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Arbuscular mycorrhizae in a long-term field trial comparing low-input (organic, biological) and high-input (conventional) farming systems in a crop rotation

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Abstract Arbuscular mycorrhizal (AM) root colonization was studied in a long-term field trial in which four farming systems currently in use in Switzerland were continuously applied to a randomized set of plots at a single field site from 1978 till 1993. There were two low-input farming systems (organic and bio-dynamic) and two high-input (conventional) farming systems (according to Swiss guidelines of integrated plant production with and without farmyard manure). The systems had an identical 7-year crop rotation and tillage scheme and differed essentially only in the amount and type of fertilizer supplied and in plant protection management. The percentage of root colonization by AM fungi was determined in field samples 2–3 times over the growing season in crops in the rotation, namely in winter wheat (*Triticum aestivum* L. cv. Sardona), vetch-rye and grass-clover. We found the percentage of root length colonized by AM fungi to be 30–60% higher ($P \leq 0.05$) in the plants grown in soils from the low-input farming systems than in those grown in conventionally farmed soils. Approximately 50% of the variation of AM root colonization was explained by chemical properties of the soils (pH, soluble P and K, exchangeable Mg), the effect of soluble soil P being most pronounced. The potential of the field soils from the differently managed plots to cause symbiosis with AM fungi was tested in a glasshouse experiment, using wheat as a host plant. Soils from the low-input farming systems had a greatly enhanced capacity to initiate AM symbiosis. The relative differences in this capacity remained similar when propagules of the AM fungus *Glomus mosseae* were experimentally added to the soils, although overall root colonization by AM fungi was 2.8 times higher.

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Introduction

Arbuscular mycorrhizal (AM) symbiosis is widespread in agricultural plants. It is believed to ameliorate plant mineral nutrition, to enhance water stress tolerance and to contribute to a better soil aggregate formation, which is important for soil structure and stability against erosion (Smith and Read 1997). These are key factors for successful low-input farming. Hence, the formation and functioning of the AM symbiosis is expected to play an important role in sustainable agriculture (Schreiner and Bethlenfalvay 1995).

In arable land, AM symbiosis is influenced by various management practices such as the degree and type of fertilization, plant protection, crop rotation, fallow period and soil tillage (Bethlenfalvay 1992; Johnson and Pfleger 1992). Although it is common to study the effect of single factors on mycorrhizae formation, interactions of these factors may also be important. Therefore, long-term investigations on the effects of different farming systems as a whole are of interest. The role of AM symbiosis may be of particular importance for agroecosystems in which synthetic mineral fertilizers are replaced by organic ones, used at a low dosage as in "biological" farming. In this paper, the term biological farming, synonymous with "organic" farming, is used as defined in the EU directive EWG 2092/91. In these types of low-input systems, plants may benefit particularly from the mycorrhizal relationship by an increased capability to take up mineralized soil nutrients present only at low concentrations.

Some information on this is already available, based on farm comparisons. In neighbouring rye fields, the rate of colonization of the roots by AM fungi, as well as the root length colonized, were about tenfold higher under biological farming than under conventional

farming (Sattelmacher et al. 1991). The authors suggested that these differences were due to the high input of fertilizers and pesticides applied in the conventional field as well as to the influence of a different crop rotation. In winter wheat a two- to threefold increase in colonization by AM fungi at a biological farm site compared with a site of a neighbouring conventional farm was found (Ryan et al. 1994). It was concluded that the amount of soluble P was the main cause for these differences. Although neighbouring-farm studies have the advantage of reflecting actual farming practice, they may be criticized since it is doubtful that soil and climatic conditions are identical at each farm and since replicates are often lacking.

Replicated field studies comparing AM symbiosis under biological and conventional farming practices have been applied hitherto only to short-term trials. In a plot trial with strawberries, Werner et al. (1990) found an increase in the degree of AM root colonization upon transition from conventional to biological management already in the second year after conversion. Similarly, in field experiments in a rotation including potato and wheat, a change from conventional, high-input agriculture to a low-input system resulted in a three- to fourfold increase in AM root colonization 4 years after conversion (Limonard and Ruissen 1989).

In a standardized glasshouse study, plants had a two- to tenfold higher AM colonization of their root systems in soils taken from two low-input farming systems in the eight and ninth year as compared to soils taken from a conventional high-input farming system, whilst results of plants grown in the corresponding field plots remained inconclusive (Douds et al. 1993). The more diverse crop rotation in the low-input systems, including cover crops planted between cash crops, was thought to play the decisive role in the increased AM infection potential of these soils.

In the present study we investigated the occurrence of AM symbiosis in a field-plot trial in which two biological and two conventional farming systems had been continuously maintained since 1978 (Mäder et al. 1999). The biological systems had about 70% less input of available N and about 50% less input of P and K than the conventional systems. No synthetic pesticides were applied in the biological systems. Nevertheless, the average yields were only reduced by 19–24% in the second 7 year crop rotation. Moreover, the soil aggregate stability was enhanced in the biological systems as assessed by the water percolation method (Siegrist et al. 1998), and the microbial activity was significantly greater (Mäder et al. 1996). Thus, the microbial contribution to the plants' P supply was higher in the biological systems as compared to the conventional ones (Oberson et al. 1996).

We hypothesized that AM symbiosis played an important role in the unexpectedly high productivity of the biological low-input systems. We therefore assessed the degree of AM root colonization in different crops grown in the biologically and conventionally managed field plots. Moreover, the AM infection potential of soils taken from the field plots was tested in the glasshouse. Special emphasis was put on wheat and grass-clover, since these two cultures are frequently included in crop rotations in Switzerland. We expected the potential differences in AM root colonization between the farming systems to be insignificant in the grass-clover crop, since no pesticides were applied to this crop.

Materials and methods

Experimental site and soil characteristics

The study was performed in the framework of the DOC trial, a long-term experiment in which two biological production systems (bio-dnamic and organic) and two conventional systems (with and without manure) have been applied continuously to randomized soil plots since 1978 (Table 1). Results with respect to soil properties, yield and quality of crops after the first 14 years have been published (Besson and Niggli 1991; Niggli et al. 1995). The soil type is a luvisol (sandy loam) on deep deposits of alluvial loess containing 15% sand, 70% silt and 15% clay. The soil analyses (0–20 cm) showed that upon employing the different farming systems for 14 years, soil acidity was slightly increased in the biodynamic system (D2) compared with the other systems. Soil organic matter content remained similar in all treatments. The distinctly higher soluble P and K contents in the conventional system with manure (C2) as compared with the biological ones reflected the higher nutrient input in these system (Mäder et al. 1999).

The field experiment was set up in 1978 at Therwil, in the vicinity of Basle, by the Swiss Federal Research Station for Agroecology and Agriculture (Zurich) in cooperation with the Research Institute of Organic Agriculture (Frick, Switzerland). The four farming systems differed mainly in fertilization strategy and plant protection management (Table 1). The biological systems were fertilized exclusively with farmyard manure (FYM) and slurry corresponding to 0.6/1.2 livestock units ha^{-1} (treatments D1/D2 and O1/O2, respectively). One conventional system was fertilized with the same amount of FYM as the biological systems and, in addition, with fertilizer up to a total level corresponding to the plant-specific Swiss standard recommendation (C2), or a lower input of mineral fertilizer (C1). The other conventional system (M) was amended exclusively with mineral fertilizers to the same level as C2 for P and K but not for N. Thus, treatments D1, O1 and C1 received half the amount of nutrients as D2, O2, C2 (Mäder et al. 1999). A control received neither fertilizer nor pesticides.

Plant protection was conducted according to the guidelines for bio-dynamic and organic systems (Table 1). In the conventional systems, pesticides were only applied, according to an integrated scheme of plant protection, if economic thresholds were surpassed with respect to loss of crops. Plant protection in the unfertilized control was the same as in the bio-dynamic system.

The crop rotation was identical in all systems, namely: (year 1) potatoes followed by rape as green manure, (year 2) winter wheat (*Triticum aestivum* L. cv. Sardona) followed by a vetch-rye fodder intercrop, (year 3) beetroots, (year 4) winter wheat, (year 5) winter barley and (year 6, 7) 2 years of grass-clover meadow. Soil tillage was similar in all treatments. The soils were ploughed to a depth of 18–20 cm before planting potatoes, winter wheat and beetroots.

The field trial was designed as a randomized block with four replicates including three crops planted simultaneously but temporally shifted in each treatment every year. Each plot was 5×20 m. The mean precipitation was 785 mm $year^{-1}$ and the annual mean temperature 9.5 °C.

Table 1 Main differences of farming systems applied to the plots, and soil characteristics of the DOC field trial. Soil properties (topsoil 0–20 cm) of the plots were assessed after 14 years of different cultivation. Soil sampling occurred after harvesting in autumn 1991. Adapted from Besson and Niggli (1991) and Alföldi et al. (1993). *FYM* Farmyard manure

Parameter	Farming systems							
	Control	Biological				Conventional		
	Unfertilized	Bio-dynamic		Organic		With manure		Without manure
	N	D1[a]	D2[b]	O1[a]	O2[b]	C1[a]	C2[b]	M[b]
Main differences								
Fertilizers	Without	Composted FYM and slurry		Slightly rotted FYM and slurry		Stacked FYM, slurry and mineral fertilizers		Exclusively mineral fertilizers
Plant protection								
Weed control	Mechanical	Mechanical		Mechanical		Mechanical and herbicides		Mechanical and herbicides
Disease control	Rock powder	Rock powder		Rock powder, Cu		Chemical (thresholds)		Chemical (thresholds)
Insect control	Plant extracts bio-control	Plant extracts bio-control		Plant extracts bio-control		Chemical (thresholds)		Chemical (thresholds)
Special applications	Bio-dynamic preparations	Bio-dynamic preparations				Plant growth regulators		Plant growth regulators
Soil properties								
$pH(H_2O)$	6.2[c] abc	6.4 cd	6.5 d	6.2 bc	6.2 bc	6.0 a	6.1 ab	6.0 ab
$C_{organic}$ (%)	1.40 ab	1.56 bc	1.68 c	1.44 ab	1.53 abc	1.37 a	1.41 ab	1.46 ab
P (CO_2)[d] (mg P_2O_5 100 g^{-1})	0.10 a	0.17 abc	0.28 d	0.16 ab	0.25 cd	0.19 bc	0.46 e	0.32 d
K(CO_2)[d] (mg K_2O 100 g^{-1})	0.37 a	0.46 ab	0.58 b	0.48 ab	0.54 b	0.61 b	1.29 c	0.58 b
Mg $(CaCl_2)$[e] (mg Mg 100 g^{-1})	6.1 a	7.5 bc	8.5 cd	7.6 bc	9.2 d	6.7 ab	7.4 bc	7.5 bc

[a] "Low" fertilizer level
[b] "High" fertilizer level
[c] Each value represents the mean of 12 plots ($n = 12$); values with *different letters* within one row are statistically significant ($P \leq 0.05$)
[d] (CO_2) = P and K measured in an extract with CO_2–saturated water
[e] $(CaCl_2)$ = MgO measured in an extract with $CaCl_2$

Soil sampling and assessment of root colonization by AM fungi and soil chemical analyses

To estimate the root colonization by AM, three soil cores (5 cm diameter, 20 cm depth) $plot^{-1}$ $date^{-1}$ were sampled several times during the growing season in 1989, 1990, 1991 and 1993. The soil cores were bulked to give one sample. There were four replicate plots farming $system^{-1}$ $crop^{-1}$. Roots contained in the soil cores were washed free of soil by wet sieving (mesh size 1 mm) with tap water and separated by hand from organic debris. Thereafter, the roots were cleared and stained with trypan blue in lactophenol according to Phillips and Hayman (1970). The percentage of root length colonized by AM fungi was determined microscopically with the gridline-intersection method according to Giovannetti and Mosse (1980) at a magnification of ×30–40.

At four sampling dates over the growing season in 1989 and at two sampling dates in 1990, the soil $pH(H_2O)$, soluble P and K content in a soil extract with CO_2–saturated water and the exchangeable Mg content in a $CaCl_2$ extract were determined [for methods, see Alföldi et al. (1993)].

Glasshouse experiment to assess the AM infection potential of field-trial soils with and without adding an AM fungus inoculum

A container system as described by Wyss et al. (1991) was used to assess the AM infection potential of the soils taken from the plots of the DOC field trial. It consisted of a central container and two lateral containers, the adjoining walls of which were composed of nylon screens (60-μm mesh; Zürcher Beuteltuchfabrik, Rüschlikon, Switzerland). Each lateral container was subdivided into five compartments in order to allow sampling of individual test plants without disturbing the neighbouring ones. Hyphae of AM fungi but not roots of cultivated plants can penetrate the screens. The potential of the soils to promote symbiosis was tested in the presence and absence of an introduced AM fungi inoculum under otherwise identical conditions. For this, winter wheat was cultivated as the test plant in soil samples from the plots in the lateral containers, and soybean (*Glycine max* L. cv. Maple Arrow) inoculated with *Glomus mosseae* [(Nicol. and Gerd.) Gerd. and Trappe] or with an AM-free mock inoculum was cultivated on sterilized, standardized soil in the central container.

Soil taken from the plots of the field trial containing the indigenous AM fungi was carefully homogenized by hand and was then filled into the lateral containers to enable symbiosis between the test plants and AM fungi. Seeds of winter wheat were surface sterilized for 5 min in 5% sodium hypochlorite, rinsed 3 times with sterile water and allowed to germinate for 3–4 days in autoclaved vermiculite (2–4 mm Vermex M/803; Vermica, Bözen, Switzerland) before they were planted separately into each compartment of the two lateral containers. There were two plants $plot^{-1}$ (eight plants $treatment^{-1}$ $sampling\ date^{-1}$).

The lateral containers with the test plants were joined to a central container with or without an inoculum of AM fungi. To

assess the infection potential of solely the indigenous community of AM fungi, the central container was filled with a steam-sterilized (20 min, 121 °C) mixture of sand, loam and organic matter (3:2:1, v:v:v) and a mock inoculum free of AM fungi was added as described by Wyss et al. (1991). Twenty days after joining the central and lateral containers, the degree of AM root colonization was assessed on the winter wheat test plants in the lateral container as described.

To assess the infection potential of the field-plot soils in the presence of an external AM fungal inoculum, the central container contained soybean plants colonized by the fungus *G. mosseae*. In this case, the central container was filled with a steam-sterilized soil mixture as before, but was supplemented with an AM inoculum as according to Wyss et al. (1991). This inoculum contained soil, AM hyphae, spores and roots of *Tagetes sp.* colonized by *G. mosseae.* Thereafter, 3- to 4-day-old soybeans, obtained from surface-sterilized seeds and germinated as the wheat plants, were planted and grown for 4 days in the central container to allow the AM symbiosis to establish. Then central and lateral containers were joined.

Statistical analysis

Data were analysed using ANOVA. Measurements for which significant treatment effects were found were characterized further using Tukey's method of multiple comparisons. Moreover, regression analyses were performed to assess the influence of the chemical soil properties on AM root colonization. Additionally, the effect η was calculated after Rosenthal and Rosnow (1985), which characterizes the variance of a parameter caused by a factor, such that: $0 \leq \eta \leq 1$; if $\eta \geq 0.25$, it is intermediate; if $\eta \geq 0.5$, it is high.

Results

Field studies in different crops

In the field studies, the plots of the treatments with a "high" fertilization level (the fertilization intensity recommended as standard for farms in Switzerland: D2, O2, C2, M) and the unfertilized control were sampled and compared. Root colonization by AM fungi was highest in the control, intermediate in the biological systems (D2, O2) and lowest in the conventional systems (C2, M). In vetch-rye and grass-clover, AM root colonization was enhanced by 30–60% in the biological farming systems, compared with the conventional systems, and this difference was statistically significant (Fig. 1A, C). In winter wheat, the differences between the farming systems were not significant when the data of the unfertilized control were included (Fig. 1B). However, when these data were excluded, the differences between the farming systems were significant ($P \leq 0.05$). Summarized over all crops, AM colonization of field-plant roots of biologically farmed plots (D2, O2) increased by about 40% compared with the conventional plots (M, C2) (Fig. 1D). A two way-ANOVA (without data of the control) revealed highly significant effects ($P \leq 0.001$) for the factors "farming systems" and "crop", without interactive effects. Thus, AM root colonization increased in the same order of treatments for all crops, and was highly dependent on both factors.

In each of the three crops investigated, both the factors "farming systems" and "sampling date" were significant ($P \leq 0.001$), reflecting the distinct dynamics of AM root colonization over time. AM fungal structures were never detected in winter wheat when it had reached the two to three leaf stage in late autumn. Moreover, in both years of investigation (1990/1991), the AM symbiosis established at a low level by the tillering stage in March/April did not increase to a level higher than about 12% until maturity was reached at the end of July. In contrast, the vetch-rye mixture, sown

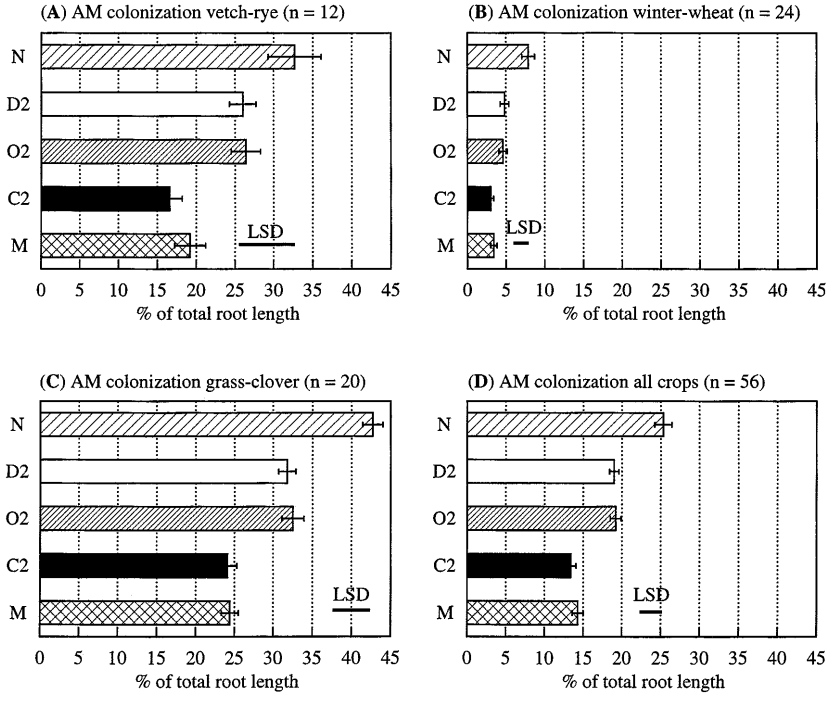

Fig. 1A–D Influence of farming systems on the mycorrhizal colonization of roots of field plants grown in unfertilized (*N*), biologically (*D2*, *O2*; "high" fertilizer level) and conventionally (*C2*, *M*; "high" fertilizer level) cultivated plots of the DOC field trial. For farming systems see Table 1. Means of three observations in vetch-rye in 1989/1990 (**A**), six observations in winter wheat in 1990/1991 (**B**), five observations in grass-clover in 1993 (**C**) and means of all crops (**D**). Each observation includes four field-plot replicates treatment^{-1}. *Error bars* indicate SE of means. *LSD* Least significant difference (Tukey test, $P \leq 0.05$)

without ploughing-in of the winter wheat stubbles after harvesting in 1989/1990, was rapidly colonized by AM fungi (1989, 15–30%; 1990, 29–61% of total root length) in all farming systems. In the grass-clover meadow, AM root colonization had reached only 5–13% by the end of September, 8 weeks after sowing. Thereafter, a rapid increase in root colonization occurred in the period between autumn of the sowing year and the first cut in the following year (1993; 27–53%). Root colonization only slightly increased further in the second year of the grass-clover meadow. A two-way ANOVA which included the farming systems D, O and C revealed the factors "fertilizer level" ($P \leq 0.05$) and "farming systems" ($P \leq 0.001$) as significant. Nevertheless, the effect of the farming systems was more pronounced ($\eta = 0.6$) than that of fertilizer level ($\eta = 0.4$).

Glasshouse experiment to test the AM infection potential of soils from the DOC field trial with their indigenous community of AM fungi and after an additional inoculation with *G. mosseae*

In the 1989/1990 season, the AM infection potential of the soils from the field trial was tested. For comparison, the colonization of field-grown plants was also examined. These results, which included "low" and "high" fertilization levels, showed the same trend as those of the experiment discussed above (Fig. 2A). When the soils were tested experimentally in the glasshouse, root colonization by indigenous AM fungi was significantly higher in the biologically cultivated soils (D1 and D2, O1 and O2) as compared to the conventionally cultivated soils (C1 and C2, M) 20 days after planting (Fig. 2B,C). The colonization reached levels of between 8% and 14% of root length irrespective of the fertilizer level applied ($P = 0.89$) (Fig. 2B). Upon inoculation with *G. mosseae*, root colonization was much higher and varied between 24% and 39% under the same growth conditions, indicating that the level of the natural population of AM fungi was far from that which was required to saturate the soil in terms of infection potential (Fig. 2C). However, the differences in AM root colonization between the farming systems remained conspicuous after inoculation (Fig. 2B, C).

In a regression analysis comparing the formation of mycorrhizae with chemical soil properties (pH, P, K, Mg), only pH and P were slightly negatively correlated with AM root colonization of field grown plants ($P \leq 0.1$). In the glasshouse experiments, the AM root colonization of winter wheat correlated negatively with extractable soil P ($P \leq 0.01$) and positively with soil K ($P \leq 0.05$). In the field investigations, a statistical analysis (not shown) indicated that all measured chemical soil properties taken together explained around 50% of the effect η of the factor "treatment" and around 80% of the factor "fertilizer level", whilst in the glasshouse, only 33% of the effect η of the factor "treatments" was explained (the factor "fertilizer level" was not significant).

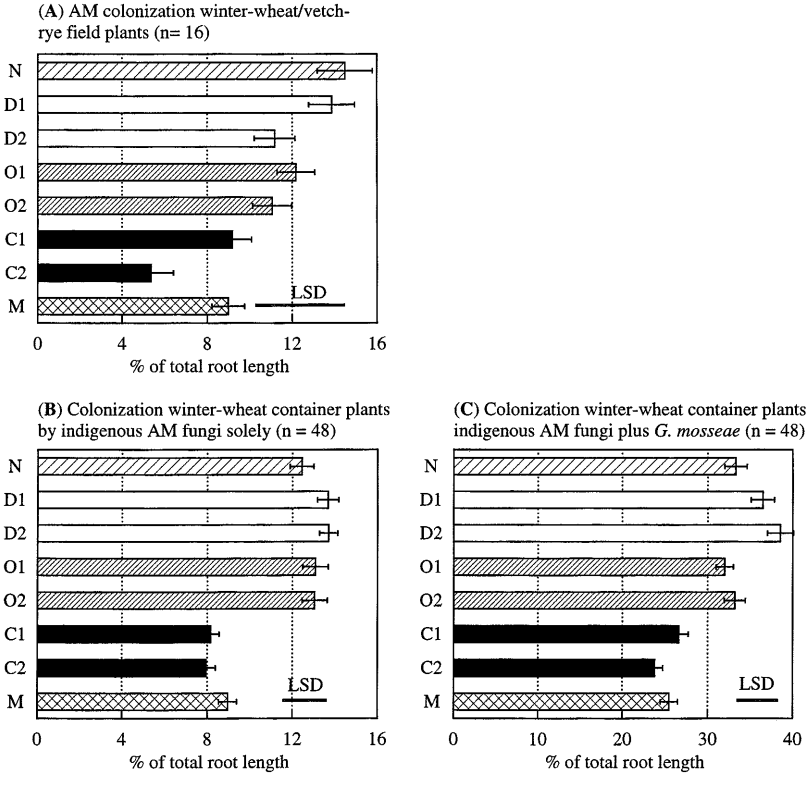

Fig. 2A–C Influence of farming systems and fertilizer level on the mycorrhizal colonization of plant roots grown in soils of unfertilized (N), biologically cultivated (*D1*, *O1* "low" fertilizer level; D2, O2 "high" fertilizer level) and conventionally (*C1* "low" fertilizer level; C2, M "high" fertilizer level) cultivated plots of the DOC field trial. For farming systems see Table 1. Each observation includes four field-plot replicates treatment^{-1}. *Error bars* represent SE of means. LSD (Tukey test, $P \leq 0.05$). **A** AM colonization of plants grown in the field plots. Means of two observations in winter wheat and two observations in vetch-rye in 1989/1990. **B, C** effect of the farming systems and the fertilizer level on the mycorrhizal colonization of winter wheat tested in the glasshouse. Mycorrhizal potential of soils with the indigenous AM populations solely (**B**) and with an additional *Glomus mosseae* inoculum (**C**) is shown. Means of samples taken on four sampling dates for winter wheat and two sampling dates for vetch-rye in 1989/1990. Note the different scales in the figures. For other abbreviations, see Fig. 1

Discussion

After 13–16 years of maintaining different cultivation practices on the field plots, root colonization by AM fungi of vetch-rye, winter wheat and grass-clover crops was enhanced by 30–60% in the biological farming systems compared with the conventional ones. Highest values were found in the unfertilized control. Even after 2 years of grass-clover crop, where no pesticides were applied, this difference persisted. Thus the different AM root colonization found reflected partly the intensity of fertilizer input and the soluble-nutrient content, especially of P, in the soils. This was in accordance with previous studies which showed P, among other macronutrients, to have the most pronounced effect on the development of AM symbiosis (Hayman 1982). In general, the percentage of AM root colonization decreases as the P status of the host plant increases (Smith and Read, 1997).

The decrease in AM root colonization with an increase in fertilizer level was most pronounced in the conventional system (C2 vs C1) but was less evident in the biological systems (D2 vs D1; O2 vs O1). This may have been due to the overall lower nutrient input in the biological than in the conventional systems. More likely, it was connected with the fact that water-soluble mineral fertilizers (NH_4NO_3, super phosphate, KCl) were only applied in the conventional systems. Also Harinikumar and Bagyaraj (1989) found that fertilizers in organic form are less inhibitory to AM root colonization than synthetic mineral fertilizers.

Although the conventional system with a "low" level of fertilization (C1) and the biological systems with a "high" level of fertilization (D2 and O2) were similar with respect to nutrient inputs, in particular with respect to P, AM root colonization was significantly lower in C1 than in D2 and O2 in the glasshouse experiment. This suggested that, besides the measured chemical soil properties, other soil properties such as pesticide residues may have influenced the AM root colonization. There were nine fungicide, two insecticide and six herbicide applications 7-year crop rotation^{-1} in the conventional systems (Niggli et al. 1995). In the organic system, only Cu was used at a low rate (1.5 kg Cu ha^{-1} crop rotation^{-1}) and no pesticides at all in the bio-dynamic one (Besson and Niggli 1991). Besides the fungicides (Schreiner and Bethlenfalvay 1997), herbicides are also known to adversely affect AM symbiosis, on the one hand directly by lowering spore viability and hyphal growth and, on the other hand, indirectly by eliminating the weeds which can act as host plants for AM fungi (Trappe et al. 1984; Johnson and Pfleger 1992). This may be of particular importance during the cultivation of non-host plants for AM fungi, such as *Brassica napus* L. var. *napus* and *Beta vulgaris* L. ssp. *vulgaris*. These plants were used as pre-crops for winter wheat in the DOC field trial. Soil cover by weeds and weed diversity was distinctly higher in the biologically farmed plots than in the conventional ones, leading to better conditions for AM fungi in the biological systems.

It is not surprising that only relatively small differences in AM root colonization were found between the different farming systems. Firstly, crop rotation and tillage, which are known to influence AM symbiosis (Johnson and Pfleger 1992), were equal in all the farming systems of the DOC field trial, and secondly, fertilizer input, even in the conventional systems (C2 and M), was comparatively low and, accordingly, the level of soluble P and K in the soil was also low in all the systems. Considering the moderate application of pesticides in the conventional systems which respected economic thresholds, according to good agricultural practices, the conventional systems in the DOC field trial were representative of the so-called "integrated production systems". In studies comparing neighbouring farms (Sattelmacher et al. 1991; Ryan et al. 1994), where AM root colonization was enhanced three- to tenfold in biological, low-input farming systems as compared to conventional ones, soluble P content in the soil of the conventional systems was much higher than in the ones of the DOC field trial. Moreover, the rotation comprised a smaller number of crops at the conventional sites with only short periods of pasture (Ryan et al. 1994) or even a maize monoculture irregularly interrupted by rye (Sattelmacher et al. 1991). In both of the neighbouring-farm studies, the low-input farms had already been managed biologically for 30 years, which may be an additional explanation for the remarkable differences in AM root colonization between the systems.

The finding that the AM root colonization potential of the soils from the biological systems remained enhanced when inoculated with *G. mosseae* suggested that, primarily, soil properties such as nutrient content, pesticide residues, biological activity and soil structure were responsible for the differences, and not the number of infectious AM propagules. Thus, in order to enhance AM symbiosis, farming practices should be chosen that favour optimal soil properties for the development of AM symbiosis.

Regarding the increase in AM root colonization obtained in all the soils irrespective of the farming system after inoculation with *G. mosseae*, the question arises how cultivation techniques of arable soils can be improved by appropriate crop rotations with good AM fungal host plants or by reduced-tillage or no-tillage systems. Hitherto, much emphasis has been put on finding new strains of AM fungi and developing techniques to inoculate them into agricultural soils in order to replace or reinforce the indigenous populations. At present, routine inoculation in large-scale, highly developed farming systems is generally not achievable because of the expense of producing the inoculum and the sheer bulk of inoculum required (Smith and Read 1997). Hence, management of indigenous populations of AM fungi is currently the more promising option. However,

in relatively small-scale operations, such as nursery production, routine inoculation is certainly feasible and likely to be highly advantageous in increasing growth rates and uniformity of the products (Smith and Read 1997). Field trials are needed to show if AM inoculation of the DOC field soils definitely results in a generally increased AM root colonization of the field plants, and if this stimulates increased yields.

The question remains whether AM fungi may have influenced the evolution of yield in the different farming systems of the DOC trial. This question is difficult to answer because of the lack of a non-mycorrhizal control in the field. There is some circumstantial evidence, however, that AM fungi may have substantially contributed to plant nutrition in the biological low-input farming systems: whilst the yield of the biologically cultivated grass-clover system, which was highly colonized by AM fungi, was only reduced by 10–12% compared to the conventional system, the yield of winter wheat, which was only colonized to a minor extent, was reduced by 19–26%. The greatest yield decrease (34–45%) was observed for potatoes, where no colonization by AM fungi was detected (Mäder et al. 1999).

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