How do monocultures of fourteen forest tree species affect arbuscular mycorrhizal fungi abundance and species richness and composition in soil?

Katarzyna Rożek⁴⁎, Kaja Rola⁵, Janusz Błaszkowski⁶, Tomasz Leski⁷, Szymon Zubek⁸

⁎ Corresponding author.

E-mail addresses: katarzyna.rozek@doctoral.uj.edu.pl (K. Rożek), kaja.skubala@uj.edu.pl (K. Rola), janusz blaszkowski@zut.edu.pl (J. Błaszkowski), tleski@man.poznan.pl (T. Leski), szymon.zubek@uj.edu.pl (S. Zubek).

https://doi.org/10.1016/j.foreco.2020.118091

Received 17 January 2020; Received in revised form 12 March 2020; Accepted 13 March 2020

Available online 19 March 2020

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1. Introduction

Numerous abiotic and biotic factors affect the structure and functioning of soil microbial communities. Significant factors responsible for such effects include the climate zone, ecosystem type, physical and chemical properties of soil as well as plant species identity and specificity (van der Heijden et al., 1998; Dumbrell et al., 2011; Bainard et al., 2011, 2014; Liu et al., 2012; Hazard et al., 2013; Helgason et al., 2014; Molina and Horton, 2015). Although arbuscular mycorrhizal fungi (AMF) constitute one of the most common and widespread groups of soil organisms and are symbionts of a majority of plant species, neither their diversity nor their interaction with plants in certain ecosystems are completely understood (Davison et al., 2015; Stürmer et al., 2018). Among these ecosystems are forests of the temperate climate zone. An overwhelming number of studies to date on plant-microbial interactions related to these ecosystems have focused on the dominant mycorrhizal type, ectomycorrhizas (Smith and Read, 2008; Veresoglou et al., 2017); however, the presence of endomycorrhizas, including arbuscular mycorrhiza (AM), among overstorey and understorey plant species has been noted as well (Wang and Qiu, 2006). Despite the presence of AMF in such ecosystems, knowledge concerning their diversity and interactions in European forests of the temperate climate zone is still insufficient (Patreze et al., 2012). AMF have been studied so far at this angle in Europe only in several locations of Belgium (Boeraeve et al., 2019a, 2019b), Estonia (Öpik et al., 2003; Moora et al., 2004; Uibopuu et al., 2009, 2012; Davison et al., 2012; Koorrem et al., 2012; Saks et al., 2014; Gerz et al., 2016), Germany (Wubet et al., 2003), Great Britain (Helgason et al., 1998, 1999, 2002, 2007; Dumbrell et al., 2011), and...
Poland (Rożek et al., 2019).

Soil chemical properties and microbial community structure and functioning are affected by overstory species (Malchair and Carnol, 2009; Malý et al., 2014; Reich et al., 2005); however, specific mechanisms of this interaction remains vague. On the one hand, variations in overstory species distribution and abundance affect spatial and temporal pattern of cation cycling and acidity of soils (Zinke, 1962; Finzi et al., 1998). On the other hand, variations in soil properties affect complexity of forest cover types (Alban, 1982; Bockheim, 1997). Fluctuations in these interactions are probably linked with variations in the quantity and quality of litters as well as root exudates and associated effects on the neighbours as well as microbial communities (Zinke, 1962; Alban, 1982; Muys et al., 1992; Bockheim, 1997; Finzi et al., 1998; Reich et al., 2005; Nettan et al., 2019). Litters of coniferous species contains lower amount of exchangeable cations in relation to deciduous species. Variation in tree species identity affects mineral weathering of parent materials as well as mineralisation and recycling of Ca in soils. Next, litters and content of Ca as well as pH in soils affect C and N cycling because higher pH is often associated with higher microbial biomass and higher rates of litter decomposition, soil respiration and net N mineralization, especially in soils of forest ecosystems (Zinke, 1962; Persson et al., 1989; Lelong et al., 1990; Muys et al., 1992; Quideau et al., 1996; Simmons et al., 1996; Finzi et al., 1998; Andersson et al., 2000; Dijkstra, 2003; Reich et al., 2005; Oostra et al., 2006; Hobbie et al., 2007). Moreover, overstory composition shapes understory species diversity and cover by light availability and enhancing the spatial heterogeneity of soil fertility (Muller, 2003; Neufeld and Young, 2003; Gilliam, 2007). Biomass quality and quantity of herbaceous species influence energy flow and nutrient cycling in forest ecosystems (Muller, 2003; Gilliam, 2007). Additionally, mycorrhizal status of forest plant species may affect the abundance of AMF propagules in soils (Rożek et al., 2019). Finally, microbial relationships of native plant species of forest ecosystems may be vulnerable to disruption through the novel biochemistry of alien plants (Callaway et al., 2005, 2008; Reinhart and Callaway, 2006). Nevertheless, the aforementioned interactions have not yet been sufficiently explored (Nadrowski et al., 2010), and no comprehensive studies have been conducted on the impact of overstory species identity on AMF abundance and species richness and composition in relation to herbaceous plant cover and soil chemical properties.

Suitable system for studying the impact of overstory species on AMF communities exists in the Siemianice Experimental Forest (western Poland), which is unique on a global scale. This area comprises 14 different tree species, planted in 1970 and 1971 as monoculture plots on the same soil type. Environmental factors have affected the entire area on a comparable scale. These conditions, unlike those in scattered wild forest complexes where various factors operate simultaneously to an uncontrollable extent, enable differentiation of the impact of particular tree species on AMF communities. A number of studies in this forest have already been conducted by international research groups. Their authors focused on ecosystem processes (Hobbie et al., 2006, 2007, 2010), ectomycorrhizas (Dickle et al., 2006; Trocha et al., 2012), fungal phenology (Dickle et al., 2010), plant invasions (Knight et al., 2008; Jagodziński et al., 2019), leaf and root life spans (Withington et al., 2006), leaf and root litter decomposition (Hobbie et al., 2006, 2010; Goebel et al., 2011), root distribution, phenology, and morphology (Dauer et al., 2009; Withington et al., 2003), and earthworms and the physical and chemical properties of soil (Reich et al., 2005; Dauer et al., 2007). The relationship between overstory species and AMF communities has not been explored. Thus, we studied the impact of overstory species identity on AMF abundance and species richness and composition in relation to herbaceous plant cover and soil chemical properties. The effects of 14 tree species grown in monospecific plots were compared, including groupings of deciduous vs coniferous, native to Poland/Europe vs alien, and forming vs not forming AM. We hypothesised that the tree species identity, as well as groups of species representing deciduous/coniferous trees, trees of native/alien origin, and trees forming or not forming AM, differentially affect AM presence, AMF abundance, and AMF species richness and composition in soil.

2. Materials and methods

2.1. Study site and sampling

The study was conducted in the Siemianice Experimental Forest, western Poland (51°14.87′ N, 18°06.35′ E, 150 m a. s. l.). This region is characterised by a transitional climate, between maritime and continental, with a mean temperature of 8.2 °C and mean annual precipitation of 591 mm. Soils are composed of 80% sand and 15% silt (Szymański, 1982; Reich et al., 2005; Hobbie et al., 2006). The site was a stand of Pinus sylvestris L. prior to clearing, stump removal, and ploughing to a depth of 60 cm (Dickie et al., 2010). The forest was established in 1970 and 1971 with seedlings, one and two years old, of 14 tree species, namely Abies alba Mill., Acer platanoides L., A. pseudoplatanus L., Betula pendula Roth, Carpinus betulus L., Fagus sylvatica L., Larix decidua Mill., Picea abies (L.) H. Karst., Pinus nigra Arn., P. sylvestris L., Pseudotsuga menziesii (Mirb.) Franco, Quercus robur L., Q. rubra L., and Tilia cordata Mill. Among the tree species were groups of coniferous (A. alba, L. decidua, P. abies, P. nigra, P. sylvestris, P. menziesii) and deciduous (A. platanoides, A. pseudoplatanus, B. pendula, C. betulus, F. sylvatica, Q. robur, Q. rubra, T. cordata); native (A. alba, A. platanoides, A. pseudoplatanus, B. pendula, C. betulus, F. sylvatica, L. decidua, P. abies, P. sylvestris, Q. robur, Q. rubra, T. nigra, P. cordata) and alien to Poland or Europe (P. nigra and P. menziesii, Q. rubra, respectively) (Witkowska-Zuk, 2012); and forming (A. platanoides, A. pseudoplatanus, P. menziesii) or not forming AM (A. alba, B. pendula, C. betulus, F. sylvatica, L. decidua, P. abies, P. sylvestris, Q. robur, Q. rubra, T. nigra, P. cordata) (Wang and Qiu, 2006; Hempel et al., 2013). The seedlings of all species were planted in 20 × 20 m plots, with spacing of 1 × 1 m, in 2 adjacent areas (Szymański, 1982; Reich et al., 2005). The number of plots for A. alba was 2 (the majority of A. alba trees on the third plot had fallen down several years ago); for A. platanoides, A. pseudoplatanus, B. pendula, C. betulus, F. sylvatica, L. decidua, P. abies, P. sylvestris, Q. robur, Q. rubra, T. nigra, P. cordata); 3; for L. decidua, P. abies, P. menziesii, and Q. robur, 6. The numbers of plots for particular groups of trees were as follows: deciduous (27) and coniferous (26); native (41) and alien (12); forming (12) and not forming AM (41).

To avoid the edge effect, a sampling plot, 1 × 1 m, was established in the central part of each plot. Plant species richness and plant cover were evaluated (see Section 2.2). Then, 3 soil-root subsamples were collected to a depth of ~20 cm using a shovel. ‘O’ layers were removed before sampling. Subsamples were placed in foil carriers and homogenised to form one composite soil-root sample for each plot. Randomly selected fragments of a root composite sample, originating from overstorey and/or understory species, depending on a plot, were transferred to fill a 60 ml plastic container and preserved in 50% ethanol. Soils were transferred into new foil carriers and then stored at 4 °C. To avoid contamination, each sample was collected and processed using a sterile kit. Before sampling the next plot, the shovel was cleaned of soil particles, sprayed with ethanol, and fired. Altogether, 54 soil samples and 54 corresponding root samples were collected on 3 and 4 June 2018 from 53 plots. Given the presence of only two plots of A. alba, sampling was doubled in one plot by establishing 2 separate sampling plots to achieve 3 replications. Soils were used for analyses of chemical properties (see Section 2.3); Stefanowicz et al., unpublished), AMF abundance (Section 2.4), and AMF species richness and composition (Section 2.5); roots were used for assessment of AM presence and AMF colonisation rate (Section 2.6).

2.2. Plant species richness, plant cover, and light intensity

Within each plot, vascular plant species were recorded to assess
plant species richness. Plant species were identified according to Rutkowski (2014). Cover of vascular plants and bryophytes was estimated on a percentage scale within each plot using digital photos of vegetation within plots. The borders of each sampling plot were clearly marked with a coloured cord. Then we used a Nikon D5300 Digital Camera attached to portable camera tripod to photograph vegetation cover within sampling plots. The pictures were taken from 1.5 m above the ground at downward angle of 90˚ with the same field of view, resolution and other settings. Bubble level was used to ensure that the tripod, camera, and resulting images were exactly vertical. Subsequently, the vegetation coverage was estimated manually by using Motic Images Plus 2.0 software (Hong Kong, Asia) and converted into a percentage of the sampling plot surface.

Light intensity (µmol m−2 s−1) was recorded at each study plot with a Kipp & Zonen PAR Quantum Sensor. The measurements were taken in the middle of a cloudy day from 5 randomly selected locations, at a height of 150 cm above the plot. Average values were treated as a single observation in subsequent analyses.

2.3. Chemical analyses of soils

Soil samples were sieved (2 mm) and subjected to analyses for chemical properties (Stefanowicz et al., unpublished). Their pH in H2O (1:5; w:v) was measured with a Hach Lange HQ40D multi meter (ISO 10390, 1994). Contents of total and organic C were analysed with a LECO RC-612 analyser and total N with a Foss Tecator 2300 Kjeltec 10390, 1994). Contents of total and organic C were analysed with a Foss Tecator Digestor 40 unit in hot concentrated HClO4. For calibration purposes Six Cation Standard II and Seven Anion Standard I, II, and III were used. In order to assess the quality of analyses of other available/exchangeable cations, ISE-859, ISE-912, and ISE-995 were used.

Available P (Olsen P) was extracted with 0.5 M citrate (pH 8) and incubated at 121 °C for 30 min. After centrifugation (10 000 g; 5 min), the supernatants were collected and then pooled. The extraction procedure was repeated at least 5 times. In order to evaluate EEG content, 1 g air-dried soil samples were extracted with 8 ml 20 mM citrate (pH 7) and incubated at 121 °C for 30 min. After centrifugation (10 000 g; 5 min), the supernatants were collected and then pooled. Both TG and EEG contents were assessed using the Bradford method in which 2 ml of extracts with 0.5 ml of Bradford reagent were incubated for 5 min in 22 °C and measured photometrically at λ500 nm using a Hach-Lange DR 3800 colorimeter. Quick Start Bovine Serum Albumin Standard Set (Bio-Rad) was used for calibration purpose (Wright and Upadhyaya, 1996; Galążka and Gawryjolek, 2015).

2.5. AMF spore number and species richness and composition in soils

AMF spores were extracted from soil samples by centrifugation in 50% sucrose solution, using a filtering method (Brundrett et al., 1996). The spores were transferred to a Petri dish and counted under a Nikon Eclipse 80i light microscope with differential interference contrast (DIC), and named in accordance with the Index Fungorum (http://www.indexfungorum.org/index.htm, accessed 15 January 2020). All slides were located in the Department of Ecology and Protection of Environment, West Pomeranian University of Technology, Szczecin, Poland.

2.6. AMF presence in roots and degree of AMF root colonisation

Roots were stained in accordance with the method of Phillips and Hayman (1970), with modifications (Zubek et al., 2011). From each sample, 30 randomly selected ~1 cm long fragments of fine and living roots were placed on slides with glycerol/lactic acid (1:1; v:v) and crushed with cover slides. AMF presence in root fragments was rated in accordance with the method of Trouvelot et al. (1986), using a Nikon Eclipse 80i light microscope with differential interference contrast (DIC). Parameters of the degree of AMF colonisation, such as mycorrhizal frequency (F%), relative mycorrhizal root length (M%), and relative arbuscular richness (A%), were calculated (Trouvelot et al., 1986).

2.7. Statistical analyses

Principal component analysis (PCA) was used to visualise the differences in habitat properties, including vegetation and soil chemical parameters, between plots representing particular tree species. The analysis was based on a correlation matrix. Following Levene’s test to assess the equality of variances, Student’s t-tests were applied to test the differences between deciduous and coniferous plots in terms of habitat parameters.

Following the Brown-Forsythe test to assess the equality of variances, a one-way analysis of variance (ANOVA) followed by Tukey’s HSD test was applied to test the differences in AMF spore number and AMF biochemical markers, namely EEG, TG, PLFA 16:1o5, and NLFA 16:1o5, between plots representing particular tree species. Mycorrhizal parameters (F, M, A) were not analysed due to low number of samples with colonized roots. Prior to the analysis, the variables were Box-Cox subjected to mild alkaline methanolysis. Fatty acid methyl esters (FAMEs) were identified using a Varian GC-MS system (Varian 3900 and Saturn 2100T) and the NIST library. Fatty acids were identified relative to the Matreya LLC standards (Stefanowicz et al., 2016, 2019).

TG and EEG were measured in accordance with the method of Wright and Upadhyaya (1996) with some modifications. In order to evaluate TG content, 1 g air-dried soil samples were extracted with 8 ml of 50 mM citrate (pH 8) and incubated at 121 °C for 1 h. After centrifugation (10 000 g; 5 min), the supernatants were collected and then pooled. The extraction procedure was repeated at least 5 times. In order to evaluate EEG content, 1 g air-dried soil samples were extracted with 8 ml 20 mM citrate (pH 7) and incubated at 121 °C for 30 min. After centrifugation (10 000 g; 5 min), the supernatants were collected and then pooled. Both TG and EEG contents were assessed using the Bradford method in which 2 ml of extracts with 0.5 ml of Bradford reagent were incubated for 5 min in 22 °C and measured photometrically at λ500 nm using a Hach-Lange DR 3800 colorimeter. Quick Start Bovine Serum Albumin Standard Set (Bio-Rad) was used for calibration purpose (Wright and Upadhyaya, 1996; Galążka and Gawryjolek, 2015).
transformed to achieve normal distribution. In the case of AMF species numbers, which turned out not to be variables characterised by normal distribution, the nonparametric Kruskal-Wallis test was applied. Following the Brown-Forsythe test, separate Student’s t-tests were performed in order to reveal significant differences in the above-mentioned parameters between plots representing deciduous/coniferous trees (tree species groups), trees of native/alien origin, and trees forming or not forming AM (mycorrhizal status). For AMF species number, the non-parametric Mann-Whitney U test was applied.

Permutational multivariate analysis of variance (PERMANOVA) was performed to test for differences between plots representing deciduous and coniferous trees in terms of AMF species composition (Anderson, 2001), along with post-hoc pairwise comparisons between particular groups. The analysis was based on the matrix of the presence/absence of AMF species using the Jaccard coefficient, with 1000 permutations for each test. Subsequently, we evaluated which species were most responsible for differentiating AMF communities, using similarity percentage (SIMPER) analysis (Clarke, 1993). Since groups of plots representing both native/alien tree species, and trees forming/not forming AM had unequal sample size, the PERMANOVA was not conducted due to the fact that in the case of unbalanced designs the results would prove to be largely affected (Anderson and Walsh, 2013).

Possible associations between AMF parameters and habitat properties were tested using canonical correlation analysis, preceded by factor analysis (FA), in order to obtain uncorrelated variables. Factors were extracted using PCA; factors with eigenvalues > 1 were then varimax-rotated. Then, canonical correlation analysis was performed in order to identify and measure associations between two sets of variables (i.e. Set I corresponding to habitat properties and Set II related to AMF parameters) and to find the features needed to explain these correlations.

Statistical calculations were performed using STATISTICA 12 (StatSoft, Tulsa, OK, USA) and PAST 3.22 (Hammer et al., 2001).

3. Results

3.1. Habitat characteristics

The PCA ordination showed similarities between study plots in terms of habitat properties (Fig. 1). The plots were rather evenly scattered; however, plots representing coniferous and deciduous trees were separated slightly along the second axis. Plots with coniferous trees were characterised by significantly higher bryophyte cover and significantly lower pH, whereas plots with deciduous trees were characterised by higher concentrations of total Ca, K and Mg (Student’s t-tests; p < 0.05; Table 1).

3.2. AMF abundance and species richness and composition in soils

The overall AMF spore number averaged 77.5 ± 249.9 (SD) and ranged from 1 to 1765 per 50 g of soil. Overall AMF species richness averaged 1.2 ± 0.5 (SD) and ranged from 1 to 3 per 50 g of soil. Altogether, 8 AMF species were found in 54 soil samples (Fig. 2, Table 2). In 43 of 54 samples, only a single AMF species was recorded; however, in 10 samples, 2 species were noted. In only one sample were 3 AMF species present simultaneously. The most frequently occurring AMF spores were those of Funneliformis constrictus, noted in 15 soil samples; in 9 samples, these spores were present alone, in 6 samples with other species. The other recorded species were: Diversispora epigaea (found in 9 samples), Acaulospora lacunosa (8), Rhizophagus fasciculatus (6), Glomus macrocarpum (4), Glomus rubiforme (2), Acaulospora cavernata (1), and Scutellospora diporuprescens (1). AMF spore numbers and AMF species numbers did not differ statistically between plots with particular tree species (Fig. 2) or between groups of tree species.

AMF species composition differed significantly between plots with deciduous and coniferous tree species (PERMANOVA; F = 1.78, p = 0.043). Four AMF species proved to be more frequent in plots with deciduous trees, i.e. F. constrictus, D. epigaea, R. fasciculatus, and G. macrocarpum, whereas only one AMF species, A. lacunosa, proved to be confined to a greater extent to plots with coniferous trees. Three AMF species, i.e. G. rubiforme, S. diporuprescens, and A. cavernata, were present only in plots with deciduous trees (Table 2).

Concentrations of TG and EGG in soils did not differ significantly between plots with particular tree species and their groups. Concentrations of NLFA 16:1ω5 were higher in A. pseudoplatanus plots than in A. alba, B. pendula, C. betulus, F. sylvatica, P. abies, P. menziesii, P. nigra, Q. robur, and Q. rubra (Fig. 3). Although ANOVA revealed significant differences in the case of PLFA 16:1ω5 (p = 0.037), the post-hoc analysis revealed no significant differences between tree species. Concerning the comparison of different groups of trees, concentrations of PLFA 16:1ω5 were higher in soils of deciduous and AM-type than those of coniferous and non-AM tree species. Concentrations of NLFA 16:1ω5 were also higher in soils of deciduous tree species (Fig. 4). No significant differences were found between groups of native and alien tree species.

3.3. AM presence and degree of AMF root colonisation

The presence of AM was noted in roots in only 5 of 54 samples. The mycorrhizal frequency parameter (FAMF%) varied between 4.8% in one P. abies plot to 81.5% in one A. pseudoplatanus plot. In the same samples, the relative mycorrhizal root length parameter (MAMF%) ranged between 3.3% and 13.4%, respectively. The presence of arbuscules was observed in only 3 of 5 samples where AM was found. The relative arbuscular richness parameter (AMFω%) varied between 5.9% in one L. deciduus plot and 11.3% and 11.6% in one of A. pseudoplatanus and Q. robur plots. The mycorrhizal parameters were strongly correlated (Pearson’s r ranged from 0.89 to nearly 1), and thus only MAMF% is presented (Fig. 2) and included in further analyses.

3.4. Relationships between habitat properties and AMF parameters

Factor analysis enabled us to reduce the number of variables describing the habitat properties (Set I) to four factors, which jointly explain 74.05% of total variation (Table 3; Fig. S1). Three factors were derived from the pool of AMF variables (Set II), accounting for 65.26% of total variation (Table 3; Fig. S2). As regards Set I, we interpreted Factor 1 as being related to essential macronutrient levels and soil acidity. Factor 2 was mainly associated with soil fertility, as defined by contents of organic matter, NO3-form nitrogen, and S-SO4-form sulphur. Vegetation parameters were highly correlated with Factor 3, whereas Factor 4 was associated with the level of forest floor lighting. As regards Set II, Factor 1 was related to both AMF species richness and 16:1ω5 NLFA concentration (spore biomass). Factor 2 was associated with concentrations of total and easily extracted glomalin and was interpreted as an equivalent of AMF mycelia abundance. Factor 3 was interpreted as a measure of AMF hyphal abundance in soil (PLFA 16:1ω5) and in roots (M: relative mycorrhizal root length).

Canonical correlation analysis showed that only the correlation of the first pair of canonical variables was statistically significant (R = 0.80, p < 0.05; Table 4). Factor 1 from Set I, relating to most macronutrients and pH, was positively correlated with Factor 1 from Set II, which was associated with AMF species number and NLFA. This means that high concentrations of essential elements in soil caused an increase in AMF species richness and NLFA concentration in soil. Similarly, the same Factor 1 from Set I was positively correlated with Factor 3 from Set II, which was related to the degree of AMF root colonisation (MAMF%) and 16:1ω5 PLFA concentration in soil. Put another way, AMF abundance in soil and roots increased along with increasing soil alkalinity and macronutrient levels in soil. This factor explained about 19.9% of the variation. The remaining factors from Set I, with low loadings, were of no help in explaining variation in AMF parameters. As regards the second pair of canonical variables, Factor 2 from...
Set I, relating to soil fertility as defined by contents of organic matter, NO$_3$-form nitrogen, and S-SO$_4$-form sulphur, was negatively correlated with Factor 2 from Set II, which in turn was negatively associated with glomalin content in soil, i.e. the higher the level of detected glomalin content, the greater the content of carbon present in soil. Nevertheless, the second pair of canonical variables were not significant ($R = 0.64$, $p > 0.05$; Table 4).

4. Discussion

No complex studies on relationships between AMF community characteristics and overstorey species identity in European forests of the temperate climate zone have been conducted to date. In the present study, we focused on the impact of large numbers of tree species, representing groups of deciduous/coniferous, alien/native to Poland/Europe, and species forming/not forming AM, on AMF abundance and species richness and composition in relation to herbaceous plant cover and soil chemical properties. Our study showed that overstorey species identity has slight impact on AMF community. However, simultaneous effects of factors in the case of groups of deciduous/coniferous and species forming/not forming AM caused the variations in AMF abundance as well as species composition.

Our observations of AMF spore number and AMF species richness are in line with previous reports, in which their values fluctuated around approximate low in forests of the temperate climate zone (Rożek et al., 2019). The values obtained in our study diverge from those of other European ecosystems as high average values observed in grasslands and vineyards as well as moderate values found in maize

Table 1

| Parameter                  | Plots with deciduous trees (mean ± SD) | Plots with coniferous trees (mean ± SD) | t     | p    |
|----------------------------|----------------------------------------|----------------------------------------|-------|------|
| Total C (%)                | 1.45 ± 0.57                           | 1.34 ± 0.70                           | 0.65  | 0.52 |
| Organic C (%)              | 1.42 ± 0.55                           | 1.31 ± 0.68                           | 0.66  | 0.51 |
| Total N (%)                | 0.12 ± 0.05                           | 0.12 ± 0.09                           | 0.42  | 0.67 |
| N-NH$_4$ (mg kg$^{-1}$)    | 2.22 ± 2.00                           | 2.08 ± 1.91                           | 0.27  | 0.79 |
| N-NO$_3$ (mg kg$^{-1}$)    | 0.93 ± 1.88                           | 1.53 ± 1.70                           | −1.24 | 0.22 |
| Olsen P (mg kg$^{-1}$)     | 118.02 ± 17.33                        | 116.68 ± 19.81                        | 0.27  | 0.79 |
| Total K (mg kg$^{-1}$)     | 509.90 ± 645.10                       | 306.59 ± 432.18                       | 1.36  | 0.18 |
| Total Mg (mg kg$^{-1}$)    | 634.88 ± 506.76                       | 459.67 ± 324.12                       | 1.51  | 0.14 |
| Total Ca (mg kg$^{-1}$)    | 468.02 ± 267.56                       | 339.66 ± 169.96                       | 2.10  | 0.04 |
| Exchangeable K (mg kg$^{-1}$) | 37.84 ± 14.34                     | 23.13 ± 11.01                        | 3.88  | < 0.001 |
| Exchangeable Mg (mg kg$^{-1}$) | 37.90 ± 23.80                   | 23.74 ± 9.66                        | 2.87  | 0.01 |
| Exchangeable Ca (mg kg$^{-1}$) | 101.70 ± 107.85                  | 43.07 ± 39.93                      | 2.65  | 0.01 |
| S-SO$_4$ (mg kg$^{-1}$)    | 0.78 ± 0.40                           | 0.99 ± 0.72                           | −1.31 | 0.20 |
| pH                         | 4.82 ± 0.52                           | 4.35 ± 0.29                           | 4.06  | < 0.001 |
| Light (µmol m$^{-2}$ s$^{-1}$) | 34.56 ± 38.36                 | 54.57 ± 46.16                       | −1.73 | 0.09 |
| Vascular plant species richness | 3.59 ± 2.41                      | 4.56 ± 2.87                         | −1.34 | 0.19 |
| Vascular plant cover (%)   | 19.36 ± 24.67                         | 27.67 ± 31.94                         | −1.07 | 0.29 |
| Bryophyte cover (%)        | 6.00 ± 8.26                           | 26.58 ± 26.58                         | −3.84 | < 0.001 |
fields, arable areas with crop rotation and low or intermediate inputs, and arable areas with maize monocropping and high inputs (Oehl et al., 2003, 2005). To avoid underestimation of AMF species richness, which may result from spore sampling from particular soil depth performed once in our research, further studies in different seasons and soil depths as well as on extra- and intra-radical mycelia are needed (Oehl et al., 2005; Hempel et al., 2007; Njeru et al., 2015).

In this study, 8 AMF species were detected. All, except for *A. caerulescens*, which is acknowledged as a rare species (Bllaszkowski, 1994; Gai et al., 2006), are globally widespread and present in numerous ecosystems, both natural and those of anthropogenic origin, in Europe and beyond (e.g. Buchholz, 1912; Khan, 1978; McGee, 1986; Díaz et al., 1992; Blaszkowski, 1994; Hamel et al., 1994; Blaszkowski et al., 2002; Iwaniuk and Blaszkowski, 2004a, 2004b; Takács and Bratek, 2006; Zubek et al., 2008). The most frequent was *F. constrictus*, in line with earlier observations where it is one of the most frequently occurring species in Poland, Europe, and worldwide (e.g. Hamel et al., 1994; Iwaniuk and Blaszkowski, 2004a, 2004b). Additionally, all AMF species, except *S. diplospores*, are present in several forest ecosystems. Two species, *F. constrictus* and *G. rubiforme*, occur frequently and are globally widespread in these ecosystems; the other two, *G. macrocarpum* and *R. fasciculatus*, though widespread, do not occur frequently (e.g. Tadych and Blaszkowski, 2000; Blaszkowski, 2012; Rożek et al., 2019).

Bainard et al. (2011), studying tree-based intercropping systems in Canada, found that the deciduous and AM-forming trees *Fraxinus americana* and *Populus deltoids × nigra* were characterised by greater AMF richness and similar communities in soils collected from their respective tree rows than coniferous and non-AM *Picea abies*. In our study, AMF species number differed neither between plots with particular tree species nor between their groups. However, notable divergence was found in AMF species composition between plots of deciduous and coniferous trees. Some fungal species are linked with only one of these sites. This is probably a result of dissimilarity in pH and concentrations of elements in the soils. Earlier observations showed that the presence of essential elements is connected with composition of AMF community structure (Casazza et al., 2017). Simultaneously, pH may be linked with the vertical distribution (Liu et al., 2019) and selection (Johnson, 1993) of AMF species, which may be related in turn to the decline or elimination of some AMF species and the simultaneously increasing abundance of others, leading to disturbances in species evenness, richness, and diversity (Wang et al., 2011).

The low frequency of AMF root colonisation found in our study may be a result of the scant presence of herbaceous species, which are overwhelmingly AM positive (Wang and Qiu, 2006; Rożek et al., 2019), and the simultaneous prevalence of non-AM overstorey species (Veresoglu et al., 2017). Additionally, the low frequency of AMF colonisation of AM positive overstorey species may be the result of the scant presence of AMF propagules in soil (Fisher and Fulé, 2004) and the co-existence of AM and ectomycorrhizas, which is probably linked with the separate presence of both mycorrhizal types at different soil depths (Lodge, 1989; Neville et al., 2002; Karlischi et al., 2010).

Among all studied soil chemical properties, only some sets of factors influenced AMF parameters. AMF abundance increased along with increasing contents of macronutrients and soil alkalinity characterising plots with deciduous trees. This agrees with previous observations according to which AMF abundance depends on the amount of nutrients, such as Ca, K, and Mg, at particular sites, as well as pH; however, this relationship may be either positive or negative, and is linked with the specific conditions at particular sites (Ochoa-Meza et al., 2009; Casazza et al., 2017; Reyes et al., 2019). Moreover, Göransson et al. (2008) found that AMF colonisation in grasses of oak forests is more common in soils with relatively high pH values. A similar result regarding pH was observed in forbs colonising beech forests (Postma et al., 2007). Additionally, increased amount of macronutrients in soil promotes plant development, which may enhance allocation of C to AMF increasing their abundance (Smith and Read, 2008; Garcia and...
The balance of the experimental design, namely low numbers of AM relative to non-AM trees as well as alien relative to native species might have prevented detection of differences between these groups in habitat properties and AMF community characteristics. Similarly, the low presence of AMF at the site could have also prevented the ability to reveal differences among tree species or their groups.

In conclusion, our study showed that the tree species identity, considered as a single factor, has a slight impact on determination of AMF community characteristics in temperate forests. Variation in AMF abundance and species composition results from the effects of several factors, as pH and element concentrations in soils, acting within tree species groups. Our research can serve as a valuable starting point for further studies on AMF communities in forest ecosystems. This issue appears to be important, especially considering predicted global climate changes and related changes in the range of occurrence of many forest species.

### Table 2
The arbuscular mycorrhizal fungi (AMF) species responsible for differentiating AMF communities between plots with deciduous and coniferous tree species (SIMPER analysis).

| AMF species                  | Average dissimilarity (%) | Contribution to dissimilarity (%) | Cumulative contribution to dissimilarity (%) | Average frequency deciduous | Average frequency coniferous |
|------------------------------|---------------------------|-----------------------------------|---------------------------------------------|----------------------------|----------------------------|
| Funneliformis constrictus    | 26.39                     | 33.83                             | 33.83                                       | 0.407                      | 0.148                      |
| Diversispora epigaea         | 17.75                     | 22.75                             | 56.57                                       | 0.185                      | 0.148                      |
| Acaulospora laccata          | 13.16                     | 16.86                             | 73.43                                       | 0.074                      | 0.222                      |
| Rhizopagus fasciculatus      | 10.41                     | 13.34                             | 86.78                                       | 0.148                      | 0.074                      |
| Glomus macrocarpum           | 5.181                     | 6.64                              | 93.42                                       | 0.111                      | 0.037                      |
| Glomus rubiforme             | 3.018                     | 3.868                             | 97.29                                       | 0.074                      | 0                                  |
| Scutellospora dipparurescens | 1.059                     | 1.357                             | 98.64                                       | 0.037                      | 0                                  |
| Acaulospora cavastrata       | 1.059                     | 1.357                             | 100                                         | 0.037                      | 0                                  |

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Fig. 3. Concentrations (mean ± SD) of easily extracted glomalin, total glomalin, and PLFA 16:1ω5 and NLFA 16:1ω5 in the soil of plots with particular tree species, including the results of one-way ANOVA. The various letters above the bars indicate statistically significant differences according to Tukey’s HSD test (p < 0.05). Although ANOVA revealed significant differences in the case of PLFA 16:1ω5 (p = 0.037), the post hoc analysis revealed no significant differences between tree species. For tree species names, see Fig. 2 legend.
tree species (Dyderski et al., 2018). Moreover, recent studies suggest that global changes among symbiotic guilds can be expected over the next several decades. It is assumed that, in temperate forests, ectomycorrhizal tree basal area will decrease and AM tree basal area will increase (Steidinger et al., 2019). This may mean that AMF occurring in forests will gain in importance in the near future.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to the authorities of the Siemianice Experimental Forest, especially to Janusz Szpyt, Eng. D., of the Department of Silviculture, Poznan University of Life Science, for their permission to conduct the study. The research was funded by the National Science Centre, Poland [grant number 2017/27/N/NZ8/00999], and also received financial support, in part, from the Institute of Botany, Faculty of Biology, Jagiellonian University in Cracow [grant numbers K/ZDS/008054, N18/DBS/000002].

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118091.

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Table 3
Factors (PCA) derived from habitat properties (including soil chemical parameters and vegetation variables) and arbuscular mycorrhizal fungi (AMF) parameters. Only variables with factor loadings > 0.6 are listed.

| Factor no. | Variables (factor loadings in parentheses) | Variation explained (%) |
|-----------|-------------------------------------------|------------------------|
| Habitat properties (Set I) | | |
| 1 | exchangeable Mg (0.94), exchangeable K (0.91), exchangeable Ca (0.91), total Mg (0.87), total K (0.84), total Ca (0.83), pH (0.69), N-NH4 (0.61) | 35.69 |
| 2 | S-SO4 (0.82), organic C (0.77), total C (0.76), N-NO3 (0.73) | 19.50 |
| 3 | vascular plant cover (-0.84), plant species number (-0.84), bryophyte cover (-0.74) | 12.29 |
| 4 | light (0.65) | 6.57 |
| AMF parameters (Set II) | | |
| 1 | AMF species number (0.86), NLFA (0.81) | 27.34 |
| 2 | total glomalin (-0.84), easily extracted glomalin (-0.81) | 21.46 |
| 3 | M (0.88), PLFA (0.72) | 16.45 |

Table 4
The results of canonical correlation analysis testing the associations between habitat properties (Set I) and AMF parameters (Set II) based on the factors extracted by factor analysis (FA). For explanation of Factor numbers see Table 3.

| Habitat properties (Set I) | Root 1 | Root 2 |
|--------------------------|--------|--------|
| Factor no. 1 | −0.955 | −0.258 |
| Factor no. 2 | 0.277 | −0.907 |
| Factor no. 3 | 0.109 | 0.031 |
| Factor no. 4 | −0.005 | −0.331 |
| Canonical R | 0.797 | 0.635 |
| P value | 0.0002 | 0.4652 |
| Redundancy of Second set (%) | 15.87 | 10.07 |
| AMF parameters (Set II) | Root 1 | Root 2 |
|--------------------------|--------|--------|
| Factor no. 1 | −0.793 | −0.224 |
| Factor no. 2 | −0.219 | 0.973 |
| Factor no. 3 | −0.568 | −0.062 |
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