycorrhizal inocula (**I**). *G. pratense* and *P. vulgaris* showed clear positive growth response to old forest inoculum compared to young forest inoculum (**II**). *V. chamaedrys* had higher growth response to the old forest stand only in the case of root biomass (**II**). *T. pratense, H. maculatum* and *G. rivale* from paper **I** and *F. vesca, P. lanceolata and P. veris* from paper **II** showed no difference in response to old and young forest stands. In contrast, *S. virgaurea* responded more positively to young forest inoculum (**II**). These results confirm that there is the specific compatibility between host plants and AM fungi as has been shown earlier (Smith and Read 2008; Öpik et al. 2009; Davison et al. 2011). The previous experiments have found that different natural AM fungal communities have a different effect on plant performance (Corkidi et al. 2002; Moora et al. 2004; Sigüenza et al. 2006; Johnson et al. 2008). The communities of AM fungi vary greatly in natural ecosystems and their distribution is affected by various factors including soil, host plant, abiotic and biotic conditions and land use intensity (Xavier and Germida 1999; Oehl et al. 2003, 2010; Fitter 2005; Kernaghan 2005; Dumbrell et al. 2010a,b). The differences in AM fungal communities may have large effects on the plant communities and ecosystem processes (van der Heijden et al. 2006; Vogelsang et al. 2006; Scheublin et al. 2007; Klironomos et al. 2011). However, the results of this study add new evidence about the influence of land use intensity on AM fungal communities and hence its effect on plant growth (**I, II**). Agricultural and forest management practises have shaped AM fungal communities which have different impact on the growth of forest understorey plant species. Plant biomass of naturally growing individuals showed that the growth response of plant species in experimental conditions was in accordance with plant growth in the field (**II**). Namely, the naturally growing *G. pratense* and *P. vulgaris* plants were also larger in old forest stands than in young forest stands (**II**).

4.2. Community composition of AM fungi in plant roots and its relation to the forest management intensity

Many studies have shown that land use intensity affects the diversity and community composition of AM fungi in plant roots (Helgason et al. 1998; Daniell et al. 2001; Šmilauer 2001; Alguacil et al. 2008; König et al. 2010; Schnoor et al. 2011). Increased human activity can be detrimental to mycorrhizae (Xavier and Germida 1999). The current study revealed that although the AM fungal communities in the experimental plant roots showed overlapping composition in treatments there was still significantly different composition (**I**). When data from all three plant species were pooled, plants inoculated with arable field fungi hosted a different AM fungal community than plants grown with old forest inocula (**I**). AM fungal communities from old and young forest inoculum showed similar composition (**I**) which is accordance with the previous study of Öpik et al. (2008). In contrast, in the study of Davison et al. (2011), they collected roots of more species from the understorey of Koeru forest and were able to show the differences between AM fungal communities in host roots when grown in old and young stands. Further observations and experiments are needed to confirm the possibility that the AM fungal communities are different in successionally old and young forest.

The distinctive mycorrhizal communities emerged in the roots of three experimental plant species growing with the same inocula (**I**). For instance, *G. rivale* and *T. pratense* were colonized by different fungal communities when inoculated with the three natural inocula, and *H. maculatum* showed similar communities of fungi in roots when inoculated with the three natural inocula (**I**). AM fungal taxon richness was higher in *T. pratense* roots than in *H. maculatum* and *G. rivale* roots (**I**). Earlier studies have reported the host preference as well (Helgason et al. 2002; Smith and Read 2008), and it is in accordance with our findings (**I**), where plant species exhibited selectivity in their associations with fungal partners.

4.3. The role of AM fungi on seedling recruitment and its dependence on soil fertility

The results of this study showed that AM fungi influence the success of seedling recruitment in forest ecosystem, and it was more pronounced under low nutrient availability for plants (**III**). In particular, emergence of a common forest understorey species *O. acetosella* was unaffected by experimental manipulations, but seedlings growth was significantly enhanced by natural activity of AM fungi when soil fertility decreased (**III**). Earlier studies have reported that seedlings growing in low soil fertility conditions may experience more nutrient stress, and hence symbiosis with AM fungi could alleviate the

nutrient stress for plants (van der Heijden and Horton 2009). Suppression of AM fungi under low soil resources may therefore result in inhibited seedling growth. Results received with *O. acetosella* plants are in accordance with this expectation. In contrast to the behavior of *O. acetosella*, emergence of *P. vulgaris* was positively influenced by natural activity of AM fungi, but seedlings growth showed no significant response to experimental manipulations (**III**). *O. acetosella* and *P. vulgaris* have been characterized by different authors as a forest specialist and generalist plants, respectively (see Santos-González et al. 2007; Öpik et al. 2009). *O. acetosella* as forest habitat specialist harbors a high number of AM fungi in its roots when growing in this study area (Öpik et al. 2009; Davison et al. 2011). In contrast, *P. vulgaris* as forest generalist harbors lower numbers of fungi in their roots than habitat specialist (Santos-González et al. 2007; Öpik et al. 2009; Davison et al. 2011). The growth of generalist *P. vulgaris* did not depend on the presence of AM fungi even in low soil fertility condition (**III**). It seems thus that AM fungi have a stronger influence on those plants that are specialized to the habitat than for the habitat generalist plant species.

4.4. The competition between AM and ECM fungi and its effect on plant performance

The competition for nutrients is one of the main forces influencing plant coexistence within limited space (Aerts et al. 1999; Smith and Read 2008). Some studies have demonstrated that there is competition between mycorrhizal fungi colonizing the same root system as well. For instance, Kennedy et al. (2007) showed competition between ECM fungi when colonising same *Pinus muricata* roots. Also, AM fungi compete for root space, and the best competitors can be the worst mutualists and vice versa (Bennett and Bever, 2009). According to the best of our knowledge, no studies have been performed to examine the competition between two different types of mycorrhizal fungi, notably between AM and ECM fungi. The results of this study demonstrated, however, that there was no competition between AM and ECM fungi (**IV**). AM fungal colonization in *A. platanoides* roots and ECM fungal colonization in *B. pendula* roots was not affected by the inoculation of neighbour plant (**IV**). ECM fungi had strong positive effect on *B. pendula* growth: the shoot, root and total biomass was three times higher when plants were inoculated with ECM fungi compare to non-inoculated plants (**IV**). Also, *B. pendula* had tendency for higher biomass (non-significant) when neighbour plant was infected with AM fungi (**IV**). AM and ECM fungi may access different soil nutrient pools (Michelsen et al. 1998) which improves nutrient availability for *Betula* plants when AM and ECM fungi are both present. In the current study, AM and ECM fungal inoculation had no influence on *A. platanoides* growth (**IV**). The interaction between AM and ECM fungal inoculation treatments was still

significant when *Acer:Betula* total biomass ratio was addressed (**IV**). In the treatment with AM-inoculated *A. platanoides* plants and non-inoculated *B. pendula* plants, significantly higher *Acer:Betula* total biomass ratio was observed, compared to treatment with no fungal inoculation of both plants (**IV**). In the study by Booth (2004), *Acer rubrum* seedlings showed also better survivorship when ECM fungi were lacking in the system. Booth (2004) speculated that in the absence of ECM network, *Acer* would be better competitor in the understorey compared with *Betula* plants. Further experimental studies employing different combinations of plant and fungal species are needed to explore the competition between different types of mycorrhizal fungi and to understand its effect on plant performance in more detail. There are examples of tree species which associate both with ECM and AM fungi; so it would be interesting to address the fungal competition in the same root system and its effect on plant performance.

5. CONCLUSIONS

The results of this study showed that arbuscular mycorrhizal (AM) fungal communities from differently managed ecosystems (from old forest, young forest and arable field) have differential effect on the growth of forest understorey plant species. *G. pratense*, *P. vulgaris* and *V. chamaedrys* showed better growth with AM fungal community from old forest stand than plants grown with young forest inoculum (**II**). *T. pratense* and *H. maculatum* responded more positively to the arable field inoculum (**I**), and *S. virgaurea* had higher growth rate with AM fungi from young forest compared to old forest inoculum (**II**). There were also plant species which showed no difference in response to old and young forest inoculum (**I, II**). For instance, *T. pratense*, *H. maculatum* and *G. rivale* species from paper **I** and *F. vesca*, *P. lanceolata* and *P. veris* species from paper **II**. These results confirm the specific compatibility between host plants and AM fungi. The communities of AM fungi are affected by various biotic and abiotic factors. Changes in the diversity and community composition of AM fungi may result in different growth responses of host plants and can have large effects on plant communities and ecosystem functioning.

Results from paper **I** provide additional evidence that plant species can have distinctive mycorrhizal fungal communities in their roots even when inoculated with the same inocula. These results are supported by the previous studies, where plants appear to display selectivity in their interactions with fungal partners. Our results showed that the community composition of AM fungi was significantly different between treatments (**I**). AM fungal inocula from old and young forest resulted in similar AM fungal communities but plants grown with AM fungi from arable field hosted a significantly different AM fungal community from those grown with old forest inocula (**I**).

The results from field experiment demonstrated that AM fungi influence the success of seedling recruitment in forest ecosystem depending on local soil fertility (**III**). The positive effect of AM fungi was stronger for those plants that are specialized to the habitat compared to habitat generalist species (**III**). AM fungi enhanced the growth of *O. acetosella* seedlings (forest specialist species) under decreased soil fertility, but did not influence the growth of *P. vulgaris* seedlings (habitat generalist species) (**III**). Suppression of AM fungal activity decreased the number of *P. vulgaris* seedlings (**III**).

Although the earlier studies have provided some evidence about the existence of competition between AM fungi or ECM fungi in plant roots, the study results from paper **IV** showed no evidence of competition between AM and ECM fungi. AM fungal colonization in *A. platanoides* roots and ECM fungal colonization in *B. pendula* roots was not affected by the inoculation of neighbour plant (**IV**). ECM-inoculated *B. pendula* plants showed three times higher biomass compared to non-inoculated plants (**IV**). However, there was not the effect of AM fungal inoculation on *A. platanoides* growth (**IV**). The interaction between the effects of both fungal inocula became evident in the

case of *Acer:Betula* total biomass ratio (**IV**), which was higher in the treatment with inoculated *A. platanoides* and non-inoculated *B. pendula* than when both plants were not inoculated (**IV**). These data suggest that *A. platanoides* may prefer growth conditions without the presence of ECM fungi, which is in accordance with previous results.

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SUMMARY IN ESTONIAN

Arbuskulaar-mükoriissete seente kooslused kuusiku ökosüsteemis ja nende mõju taimedele

Arbuskulaarne mükoriisa (AM) on kõige laiemalt levinud maismaasümbioos, mis moodustub obligatoorselt biotroofsete seente, hõimkonnast *Glomeromycota*, ja taimede (80–90% maismaataimedest) vahel. AM seentel on mitmeid taimedele kasulikke funktsioone, näiteks varustavad nad taimi toitainetega, parandavad mullastruktuuri, leevendavad patogeenide poolt põhjustatavat biootilist stressi ning mullareostuse poolt põhjustatavat abiootilist stressi. AM seened elavad peamiselt sümbioosis rohttaimedega, kuid koloniseerivad ka mitmeid troopilisi puid ja parasvöötme metsade puuliike. Samuti võivad nad olla nö. kaaskoloniseerijad puujuurtes koos ektomükoriisaseentega. Mitmed tööd on näidanud, et kasulik kooselu taimega pole AM seene jaoks peremehespetsiifiline, vaid seened pigem eelistavad neile sobivaid taimeliike. Samuti näitavad taimed mõnikord eelistusi teatud seente suhtes.

Paljudes töödes on näidatud, et AM seente mõju taimede kasvule sõltub konkreetsest taime- ja seeneliigist. Samuti varieeruvad AM seente mitmekesisus ja koosluste koosseis nii ajas kui ka ruumis. Inimtegevus omakorda võib mõjutada looduslikke seenekooslusi nii taimejuurtes kui ka mullas. Näiteks võib AM seenekooslus olla erinev suktsessiooniliselt vana ja noore metsa mullas kasvanud taimede juurtes. Samuti mõjutab AM seenekooslusi intensiivne põlluharimine ja karjakasvatamine, mille tagajärjel seente ohtrus ja liigiline koosseis juurtes muutuvad. Igasugune intensiivne maakasutus võib pärssida AM seente elutegevust ja lõhub seenemütseeli, mis omakorda viib seente aktiivsuse languseni ja liigirikkuse vähenemiseni häiritud keskkonnas. Sellised häiringud avaldavad mõju seenekooslustele ning seeläbi ka taimekooslustele.

Käesoleva väitekirja üheks eesmärgiks oli kirjeldada AM seenekooslusi kuusiku alustaimede juurtes (**I**) ning selgitada nende seente mõju taimede kasvule (**I, II**). Hetkel on veel vähe töid, kus taimi on inokuleeritud looduslike AM seenekooslustega. Näiteks on kasvuhoonekatses taimi inokuleeritud rohumaalt ja metsast pärit loodusliku AM seenekooslusega, et võrrelda nende seenekoosluste mõju taimede funktsionaalsetele parameetritele. Samuti on uuritud, kuidas intensiivne põlluharimine mõjutab loodulikke AM seenekooslusi ning seeläbi taimede saagikust. Samas ei ole varem tehtud ühtegi tööd metsahäiringute mõju kohta. Intensiivne metsamajandus võib muuta AM seenekoosluste koosseisu ning see omakorda avaldab mõju taimede kasvule, taimekooslustele ning ökosüsteemidele laiemalt. Antud töös viidi läbi kaks kasvuhoonekatset, mille tulemused näitasid, et erinevad AM seenekooslused (vana metsa, noore metsa ja põllu mullast pärinevad) mõjutavad taimede kasvu erinevalt (**I, II**). Näiteks aas-kurereha (*Geranium pratense*), harilik käbihein (*Prunella vulgaris*) ja külmamailane (*Veronica chamaedrys*) kasvasid paremini vana metsa AM seenekooslusega kui noore metsa seenekooslusega (**II**).

Aasristik (*Trifolium pratense*) ja kandiline naistepuna (*Hypericum maculatum*) eelistasid kasvada põllumulla AM seenekooslusega (**I**) ning harilik kuldvits (*Solidago virgaurea*) eelistas kasvada noore metsa mullas (**II**). Samas leidus taimeliike, mille kasvu ei mõjutanud AM seenekoosluste päritolu (**I, II**). Näiteks aasristiku, kandilise naistepuna ja ojamõõla (*Geum rivale*) (**I**) ning metsmaasika (*Fragaria vesca*), süstlehise teelehe (*Plantago lanceolata*) ja hariliku nurmenuku (*Primula veris*) (**II**) kasv ei erinenud oluliselt vana metsa ja noore metsa mullas kasvanud taimede vahel. Saadud tulemusi kinnitasid ka loodusest korjatud taimeproovid (**II**). Järelikult on taimi ja seeni, mis sobivad paremini kokku kui teised. Seda kinnitavad ka varasemad tööd. Eksperimendis kasvatatud taimeisendite juurtes kirjeldati AM seenekooslusti ja selgus, et kuigi taimede inokuleerimisel kasutati sama AM seenekooslust, siis erinevaid taimeliike koloniseerisid erinevad seenekooslused (**I**). Samuti erinesid AM seenekooslused töötluste kaupa (**I**). Põllumullas kasvanud taimede juurtes oli oluliselt erinev AM seenekooslus võrreldes vana metsa mullas kasvanud taimedega (**I**). Kuigi antud töös oli vana metsa mullast pärit AM seenekooslus sarnane noore metsa mullast pärit seenekooslusega (**I**), on nende erinevust loodusest korjatud juureproovide molekulaarse mitmekesisuse analüüsi abil tõestatud.

Käesoleva doktoritöö teiseks eesmärgiks oli selgitada, kuidas looduslik AM seente ohtrus mõjutab metsa alustaimestiku liikide idanemist ja idandite kasvu erineva mullaviljakuse tingimustes (**III**). Välieksperimendis pärsiti looduslikke AM seeni fungitsiidiga ja manipuleeriti mullaviljakust väetise (suurendamaks) ning suhkru (vähendamaks) lisamisega, mille järel jälgiti taimede idanemist ja kasvu. Töö tulemused näitasid, et AM seente ohtrus ei mõjuta hariliku jänesekapsa (*Oxalis acetosella*) idanemist. Samas oli madala mullaviljakuse puhul idandite kasv parem just loodusliku AM seente ohtrusega mullas, võrreldes viljakamas mullas kasvanud taimedega (**III**). Vastupidiselt harilikule jänesekapsale oli teise katseliigi, hariliku käbiheina (*Prunella vulgaris*), idanemine parem loodusliku AM seente ohtrusega mullas (**III**). Manipulatsioon mulla viljakuse ja AM seente ohtrusega ei mõjutanud hariliku käbiheina idandite kasvu (**III**). Varasemad tööd on näidanud, et harilikku jänesekapsast kui kitsa ökoloogilise amplituudiga liiki koloniseerivad arvukad AM seenetaksonid. Seevastu harilikku käbiheina, kui laia ökoloogilise amplituudiga taimeliiki, võivad koloniseerida väiksema arvukusega AM seenetaksonid. Töö tulemuste põhjal saab järeldada, et AM seente ohtrus mõjutab taimede idanemist ja kasvu, mis võib sõltuda mulla viljakusest. Seente mõju on eriti ilmne sellistele taimeliikide idanditele, mis on spetsialiseerunud antud kasvukohas.

Mitmed tööd on uurinud taimedevahelist konkurentsi, kus peamisteks konkurentsi põhjusteks on võitlus toitainete ja valguse pärast. Samuti on näidatud, et mükoriissed seened võivad konkureerida juureruumi pärast. Näiteks ektomükoriissed seeneliigid, aga ka AM seeneliigid, konkureerivad üksteisega koloniseerides sama taimejuurt. Samas on veel teadmata, kas AM seened ja ektomükoriissed seened võiksid ka omavahel konkureerida. Käesoleva väitekirja kolmandaks eesmärgiks oli kontrollida konkurentsisuhteid AM seente ja

ektomükoriissete seente vahel ja uurida, kuidas see mõjutab taimede kasvu (**IV**). Potikatses kasvatati koos kahte mükoriisset puuliiki, millest üks, harilik vaher (*Acer platanoides*), oli inokuleeritud AM seenega ning teine, arukask (*Betula pendula*), ektomükoriisse seenega (**IV**). Katsetaimedel hinnati seente juurekolonisatsiooni ning mõõdeti kasvuparameetreid. Seente kolonisatsioon juurtes näitas, et AM seente ja ektomükoriissete seente vahel ei esine konkurentsi. AM seente kolonisatsiooni hariliku vahtra juurtes ja ektomükoriissete seente kolonisatsiooni arukase juurtes ei mõjutanud naabertaime inokulatsioon (**IV**). Ektomükoriissed seened soodustasid arukase kasvu; see oli kuni kolm korda suurem võrreldes inokuleerimata taimedega (**IV**). Marginaalne mõju arukase kasvule oli ka naabertaime inokulatsioonil. AM seente inokulatsioon ja naabertaime ektomükoriissne inokulatsioon ei mõjutanud hariliku vahtra kasvu (**IV**). Taimede biomassi andmete põhjal arvutati vahtra ja kase biomasside suhe. Vaher:kask kogubiomassi suhe oli suurem tingimustes, kus vaher oli inokuleeritud AM seenega ja kask inokuleerimata, võrreldes tingimustega, kus kumbki taim ei olnud inokuleeritud. Sellest järeldub, et harilik vaher võib eelistada kasvutingimusi, kus ektomükoriissed seened puuduvad.

Kokkuvõttes näitavad doktoritöö tulemused, et maakasutuse intensiivsusel on väga oluline roll AM seenekoosluste ning seeläbi ka taimekoosluste mõjutajana. Nii nagu varieerub AM seenekoosluste koosseis, nii on ka nende seenekoosluste mõju taimeliikidele väga erinev. Juba taimede idanemisel ja kasvama hakkamisel on AM seentel kandev roll. Kuigi antud töös ei tuvastatud konkurentsi esinemist AM seente ja ektomükoriissete seente vahel, ei välista see pingeliste konkurentsisuhete tekkevõimalust kahe erineva seenegrupi vahel muudes olukordades.

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PUBLICATIONS

CURRICULUM VITAE

Name: Annika Uibopuu
Date of birth: 22.02.1984
E-mail: annika.uibopuu@ut.ee

Education:

1990–1999	Nõo Primary School
1999–2002	Tartu Raatuse Gymnasium
2002–2005	University of Tartu (B.Sc. in environmental technology)
2005–2007	University of Tartu (M.Sc. in environmental technology)
2007–2013	University of Tartu (Ph.D. student in environmental technology)

Professional employment:

2008–2012	University of Tartu, Institute of Ecology and Earth Sciences, lab assistant

Administrative responsibilities:

2007–2010	Member of the Eesti Looduskaitse Selts

Awards and Scholarships:

2008	Travelling grant from Kristjan Jaak Scholarship (SA Archimedes)

Research interests:
Communities of arbuscular-mycorrhizal fungi in forest ecosystems and their functions for the understorey plant species.

Publications:

Uibopuu, A., Moora, M., Saks, Ü., Daniell, T., Zobel, M., Öpik, M. 2009. Differential effect of arbuscular mycorrhizal fungal communities from ecosystems along management gradient on the growth of forest understorey plant species. *Soil Biology and Biochemistry* 41: 2141–2146.

Uibopuu, A., Moora, M., Öpik, M., Zobel, M. 2012. Temperate forest understorey species performance is altered by local arbuscular mycorrhizal fungal communities from stands of different successional stages. *Plant and Soil* 356: 331–339.

Koorem, K., Saks, Ü., Sõber, V., **Uibopuu, A**., Öpik, M., Zobel, M., Moora, M. 2012. Effects of arbuscular mycorrhiza on community composition and seedling recruitment in temperate forest understorey. *Basic and Applied Ecology* 13: 663–672.

Conference presentations:

Uibopuu, A., Öpik, M. "Native arbuscular mycorrhizal fungal communities' differential influence on the growth and metabolism of plant species". Poster. 2–6 July 2008. Conference of Plant-Microbial Interactions in Krakow, Poland.

Uibopuu, A., Öpik, M., Moora, M., Saks, Ü., Zobel, M. "The effect of arbuscular mycorrhizal fungal communities from differently managed ecosystems on plant performance". Poster. 26–30 June 2013. 56th IAVS Symposium "Vegetation patterns and their underlying processes" in Tartu, Estonia.

ELULOOKIRJELDUS

Nimi: Annika Uibopuu
Sünniaeg: 22.02.1984
E-post: annika.uibopuu@ut.ee

Haridus:

1990–1999	Nõo Põhikool
1999–2002	Tartu Raatuse Gümnaasium
2002–2005	Tartu Ülikool (B.Sc. keskkonnatehnoloogia eriala)
2005–2007	Tartu Ülikool (M.Sc. keskkonnatehnoloogia eriala)
2007–2013	Tartu Ülikool (doktorant, keskkonnatehnoloogia eriala)

Erialane teenistuskäik:

2008–2012	Tartu Ülikool, Ökoloogia ja Maateaduste Instituut, Botaanika osakond, laborant

Teadusorganisatsiooniline ja -administratiivne tegevus:

2007–2010	Eesti Looduskaitse Seltsi liige

Saadud uurimistoetused ja stipendiumid:
2008, Kristjan Jaagu välissõidu toetus (SA Archimedes)

Peamised uurimisvaldkonnad:
Arbuskulaar-mükoriissete seenekoosluste koosseis ja funktsioon metsa-ökosüsteemides.

Publikatsioonide loetelu:

Uibopuu, A., Moora, M., Saks, Ü., Daniell, T., Zobel, M., Öpik, M. 2009. Differential effect of arbuscular mycorrhizal fungal communities from ecosystems along management gradient on the growth of forest understorey plant species. *Soil Biology and Biochemistry* 41: 2141–2146.

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Uibopuu, A., Öpik, M. "Native arbuscular mycorrhizal fungal communities' differential influence on the growth and metabolism of plant speciesö. Poster. 2–6 Juuli 2008. Plant-Microbial Interactions konverents, Krakow, Poola.

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