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ORIGINAL PAPER

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Mycotrophy of crops in rotation and soil amendment with peat influence the abundance and effectiveness of indigenous arbuscular mycorrhizal fungi in field soil

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Abstract Mycotrophy of previous crops has been shown to have an impact on arbuscular mycorrhizal fungi (AMF), and the growth and productivity of succeeding crops. We studied the impact of 3 years of cultivation of eight crops with different degrees of mycotrophy, including mycorrhizal (strawberry, rye, timothy, onion, caraway) and non-mycorrhizal (turnip rape, buckwheat, fiddleneck) hosts, as well as the impact of peat amendment, on the effectiveness, amount and diversity of indigenous AMF. A field experiment having a split-plot design with peat amendment as the main plot, crop cultivation as a sub-plot and three replications, was carried out on silt clay mineral soil in 1999–2001. A well-humified dark peat was applied immediately before establishment of the field experiment. Each year, the relative mycorrhizal effectiveness of soil collected in September, in terms of shoot dry weight (RME_{DW}), was determined in a bioassay. In the 3rd year of the experiment, AMF spores were also extracted and identified from the field soil. Expressed as the mean of 3 years of cropping in unamended soil, the mycorrhizal crops strawberry and caraway maintained RME_{DW} most effectively, while the values were lower in the non-host crops buckwheat, turnip rape and fiddleneck. In addition, the numbers of AM spores detected in soil were considerably greater during 3 years of strawberry cultivation. In soil under caraway, there were high numbers of AM spores compared to the other crops. In soil amended with peat, the situation was in some cases opposite of that of unamended soil; RME_{DW} was highest in rye and onion and lowest in strawberry and caraway. The reasons behind the negative impact of peat on mycorrhizal effectiveness in strawberry soil may be due to the microbiological properties of peat. The importance of including mycotrophic species in crop rotations for maintaining high soil quality and for increasing yields of subsequent crops is discussed.

Keywords Arbuscular mycorrhiza · Cropping · Mycorrhizal effectiveness · Peat amendment · Spore density

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Introduction

Arbuscular mycorrhizal fungal (AMF) symbiosis is exceptionally common in terrestrial flowering plants (Koide and Schreiner 1992). According to some estimates, more than 80% of such plants form symbiosis with AMF (Law 1985). AMF may have a positive impact on soil quality as well as plant health and growth, especially in natural ecosystems where the AMF diversity is very high with evidence of AMF host preference (Vandenkoornhuyse et al. 2002; Gollotte et al. 2004). It has been suggested that mycorrhizal fungal diversity is a determinant of plant diversity in natural ecosystems (van der Heijden et al. 1998). AMF improve the growth of plants through increased uptake of available soil phosphorus (P) and other non-labile minerals essential for plant growth (Smith and Read 1997). AMF also stabilise soil aggregates (Miller and Jastrow 1990) by producing the glycoprotein glomalin (Wright and Upadhyaya 1996), which binds soil particles. In addition, these fungi alleviate plant stress caused by biotic (Guillemin et al. 1994; Jaizme-Vega et al. 1997; Linderman 2000) and abiotic (Rosendahl and Rosendahl 1991; Goicoechea et al. 1997; Augé 2000) stress.

Many agricultural practices used in modern farming affect indigenous AMF. The positive effects of AMF may be of minor importance in high-input agriculture (Barea and Jeffries 1995). At increasing levels of available soil P, the growth enhancement due to AMF may either vanish, and AMF may even depress plant growth (Vivekanandan and Fixen 1991; Harrier and Watson 2003). Annual tillage

breaks up the mycorrhizal network, possibly decreasing the effects of indigenous AMF on plant growth (Miller et al. 1995; Mozafar et al. 2000). Soil disturbance may decrease the density of AMF spores, the species richness, and the extraradical AMF mycelium (Boddington and Dodd 2000). However, in some cases tillage has no impact on mycorrhizal traits (Pattinson and McGee 1997).

High-input conventional cropping systems may adversely affect AMF communities in soil (Sieverding 1989; Douds et al. 1993; Galvez et al. 2001; Oehl et al. 2003, 2004). The incorporation of individual crops with various degrees of mycorrhizal dependency (MD) in the crop rotation has clearly affected the amount and function of indigenous AMF. Non-host crops and long fallow periods may reduce AMF (Harinikumar and Bagyaraj 1988; Vivekanandan and Fixen 1991; Arihara and Karasawa et al. 2001; Troeh and Loynachan 2003), but when the fallow soil was kept dry, Pattinson and Mcgee (1997) found no reduction in the rate of mycorrhizal establishment.

The growth and yield of a crop may be affected by the previous crop (Karlen et al. 1994), an important factor to consider when designing crop rotations. The reasons for this phenomenon are not fully understood, but they might be related to mechanisms such as changes in water and nutrient usage by different plant species, disease and pest interactions, allelopathy, soil quality, and biological diversity (Arihara and Karasawa 2000). It has also been suggested that AMF play a key role in crop rotation effects (Thompson 1991; Bagayoko et al. 2000). In fact, a study comprising 17 different field sites (Karasawa et al. 2001) showed that the mycotrophy (non-mycorrhizal mustard vs. mycorrhizal sunflower) of the preceding crop was the most important factor influencing the growth and yield of the successive maize crop.

Organic matter in soil clearly affects different soil organisms and processes, but its impact on AMF has not been studied to any great extent. Nutrient-rich organic niches in soil have been found to stimulate hyphal growth of AM fungi (St John et al. 1983; Hodge et al. 2001; Hodge 2003). It has even been demonstrated that the AMF species *Glomus hoi* can transfer nitrogen to its associated host from a complex organic patch in soil (Hodge et al. 2001). There are also studies showing a negative impact of peat on AMF. Biermann and Linderman (1983) found peat to inhibit AMF colonisation, but they also noticed that this effect could be reduced by adding 25% soil or sand to the substrate. In the same study, hypnum peat was less inhibitory than sphagnum peat. In a study including seven peat types, different peats interacted differently with different AM fungi (Linderman and Davis 2003). An inhibitory influence of peat on AMF has also been found by Calvet et al. (1992), Estaún et al. 1994 and Vestberg et al. (2000). According to Calvet et al. (1992), there may be a biological cause for this inhibition.

Considering the factors discussed above, we designed a field experiment to study the changes in mycorrhiza and other soil variables induced by peat amendment and crop plant production. The results of the experiment concerning earthworms, soil microbial biomass (Kukkonen et al. 2004) and soil enzyme activities (Vepsäläinen et al. 2004) have been published. In this part of the study, we hypothesised that the degree of mycotrophy of crops (non-mycorrhizal vs. mycorrhizal) and soil amendment with sphagnum peat will affect the symbiotic effectiveness and the density and diversity of indigenous AMF.

Material and methods

Field experiment

The experimental field studied was situated at the MTT Laukaa Research and Elite Plant Station in Central Finland (62°25′ N, 25°60′ E). The field (95×61 m^2) has a flat topography and the soil type is silt clay (silt 52%, clay 31%). Oats had been cultivated for 4 years using conventional methods at the experimental site before the start of the trial. The experiment was established in June 1999 and was surrounded by a barley field. There were two peat amendment treatments and eight different crop production systems arranged in a split-plot design with three replications (blocks). Sub-plots (10×5 m^2) were arranged in two rows within the main plots (36×30 m^2). The sub-plots in the rows were separated by a 2-m wide corridor. Between the main plots and rows of sub-plots there was an 8-m corridor, which was harrowed in spring, mowed in summer and ploughed in October.

The main plots, designated as A, were left unamended while the B plots were amended with well-humified (H 4–7 von Post scale; Post 1952) natural peat (300 m^3 ha^{-1}, pH 4, Vapo Oy, Finland). The peat was incorporated into the uppermost 20 cm of the soil using a rotary harrow. The amendment was estimated to increase the organic C content of the ploughed layer by one percentage point. The crop production systems consisted of eight different types of crops produced by crop-specific conventional methods. Each crop was tilled, fertilised and treated with pesticides according to the needs of the crop (Table 1). Two crops were perennial (strawberry and timothy), one was a biennial herb (caraway) and five crops (rye, buckwheat, turnip rape, onion and fiddleneck) were annuals.

On the basis of their mycorrhizal dependency, the crops could be divided into three groups, namely mycorrhiza-supporting crops, moderately mycorrhizal crops and non-mycorrhizal crops. Strawberry, onion and caraway can be regarded as mycorrhiza-supporting crops. Strawberry plants [*Fragaria×ananassa* (Weston) Loisel et al.] derived from micropropagated 'Senga Sengana' were grown in raised beds (three beds per experimental plot) mulched with black plastic. Sheep's fescue (*Festuca ovina* L.) was sown in the corridors between the strawberry beds and cut three to four times per year with a lawn mower. Onion (*Allium cepa* L. 'Stuttgarter') was replanted each year from bulbs, while the biennial caraway (*Carum carvi* L.) could be grown for 3 years without re-sowing.

Table 1 Tillage, fertilisation and pesticide treatments for different crops during the experiment

Crop	Year	Tillage[a]	N–P–K fertilization (kg ha^{-1})	Pesticide[b]
Strawberry	1999	SH	82.5–40–149	Insecticide: endosulfan (1×2,600)
	2000	–	–	Insecticides: endosulfan (1×2,600), deltamethrin (1×6.5)
	2001	–	–	Insecticides: endosulfan (1×2,600), iprodione (3×750), deltamethrin (1×6.5)
Onion	1999	SH+AP	36–30–120	Herbicide: linuron (1×1250)
	2000	SH+AP	36–30–120	Herbicide: bentazone (1×528)
	2001	AP	36–30–120	Herbicide: bentazone (1×528)
Caraway	1999	SH	36–30–120	Herbicide: linuron (1×1750)
	2000	–	30–25–100	–
	2001	–	30–25–100	–
Rye	1999	SH+AP +AH	66–24–81	–
	2000	AP+AH	80–12–36	Herbicides: MCPA (1×500), chlorpyralid (1×50), fluoroxypyr (1×100)
	2001	–	60–9–27	Herbicides: MCPA (1×500), chlorpyralid (1×50), fluoroxypyr (1×100)
Timothy	1999	SH	80–12–36	Herbicide: tribenuron-methyl (1×40)
	2000	–	200–30–90	–
	2001	–	200–30–90	–
Turnip rape	1999	SH+AP	100–15–45	Insecticides: λ-Cyhalotrin (2×7.5)
	2000	SH+AP	100–15–45	Insecticides: λ-Cyhalotrin (2×3.75)
	2001	SH	100–15–45	Insecticides: λ-cyhalotrin (1×6.25, 1×3.75), metazachlor (1×1,000)
Buckwheat	1999	SH+AP	15–12.5–50	–
	2000	SH+AP	15–12.5–50	–
	2001	SH	25–17.5–35	–
Fiddleneck	1999	SH+AP	60–9–27	–
	2000	SH+AP	60–9–27	–
	2001	SH	60–9–27	–

[a] *SH* Spring harrowing, *AP* autumn ploughing, *AH* autumn harrowing

[b] Name of active ingredient (number of applications × application rate g ha^{-1})

Two members of the Poaceae family were included in this study. Species of the Poaceae are usually regarded as only moderately dependent on mycorrhizal symbiosis. Rye (*Secale cereale* L. 'Voima' or 'Riihi') was sown each year at the end of August and harvested nearly 1 year later. In the first year, Persian clover (*Trifolium resupinatum* L. ssp. *majus* Boiss.) was grown in the rye plots as green manure before sowing of rye. Timothy (*Phleum pratense* L. 'Iki') was grown with barley (*Hordeum vulgare* L. 'Artturi') as a companion crop in 1999 and after that as a pure stand.

The crops turnip rape (*Brassica rapa* L. 'Valo'), buckwheat (*Fagopyrum esculentum* Moench 'Hruszowska') and fiddleneck (*Phacelia tanacetifolia* Benth.) were annual non-hosts of AMF. The mycorrhizal status of fiddleneck was unknown before the start of the experiment. Studies of root colonisation showed that the species is non-mycorrhizal or very slightly mycorrhizal.

Sampling

For mycorrhizal studies, samples were collected yearly in late September 1999–2001 from the 0–15 cm topsoil using a spade. A composite sample of 8–10 l was formed by collecting ten spadefuls of soil from each subplot. The samples were stored at +6°C. Before use in AM effectivity assays, the composite sample was thoroughly mixed and passed through a 2 mm sieve. From this homogenised soil sample, a 0.5 l sample was set aside for studies of AMF spore densities.

For estimation of organic C and soil chemical and physical properties, samples were collected from the depth of the whole ploughed layer (0–20 cm) using a 2-cm wide auger. A composite sample of 20–30 drillings (35 ml each) was collected from the main plots in spring 1999 (before establishment of the experiment) and from each sub-plot in autumn 2000 and 2001.

Soil analyses

Organic C $C_{org\%}$) was analysed with a LECO CN-2000 analyser in autumn 2000 and 2001. Soil pH and electrical conductivity were analysed in spring 1999 and autumn 2001 from a soil-water suspension (1:2.5, v/v). Soluble P, K, Ca and Mg were analysed from acidic (pH 4.65) am-

monium acetate (0.5 M acetic acid, 0.5 M ammonium acetate) extract (Vuorinen and Mäkitie 1955).

Mycorrhizal effectiveness

The effectiveness of indigenous AMF communities was estimated in a bioassay using flax (*Linum usitatissimum* L.) as a test plant (Kahiluoto et al. 2000). In order to create a non-mycorrhizal control, benomyl was mixed with soil at a rate of 20 mg l^{-1} soil. The relative mycorrhizal effectiveness (RME), i.e. the mycorrhizal contribution to the growth of the mycorrhizal plant, was defined by the following formula:

$$\mathrm{RME}(\%) = [(Y^{\mathrm{myc+}} - Y^{\mathrm{myc-}})/(Y^{\mathrm{myc+}})] \times 100$$

where Y_{myc+} and Y_{myc-} are the dry weights of the mycorrhizal treatment and control with inhibited AM function, respectively.

Soil mixtures were prepared and potted in 500 ml PVC pots (tubes) without drainage holes immediately after addition of benomyl suspension (0.07% strength) or plain water. Soil moisture in pots was adjusted to 65% of water-holding capacity. In each PVC tube, five pre-germinated seeds of flax (*L. usitatissimum* L. cv. Linetta) were planted to a depth of 1 cm. The initial weight of each pot was recorded. The pots were arranged in a randomised complete block design with four replicates in a growth chamber having a light intensity of 80–120 μmol m^{-2} s^{-1}. Each replicate included 48 pairs of pots (two peats × eight crops × three field replicates). Pots with untreated and benomyl-treated soils were kept adjacent to each other to ensure that conditions were as similar as possible. Pots were watered to their original weight three times a week and circulated at the same time. After emergence, the number of plants in each pot was thinned to leave three flax seedlings. The experiment was concluded 5 weeks after planting. Shoot fresh and dry weight and root AMF colonisation were then estimated. RME values were calculated using fresh weights ($\mathrm{RME_{FW}}$) and dry weights ($\mathrm{RME_{DW}}$) but only the results based on dry weights are presented here. In statistical analyses for $\mathrm{RME_{DW}}$ and AMF colonisation, the analysis variable was a mean over four replicates in the assay, because these replicates are similar subsamples from the field plot, i.e. in the statistical analyses the field plots are considered as the experimental units.

AMF spore extraction and identification

AM spores were extracted by wet sieving and decanting (Gerdemann and Nicolson 1963) followed by centrifugation in water and in 50% sucrose solution (Walker et al.

Table 2 Soil characteristics before establishment of field experiment in 1999, and in the different crops and peat treatments in 2001 (mean± SD, *n*=3)

Crop	Peat amendment[a]	C_{org} (%)	Electrical conductivity (10×mS cm^{-1})	pH (water)	Extractable P (mg l $soil^{-1}$)	Extractable K (mg l $soil^{-1}$)	Extractable Ca (mg l $soil^{-1}$)	Extractable Mg (mg l $soil^{-1}$)
Values before start of experiment	A		1.1±0.2	5.7±0.1	6.7±0.9	94.1±4.7	1,260±69	117±6
	A[b]		1.1±0.1	5.8±0.1	6.2±1.4	94.4±4.2	1,273±78	127±6
Strawberry	A	5.3±1.1	1.9±0.5	5.9±0.3	5.9±1.0	63.5±7.9	1,553±407	221±62
	B	5.9±1.8	1.8±0.5	6.0±0.3	5.9±0.8	67.4±7.5	1,480±416	249±82
Onion	A	4.9±0.7	3.0±0.9	5.4±0.1	7.7±1.9	110.6±16.1	1,123±47	194±4
	B	5.5±0.5	3.5±0.6	5.4±0.1	7.1±1.3	120.7±15.1	1,160±101	213±27
Caraway	A	5.1±0.8	1.7±0.5	5.6±0.2	7.1±1.2	114.7±22.7	1,138±132	187±30
	B	6.8±1.7	2.2±0.4	5.9±0.4	6.4±1.1	100.0±10.3	1,407±182	269±39
Rye	A	4.5±0.6	1.2±0.3	5.8±0.1	5.9±0.8	82.9±3.6	1,123±136	186±21
	B	6.2±1.2	1.5±0.1	5.8±0.2	6.5±0.7	85.7±8.2	1,203±136	228±35
Timothy	A	5.8±1.2	1.6±0.2	5.8±0.4	6.0±0.2	48.0±5.1	1,420±246	209±52
	B	5.6±0.6	1.6±0.3	5.8±0.1	5.6±0.3	51.6±2.0	1,307±80	220±9
Turnip rape	A	5.5±1.1	1.4±0.2	5.7±0.2	6.8±0.8	86.6±16.0	1,157±35	171±10
	B	5.6±1.1	1.9±0.5	5.6±0.3	5.4±0.5	85.0±6.5	887±673	210±23
Buckwheat	A	5.0±1.2	1.3±0.3	5.7±0.4	6.7±1.1	73.0±6.1	1,137±81	172±24
	B	5.8±1.3	1.5±0.1	5.7±0.2	6.3±0.3	76.6±7.3	1,233±160	227±31
Fiddleneck	A	5.3±0.6	1.4±0.4	5.6±0.1	6.6±0.9	77.6±7.6	1,120±90	178±10
	B	6.1±1.0	1.3±0.1	5.7±0.2	6.1±0.8	72.1±7.6	1,207±118	221±31
Mean	A	5.2±0.9	1.7±0.7	5.7±0.2	6.6±1.1	82.1±23.7	1,221±224	190±32
	B	5.9±1.1	1.9±0.7	5.7±0.3	6.1±0.8	82.4±21.4	1,235±305	230±38

[a] *A* Unamended, *B* amended with peat
[b] Area later amended with peat (B)

Table 3 Statistical tests for effects of peat, crop, year and their interactions on mycorrhizal variables of relative mycorrhizal effectiveness using shoot dry weights (RME_{DW}), arbuscular mycorrhizal fungal (AMF) colonisation 2000 (natural soil), AMF colonisation 2001, and AMF spore density

Effects							
Variable	Peat	Crop	Peat×crop	Year	Peat×year	Crop×year	Peat×crop×year
RME_{DW}	$F_{1,7.13}$=2.91 P=0.13	$F_{7,30.4}$=3.17 P=0.01	$F_{7,30.4}$=5.61 P<0.001	$F_{2,13.5}$=43.64 P<0.001	$F_{2,13.5}$=1.06 P=0.37	$F_{14,58.7}$=2.30 P=0.01	$F_{14,58.7}$=1.45 P=0.16
AMF colonisation 2000, unamended soil		$F_{7,16}$=0.98 P=0.48					
AMF colonisation 2001	$F_{1,30}$=15.67 P<0.001	$F_{7,30}$=13.05 P<0.001	$F_{7,30}$=0.59 P=0.76				
AMF spore density	$F_{1,4}$=0.20 P=0.68	$F_{7,28}$=40.67 P<0.001	$F_{7,28}$=0.89 P=0.53				

1982). Sieves of 500 μm and 50 μm were used for wet sieving. After centrifugation, the spores were transferred to a dish of water for examination under a dissecting microscope. Thereafter the spores were counted and characterised.

Statistical analyses

The RME_{DW} data were analysed as a split-plot design with repeated measures. In the analyses, peat was considered as

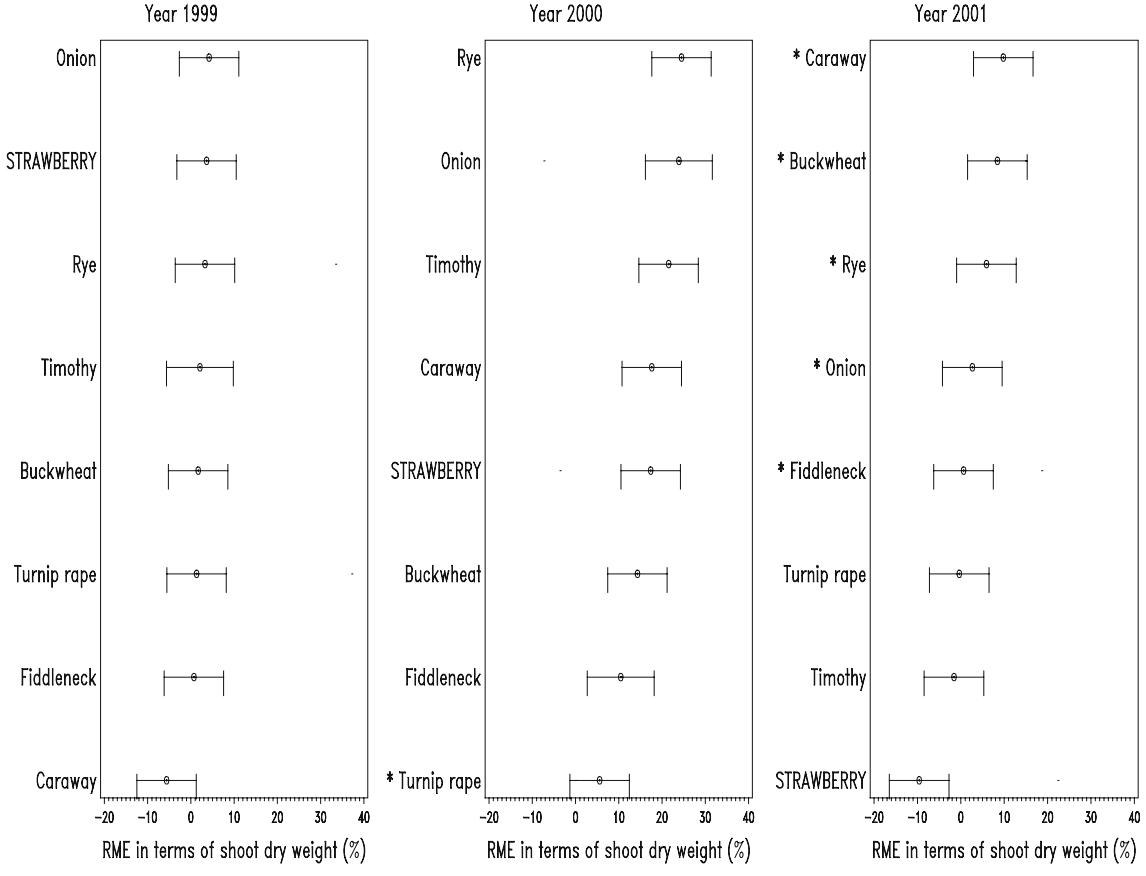

Fig. 1 Effect of crop on the relative mycorrhizal effectiveness (RME) of field soil during 1999–2001 determined in a bioassay in terms of shoot dry weight. Values are estimated means of six observations (three replicates × two peat treatments, n=6). Exceptions are timothy in 1999 and fiddleneck and onion in 2000, for which only five observations were used (n=5). *Bars* 95% confidence intervals of the means. Groups are arranged in ascending order. Crops marked with * differ from strawberry at $P \leq 0.05$

a whole-plot factor, crop as a subplot factor, year as a repeated measure, and replication as a blocking factor. Repeated measurements based on the same field plot were correlated, which was taken into account in the statistical models through covariance structures. The covariance structures were chosen by comparing biologically suitable structures using the likelihood ratio test, and the resulting covariance structure was compound symmetry. Thus, the linear model could be formulated as

$$\begin{aligned} Y_{ijkl} &= \mu + \mathrm{BLOCK}_i + \mathrm{PEAT}_j + \varepsilon_{ij} + \mathrm{CROP}_k + \mathrm{PEAT} \\ &\quad \times \mathrm{CROP}_{jk} + \delta_{ijk} + \mathrm{YEAR}_l + \mathrm{BLOCK} \times \mathrm{YEAR}_{il} \\ &\quad + \mathrm{PEAT} \times \mathrm{YEAR}_{jl} + \theta_{ijl} + \mathrm{CROP} \times \mathrm{YEAR}_{kl} \\ &\quad + \mathrm{PEAT} \times \mathrm{CROP} \times \mathrm{YEAR}_{jkl} + \gamma_{ijkl}, \end{aligned}$$

where μ is constant, and PEAT_j, CROP_k, $\mathrm{PEAT}\times\mathrm{CROP}_{jk}$, YEAR_l, $\mathrm{PEAT}\times\mathrm{YEAR}_{jl}$, $\mathrm{CROP}\times\mathrm{YEAR}_{kl}$ and $\mathrm{PEAT}\times\mathrm{CROP}\times\mathrm{YEAR}_{jkl}$ are fixed main and interaction effects for factors PEAT, CROP and YEAR. The BLOCK_I, ε_{ij} and δ_{ijk} are random (main) effects for blocks, main plots (PEAT) and subplots (CROP), respectively, all mutually independent with $\mathrm{var}(\mathrm{BLOCK}_I)=\sigma^2_{\mathrm{BLOCK}}$, $\mathrm{var}(\varepsilon_{ij}) = \sigma^2_{\varepsilon}$, and $\mathrm{var}(\varepsilon_{ijk}) = \sigma^2_{\delta}$. The $\mathrm{BLOCK}\times\mathrm{YEAR}_{il}$, θ_{ijl} and γ_{ijkl} represent random time-specific contributions for blocks, main plots and subplots (Gumpertz and Brownie 1993). For other variables YEAR was not applicable for analyses, therefore the models became simpler. For variable AMF the analysis had to be performed separately for each year 2000 and 2001, because peat amendment was applied only in 2001. The data of year 2001 were therefore analysed as a standard split-plot design and the data of 2000 as a standard randomised complete block design. Total number of AMF spores were also analysed as standard split-plot designs.

For all the models mentioned above, REML was used as an estimation method and degrees of freedom were calculated by the Kenward-Roger method (Kenward and Roger 1997). The models were fitted using the MIXED procedure of SAS version 8.2 (SAS Online Doc, ver 8. SAS Institute, Cary, N.C.). Pairwise comparisons were performed by two-sided *t*-type tests and strawberry was used as a reference crop. For total number of AMF spores, caraway was used as an alternative reference crop due to strawberry being an obviously superior crop in terms of spore densities. Model assumptions were checked by graphs: equality of variances through plotting residuals against fitted values, and normality of the response variables by inspecting model residuals using the box-plot technique (Tukey 1977). The examination of the model residuals revealed three influential outliers for $\mathrm{RME}_{\mathrm{DW}}$. The influence of the outlying values on the results was examined by comparing results of the analysis of the reduced and complete data. On checking the data, no logical reason for the exceptional values was discovered. Therefore, it could be a question of human error or a result of excess watering or of a soil-borne disease. For $\mathrm{RME}_{\mathrm{DW}}$, more emphasis is given to the results based on reduced data. The results for other variables are based on the complete data. For total number of AMF spores, natural logarithm transformation was used due to unequal variances on the original scale.

Results

Nutrients

The effects of crop-specific fertilisation and peat amendment on various soil chemical properties can be seen in Table 2. Soil analyses performed prior to the establishment of the experiment show that there were only minor differences between the untreated and peat-amended plots. In 2001, the research area had a rather high content of soil C_{org} (Table 2). Peat amendment raised soil C_{org} on average by 0.7%. EC values were slightly elevated in soil under onion, but were not affected by peat. The pH and amounts of extractable P were not affected either by crop or by peat amendment. The amount of P was low. The amount of extractable K was low in strawberry and timothy and high in onion and caraway, but was not affected by peat. In con-

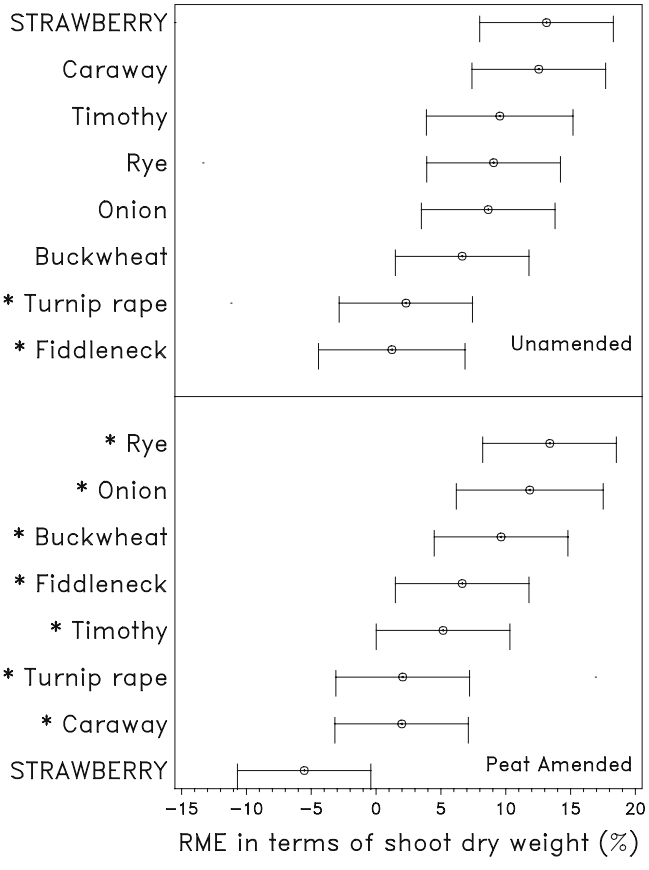

Fig. 2 Effect of crop and soil amendment (unamended vs. peat-amended soil) on the RME of field soil determined in a bioassay in terms of shoot dry weight. Values are estimated means of 3 years (1999–2001), i.e. nine observations (three replicates × three years, *n*=9). Exceptions are timothy and fiddleneck on unamended soil and onion on peat-amended soil, for which only eight observations were used (*n*=8). *Bars* 95% confidence intervals of the means. Groups are arranged in ascending order. Crops marked with * differ from strawberry at $P \leq 0.05$

trast, peat amendment lowered the amount of extractable Mg in all crops. The amount of extractable Ca was somewhat higher in strawberry and timothy than in the other crops, but did not differ due to peat treatment.

Mycorrhizal effectiveness

The estimated mean for RME_{DW} was highest in 2000, at 16.9% (95% CI=14.1–19.7%). In 1999 and 2001, the values were 1.4% (95% CI=−1.3–4.2%) and 2.0% (95% CI=−0.7–4.7%), respectively. The mean RME_{DW} were at about the same level in unamended soil and in peat-amended soil, at 7.9% (95% CI=5.7–10.1%) and 5.6% (95% CI=3.5–7.8%), respectively. The effect of crops was dependent on peat amendment ($F_{7,30.4}$=5.61 P<0.001) and year ($F_{14,58.7}$=2.30 P=0.01) (Table 3).

When looking at the crop effects for each year separately (Fig. 1), no differences in RME_{DW} values compared to those in strawberry occurred in 1999, although the RME_{DW} was close to being significantly lower in caraway (P=0.06). In 2000, turnip rape exhibited significantly lower (P=0.02) effectiveness values than strawberry. The highest AMF effectiveness this year was found in rye (RME_{DW}=24.5%; 95% CI=17.6–31.4%) and onion (RME_{DW}=23.9%; 95% CI=16.2–31.6%), and the lowest in fiddleneck (RME_{DW}= 10.4%; 95% CI=2.7–18.2%) and turnip rape (RME_{DW}= 5.6%; 95% CI=−1.3 to 12.4%). In contrast to the previous 2 years, in 2001 the lowest RME_{DW} was observed in strawberry (RME_{DW}=−9.6%; 95% CI=−16.5 to −2.7%). In 2001, all other crops except turnip rape and timothy exhibited statistically significantly higher RME_{DW} compared to strawberry (Fig. 1).

The decrease in AMF effectiveness in the soil from strawberry plots was due to a strong negative effect on RME_{DW} in peat-amended plots, as seen in Fig. 2. Expressed as a mean of 3 years of cropping in unamended soil, the mean estimated RME_{DW} was highest in strawberry (RME_{DW}= 13.1%; 95% CI=8.0–18.3%) and significantly lower in the non-host crops fiddleneck (RME_{DW}=1.2%; 95% CI=−4.4–6.9%) and turnip rape (RME_{DW}=2.3%; 95% CI=−2.9–7.4%). The second highest RME_{DW} was found in the soil from caraway plots. In soil amended with peat, however, the situation was quite the opposite (Fig. 2). Here, the lowest estimated RME_{DW} (−5.5%; 95% CI=−10.7 to −0.4%) was found in soil from strawberry plots. The

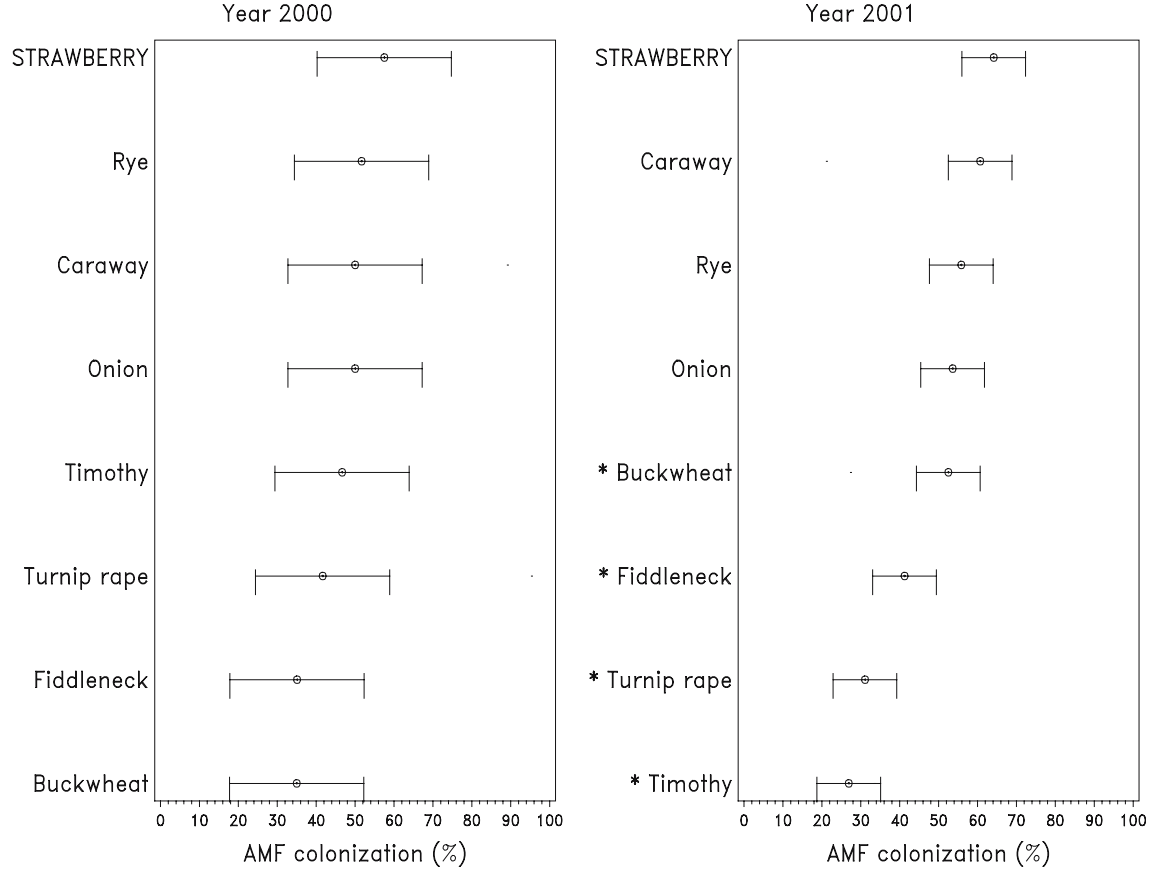

Fig. 3 Arbuscular mycorrhizal fungal (AMF) colonisation in roots of flax in a bioassay used for the determination of RME of soil from a field experiment with different crops and peat amendment. For the year 2000, values are estimated means of three observations (three replicates on natural field soil) and for the year 2001, values are estimated means of six observations (three replicates × two peat treatments). *Bars* 95% confidence intervals of the means. Groups are arranged in ascending order. Crops marked with * differ from strawberry at P≤0.05

RME_{DW} was statistically significantly higher in soil from all other crops, the highest values being found in rye (RME_{DW}=13.4%; 95% CI=8.2–18.5%) and onion (RME_{DW}= 11.9%; 95% CI=6.2–17.5%). The negative impact of peat on RME_{DW} in strawberry soil developed gradually over the 3 years (results not shown). In a comparison (1= highest RME_{DW}; 8= lowest RME_{DW}) between the eight crops, strawberry was ranked third in 1999, seventh in 2000 and eighth in 2001.

The results presented here were based on the reduced data set. Omitting the outliers somewhat lowered the standard error of means as compared with the complete data. Using the original data, fewer pairwise comparisons with strawberry were statistically significant. For example, by using the reduced data set the RME_{DW} of turnip rape in 2000 was significantly lower (Fig. 1) than that of strawberry, but this was not the case when using the complete data set. Furthermore, in peat-amended soil, the RME_{DW} was significantly higher in all crops other than strawberry when the reduced data set was used (Fig. 2), but by using the complete data turnip rape and caraway did not differ significantly from strawberry.

AMF root colonisation in RME bioassay

AMF colonisation of flax roots in the RME assay was estimated for 2000 and 2001. The results from the years 2000 and 2001 were treated separately because roots of flax plants were not stained when growing in peat-amended soil in 2000. In 2000, the estimated mean AMF colonisation percentages were lowest in flax roots growing in the soil originating from the non-mycorrhizal crops buckwheat (35.0%; 95% CI=17.8–52.2%) and fiddleneck (35.1%; 95% CI=17.8–52.3%) and highest in soil from strawberry (57.5%; 95% CI=40.3–74.7%) and rye (51.7%; 95% CI=34.4–68.9%), but these differences were not statistically significant (Table 3, Fig. 3).

In 2001, the effects of both peat amendment and crop on the level of colonisation were statistically significant (Table 3). The colonisation percentage was higher on average in amended soil (53.6%; 95% CI=47.8–59.4%) than in unamended soil (43.0%; 95% CI=37.2–48.7%). Roots of flax were colonised most heavily in soil originating from strawberry amended with peat (72.5%; 95% CI=61.3–83.7%) and least in unamended soil originating from turnip rape (21.3%; 95% CI=10.1–32.5). Calculated as the mean of both soil types, cropping of strawberry caused the highest colonisation percentage. Soil from timothy (P<0.001), turnip rape (P<0.001), fiddleneck (P<0.001) and buckwheat (P=0.04) yielded significantly lower levels of AMF colonisation compared with strawberry (Fig. 3).

AMF species and spore abundance

Only four AMF species of the phylum Glomeromycota were identified in soil collected in 2001. These all belonged

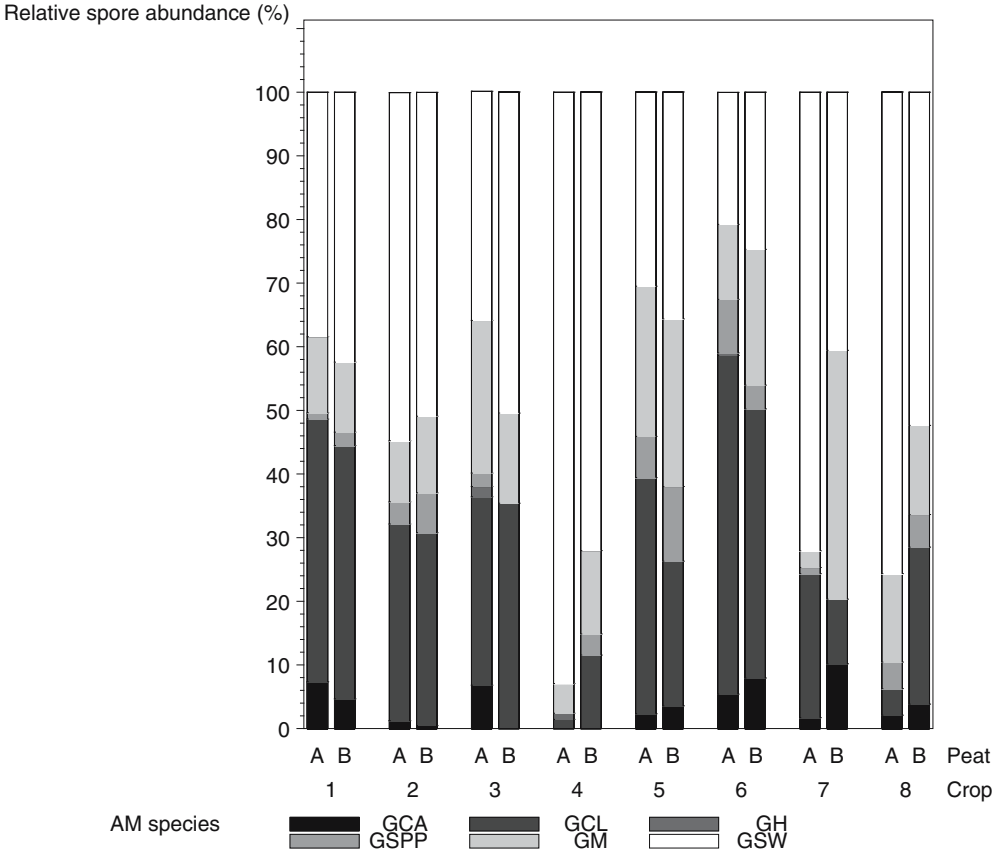

Fig. 4 Effect of crop cultivation and peat amendment (unamended vs. peat-amended soil) on relative AMF spore abundance in the 3rd year (2001) of a 3-year (1999–2001) field experiment. *A* Non-amended, *B* amended with peat, *1* strawberry, *2* rye, *3* timothy, *4* turnip rape, *5* buckwheat, *6* onion, *7* caraway, *8* fiddleneck, *GCAGlomus caledonium*, *GCLG. claroideum*, *GHG. hoi*, *GMG. mosseae*, *GSWGlomus* type "small white", *GSPPGlomus* spp

to the genus *Glomus* Tulasne & Tulasne: *G. claroideum* Schenck & Smith emend Walker & Vestberg, *G. mosseae* (Nicolson & Gerd.) Gerd. & Trappe, *G. hoi* Berch & Trappe and *G. caledonium* (Nicolson & Gerd.) Trappe & Gerd. The most commonly found species were *G. claroideum* and *G. mosseae*, which were detected from soil under all crops whether amended or not amended with peat. Spores of *G. hoi* were detected in very small numbers only in unamended soil under onion, turnip rape and timothy. The fungus *G. caledonium* was not detected at all under turnip rape and under timothy in peat-amended soil. An unidentified spore type, which we called *Glomus* sp. "small white" on the basis of its morphological appearance, was the most commonly found spore type in this study (Fig. 4). In unamended soil from the non-mycorrhizal turnip rape and fiddleneck, this spore type comprised 92.9 and 75.7%, respectively, of the total numbers of spores characterised. In caraway not amended with peat, the relative abundance of this spore type was also high at 72.0%. The relative abundance of spores of *G. claroideum*, the most commonly found identified species, was highest in soil under onion, but low in soil under turnip rape, caraway and fiddleneck. A noticeably high proportion of spores of *G. mosseae* was observed in peat-amended soil under caraway (Fig. 4).

The estimated mean number of AMF spores was 10.7% lower in peat-amended soil (72 spores 100 g dry soil^{-1}; 95% CI: 44–118) than in unamended soil (80 spores 100 g dry soil^{-1}; 95% CI: 49–132), but this difference was not statistically significant (Table 3). In some crops the difference was more pronounced, being 36% [761 (95% CI: 386–1,500) vs. 1,197 spores 100 g dry soil^{-1} (95% CI: 608–2,358)] in strawberry, 33% [95 (95% CI: 48–187) vs. 141 spores 100 g dry soil^{-1} (95% CI: 71–277)] in rye, 22% [223 (95% CI: 113–439) vs. 285 spores 100 g dry soil^{-1} (95% CI: 145–561)] in caraway and 44% [16 (95% CI: 8–32) vs. 29 spores 100 g dry soil^{-1} (95% CI: 15–57)] in turnip rape, but in fiddleneck the amounts of AMF spores were 90% higher in peat-amended soil (27 spores 100 g dry soil^{-1}; 95% CI: 14–53) than in unamended soil (14 spores 100 g dry soil^{-1}; 95% CI: 7–28). However, the interaction between peat amendment and crop was not found to be statistically significant ($F_{7,28}$=0.89 P=0.53; Table 3). The effect of crop on spore numbers was highly significant ($F_{7,28}$=40.67 P<0.001; Table 3). The highest estimated AMF spores numbers were detected in strawberry and caraway soils, 955 (95% CI: 591–1,542) and 252 (95% CI: 156–407) spores per 100 g dry soil, respectively (Fig. 5). Compared to strawberry, the spore densities were significantly lower in all other crops. The spore numbers in soil of caraway plots were also significantly higher than those in all other crops besides strawberry. The lowest total spore numbers were detected in the non-mycorrhizal crops fiddleneck (20 spores 100 g dry soil^{-1}; 95% CI: 12–32), turnip rape (22 spores 100 g dry soil^{-1}; 95% CI: 13–35) and buckwheat (31 spores 100 g dry soil^{-1}; 95% CI: 19–50).

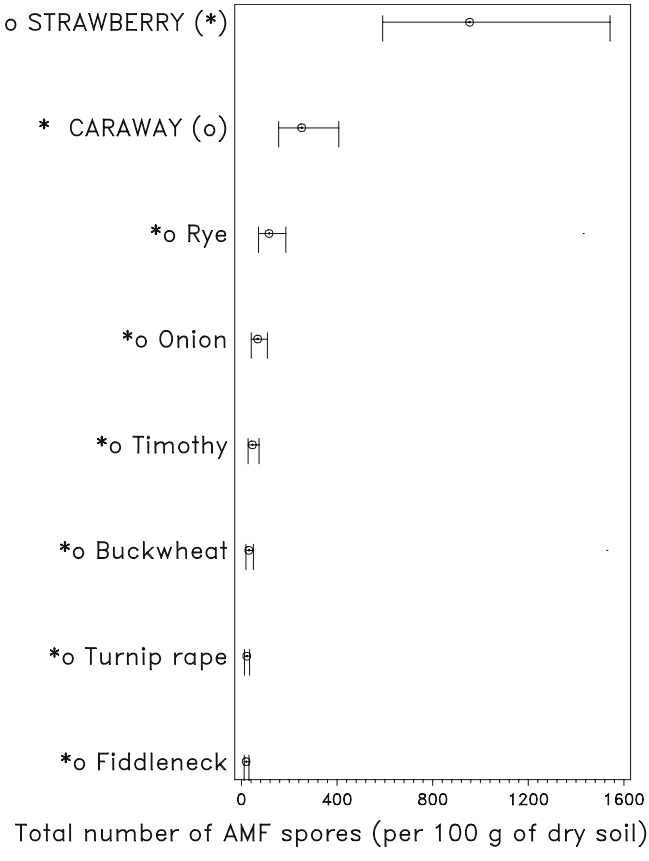

Fig. 5 Total numbers of AMF spores extracted from soil during the 3rd year (2001) of a field experiment with eight crops and peat amendment. Values are estimated means of six spore counts (replicates × peat treatment). *Bars* 95% confidence intervals of the means. Groups are arranged in ascending order. Crops marked with * differ from strawberry at P≤0.05 and crops marked with ○ differ from caraway at P≤0.05

Discussion

The impact of preceding crops on soil properties and the productivity of succeeding crops is complex. In some studies, AM fungi have been suggested to play a key role in the phenomenon known as the crop rotation effect (Thompson 1991; Bagayoko et al. 2000; Karasawa et al. 2001), which is also said to be due to several mechanisms taking place in soil (Karlen et al. 1994). Only a few studies dealing with the effects of agricultural management on indigenous field mycorrhiza also take into account the carbon cost of the symbiosis. We applied a method (Kahiluoto et al. 2000) enabling us to evaluate this aspect. The method is an ex citu assay using the highly mycorrhiza-dependent flax as test plant and benomyl to create a non-mycorrhizal control. The effect of different crops on RME_{DW} was significant. As a mean of 3 years of crop cultivation in unamended soil, the mycorrhizal crops strawberry and caraway were the most effective in maintaining RME_{DW}, while the non-host crops buckwheat, turnip rape and fiddleneck were the poorest. This result is in agreement with other studies in which mycotrophic crops have been shown to maintain mycorrhizal activity in soil, and affect growth and produc-

tivity of the succeeding crops (Arihara and Karasawa 2000; Gavito and Miller 1998; Karasawa et al. 2001), whereas non-host crops like sugar beet (Isoi 1997; Land et al. 1993), brassicaceous crops (Gavito and Miller 1998; Karasawa et al. 2001; Panja and Chaudhuri 2004) and spinach (Douds et al. 1997) have had a negative impact on various mycorrhizal variables.

In soil amended with peat, in some cases the situation was the opposite. RME_{DW} was highest in rye and onion but lowest in strawberry and caraway, showing a negative impact of peat on mycorrhiza in the soil of these mycotrophic plants. This phenomenon was especially evident in strawberry in 2001. Peat also slightly decreased the numbers of AMF spores although this difference was not significant. However, in several mycotrophic crops (strawberry, rye, caraway) and in one non-host (turnip rape) crop, the difference in spore numbers was more pronounced. The negative effects may be related to certain qualities of peat, which has been reported earlier (Biermann and Linderman 1983; Calvet et al. 1992; Estaún et al. 1994; Vestberg et al. 2000; Linderman and Davis 2003), but the mechanism behind the phenomenon is still open to debate. Calvet et al. (1992) state that certain peat products have a negative effect on the establishment of the arbuscular mycorrhizal symbiosis, although germination and early mycelial growth of the AM fungi is not affected, indicating a biological cause for the inhibition. Finnish natural peat is known to possess disease-suppressive properties (Tahvonen 1982), which are due to high concentrations of antagonistic bacteria (*Bacillus, Streptomyces*) and fungi (*Penicillium*, *Trichoderma*), and these may also interact with AM fungi.

The negative impact of peat on mycorrhizal variables observed by us differs from that seen in other studies, in which AM fungi have shown a positive response to the incorporation of other organic materials in soil (St John et al. 1983; Joner and Jakobsen 1995). Indeed, Ravnskov et al. (1999) showed that the type of organic compound might determine its impact. They found that hyphal growth of an AM fungus was enhanced by yeast and bovine serum, whereas the carbon sources starch and cellulose depressed fungal growth. The peat used by us was a well-humified dark peat. According to Arpiainen et al. (1986), this type of peat contains 5–15% cellulose, 10–25% hemicellulose, 5–30% lignins, 20–30% humic substances, 5–15% bitumen, and 5–20% proteins and amino acids. Further studies will be required to clarify whether components of natural peat could have a negative impact on AM fungi and, if so, which components are responsible.

In contrast to the other measured mycorrhizal variables, AMF root colonisation in the bioassay was significantly higher in peat-amended soil than in unamended soil (54 and 43% in 2001, respectively). The highest mean estimated colonisation (72%) was actually observed in plants growing in soil from strawberry plots amended with peat. This indicates that carbon drain could be a possible explanation for the negative effects of peat on RME_{DW}. Intraradical colonisation was high, but the density of the extraradical mycelium (ERM) might also have been high, leading to a high cost of the symbiosis. The ERM was, however, not estimated, making it difficult to draw conclusions about the reasons for the decreased RME.

The number of AM spores detected from soil increased strongly during the 3 years of strawberry cultivation. Also in soil under caraway, the AM spore number was high as compared with the other crops. Strawberry has been found to favour AMF sporulation in soil also in other studies (Vestberg et al. 2002), but, to the authors' knowledge, caraway has not been studied before in this respect. It is evident that both strawberry and caraway are very mycotrophic plant species that will increase the quantities of AMF propagules in soil, which is regarded as a positive crop rotation effect. As expected, the numbers of AM spores were low in soil under non-host crops after 3 years of cultivation.

Only a few *Glomus* species (*G. caledonium*, *G. claroideum*, *G. hoi* and *G. mosseae*) typically occurring in agricultural soils were found in this study. Relatively low AM fungal diversity in field soil has been observed also in other studies (Johnson 1993; Helgason et al. 1998; Miller et al. 1985; Talukdar and Germida 1993). However, in some other studies carried out in agricultural soils, species diversity was high (Bever et al. 1996; Ellis et al. 1992; Oehl et al. 2004), even exceeding 20 species per site and being comparable with the numbers of species often found in natural ecosystems (Douds and Millner 1999). No genera of the phylum Glomeromycota other than *Glomus* was found in this study. This finding is partly in agreement with the results of Jansa et al. (2002), who recorded AMF species belonging to only two genera in conventionally tilled soil, while five genera were present in non-tilled soil. Before establishment of the field experiment in 1999, the experimental area in Laukaa had had a long cultivation history of conventional agriculture, including frequent tillage, the use of mineral fertilisers and barley monoculture. This may explain the low AMF species diversity in the area. A 3-year cultivation of mycotrophic plants in a non-tilled system (strawberry, timothy, caraway) was not enough to restore fungal diversity.

It can be concluded that the effect of cropping, including planting of annual and perennial crops, as well as hosts and non-hosts of AMF, on indigenous soil mycorrhiza are very complex. It is clear that the use of mycotrophic crops in crop rotation will keep the indigenous mycorrhizal population at a good functional level, while non-hosts of AMF can have a negative impact. By introducing a soil treatment like peat amendment the situation can become more complex and negative plant-peat-microbe interactions can even occur. This result is in contrast to other findings from the same experiment (Kukkonen et al. 2004), which have shown that peat had positive effects on the soil by increasing microbial biomass and the number of earthworms. Furthermore, the yields of the different crops (yield results not shown in this paper) were also increased by the application of peat, especially during the 1st and 2nd year after application. The reasons for the negative impact of peat on AMF effectiveness, especially in connection with strawberry and partly in connection with caraway, may have different reasons as discussed above. The fact that the negative impact of peat increased towards the end of the experiment after 3 years indicates, however, that peat may

have caused a microbiological imbalance in the soil, favouring peat-specific microorganisms more than AMF. In our ongoing study, we will study the impact of mycorrhizal traits and other soil properties on the growth and yield of the succeeding crop.

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