Catena 182 (2019) 104135

Contents lists available at ScienceDirect

Catena

journal homepage: www.elsevier.com/locate/catena

Unexpectedly high diversity of arbuscular mycorrhizal fungi in fertile Chernozem croplands in Central Europe

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ARTICLE INFO

Keywords:
Biodiversity, cultivated soils
Ecosystem services, growth promotion
Microbial indicators
Soil type

ABSTRACT

Highly fertile soils are considered to harbor low diversity of arbuscular mycorrhizal fungi (AMF), since plants might not depend on the mycorrhizal symbiosis to efficiently assimilate soil nutrients. 'Black steppe soils' classified as Chernozems are counted among the soil types with highest natural fertility and productivity. However, information on AMF diversity from highly productive Chernozems used as croplands are extremely rare to non-existent. Our objective was to study the impact of soil tillage and fertilization intensity on AMF communities in a long-term field trial established on a silty-loamy Calcic Chernozem in the Magdeburger Börde (Central Europe). Samples were taken at harvest of maize that grew in a rotation with winter wheat, winter barley, winter oil seed rape and again winter wheat. AMF species were characterized by spore morphology. Astonishingly high spore densities (up to 41 spores g^{-1} soil) and species richness (19–33 species) of AMF were found in this highly productive Chernozem cropland, even under high-input conditions, which were, however, higher in reduced tillage than in regularly ploughed plots. AMF diversity decreased with increasing fertilizer input concerning N and P. These findings might re-stimulate the discussion about the significance of AM fungi in highly productive croplands, which was so far thought to be low. Several indicator AMF species were identified for reduced tillage (e.g. *Ambispora fennica* and *Dominikia bernensis*) or reduced fertilizer inputs (e.g. *Dominikia aurea*) or both (e.g. *Diversispora celata* and *Scutellospora calospora*), but only a few for tillage (e.g. *Funneliformis fragilistratus* and *Pacispora dominikii*). AMF indicators have to be, however, identified for each soil type and climatic condition separately, as they should be completely different from those species for instance in nutrient-poor or in acidic soils, in warmer or colder as well as in more humid or arid climates.

1. Introduction

Arbuscular mycorrhizal fungi (AMF) display a key role in nutrient cycling by transferring minerals such as P and micronutrients to their host plants and receiving carbohydrates and lipids in exchange (Bonfante and Genre, 2010; Smith and Read, 2008; Rillig et al., 2015; Keymer et al., 2017; Neuenkamp et al., 2018). AMF are important natural resources for nutrition of many agronomic crops, as for example maize, small grain cereals, sugarcane, soybeans and cotton (Smith et al., 2011; Aghili et al., 2014).

These fungi are naturally found in almost all terrestrial ecosystems and all soils with flowering plant growth (Read, 1991), ranging from shallow Leptosols in coldest climates (Oehl and Körner, 2014), acidic, infertile, young to old Andosols (Aguilera et al., 2014; Castillo et al., 2016), and deeply weathered Acrisols and Ferralsols with low nutrient contents, generally found in the tropics and subtropics (Sieverding, 1991; Tchabi et al., 2010; Pontes et al., 2017a, 2017b). They are also known from Phaeozems, Calcisols and Gipsisols of arid temperate, Mediterranean to sub-tropical climate (Caravaca et al., 2005; Oehl et al., 2005), Kastanozems, Chernozems, or alcaline Solonetz and

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https://doi.org/10.1016/j.catena.2019.104135
Received 9 October 2018; Received in revised form 16 June 2019; Accepted 18 June 2019
Available online 16 July 2019

Solonchak soils of continental climates (Hamel et al., 2015; Guo et al., 2016), to medium fertile Cambisols and Luvisols in temperate climates (Oehl et al., 2010), clay-rich Vertisols in sub-tropical to tropical basins (Soka and Ritchie, 2018), up to groundwater affected Gleysols and Histosols of very different nutrient contents in moist areas around the globe (e.g. Palenzuela et al., 2010).

Chernozems in Central to Eastern Europe (Eckmeier et al., 2007) are counted as the most fertile soils worldwide, as long as they still have well-balanced water supplies during the vegetation period and have not yet been degraded by unsustainable land uses or climate change. Information about AMF from very fertile Chernozems is scarce (Yang et al., 2010; Sommermann et al., 2018). Recently, Dai et al. (2012) reported non-significant differences in AMF species diversity among different Chernozem 'types' in Canada. Generally, AMF species richness and composition of AM fungal communities depend on host plant, climate, and soil conditions, particularly on their nutritional status (Öpik et al., 2006; De Deyn et al., 2011; Wetzel et al., 2014). Especially intensively used, nutrient-rich croplands harbor a particularly low diversity of AM fungi, since plants might not depend on the mycorrhizal symbiosis to efficiently assimilate soil nutrients, which was confirmed in Central European Luvisols and Cambisols (e.g. Oehl et al., 2003, 2010).

Some ecological indicator species for broad and narrow range of soil conditions and tropical agronomic crops were brought up first by Sieverding (1989). Further ecological studies carried out by Oehl et al. (2003, 2010) in different agro-systems of Central Europe showed dominance of some AMF species in grass- or croplands and in different soil types. They called them AMF "specialist" and "generalists" depending on whether they occurred exclusively under specific soil and agronomic conditions and in all soils under a broad range of agronomic practices. AMF bioindicator species for specific soil chemical and physical conditions and environments were found by Oehl et al. (2017), who analyzed reports from 154 Swiss locations with different climates (altitudes), land uses and soil parameters. AMF species exclusively occurring in long term no-tilled vineyards on Luvisols were identified by Oehl and Koch (2018). Such species can be named indicator AMF species for vineyards with reduced tillage. Good taxonomic knowledge is required for such investigations, when spore morphological characters are used to identify AMF species from field samples. We used such classical morphological identification methods, as they revealed to generate higher AMF species numbers than using molecular biological methods (Wetzel et al., 2014).

The objective of the present study was to investigate the impact of two tillage systems, conserving cultivator soil preparation versus conventional ploughing on the AMF species community after maize cultivation in a highly fertile Calcic Chernozem cropland in Lower Saxony, Germany, Central Europe (Körschens et al., 1998). In Lower Saxony, Chernozems reach the highest proportion of the surface area (nearly 20%) and of the agriculturally arable land (nearly 33%) as compared to all other German states (Altermann et al., 2005). For our study, samples were taken within a 23 years long term field experiment that was subjected to crop rotation comprising winter wheat, winter barley, winter oil seed rape, winter wheat and maize. Individual plots on this long-term field trial had been managed by the two soil preparation systems, where three levels of mainly nitrogen were applied as nutritional intensity subplots. We hypothesized that in these old Central European croplands AMF diversity is low due to i) the high natural fertility and productivity of these Chernozem soils, ii) the long tradition of intensive soil cultivation by ploughing and iii) the mineral nutrient fertilization, especially high nitrogen and phosphorus amendments for maize grain production. Finally, we expected that, even under such conditions of assumed low AMF diversity, AMF spore densities and species richness would be affected by soil tillage and fertilization intensity.

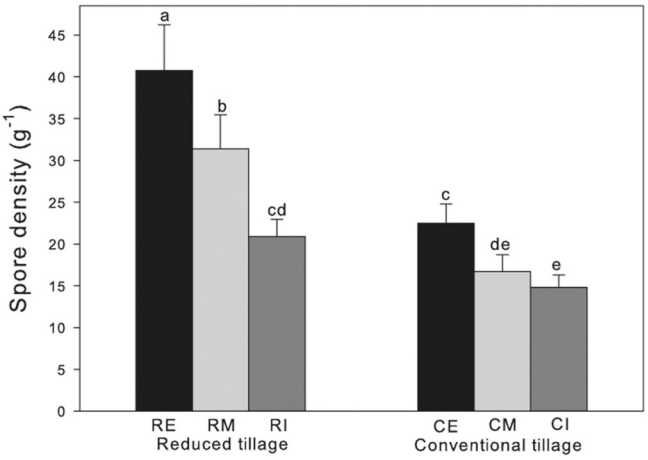

Fig. 1. AMF spore densities (g^{-1} soil) in reduced till and conventionally tilled plots of different fertilization intensity in a 23-years field experiment. Average and standard deviations are shown. Non-significant differences between differently managed plots are shown by identical miniscule letters above the corresponding columns and were determined with Fischer's Least Significant Difference (*LSD*) test at the $p < 0.05$ level after a one-way ANOVA.

2. Material and methods

2.1. Long-term field experiment

Within a long-term tillage trial, laid out in 1992 on the experimental station of the Anhalt University of Applied Sciences, in Bernburg-Strenzfeld, Germany, the effect of tillage practices on crop yield, plant availability of P and K, as well as plant nutrients, is being investigated. The farming management practices, including type of tillage and level of nitrogen and phosphorus fertilization, as well as the treatment abbreviations RE, RM, RI for Reduced tillage with different fertilization levels; CE, CM, CI for Conventional tillage with different fertilization levels used in this publication are presented in detail in Fig. 1 and Table 1. The trial location is situated in the South of the fertile Chernozem (= "Schwarzerde") plain of the Magdeburger Börde. Productivity of the stands had demonstrated clear positive effects of reduced till management for soil stability, nutrient availability, yields and earthworm populations (Deubel and Orzessek, 2011; Deubel et al., 2011; Schlüter et al., 2018).

The soil is a Calcic Chernozem having developed on Loess sediments over limestone with an effective root depth of 100 cm, with a neutral pH (7.0–7.4). Mean annual temperature at the site is about 9.7 °C and mean rainfall is about 500 mm per year (551 mm within 1981–2010; Deubel et al., 2011). Conservation tillage (stubble processing + cultivator 12–15 cm deep) is compared with conventional tillage (stubble processing + moldboard ploughing 20–30 cm deep) on five large plots (1.2 ha each) with crop rotation grain maize (*Zea mays* L.) – winter wheat I (*Triticum aestivum* L.) – winter barley (*Hordeum vulgare* L.) – winter rape (*Brassica napus* L.) – winter wheat II. Stubble processing after harvest was by mechanically crushing; all farm residues remained on the field. No other organic fertilizers were applied (Deubel et al., 2011). Three fertilizer treatments were compared per tillage system: i) 'Extensive' (reduced N supply of 60 kg N ha^{-1} as Urea Ammonium Nitrate (UAN) after sowing; ii) 'Moderate' following usual practice (120 kg N/ha^{-1} as UAN after sowing, and iii) 'Intensive' following usual practice (102 kg N/ha^{-1} as UAN after sowing, plus 18 kg N and 20 kg P ha^{-1} applied as Diammonium phosphate (DAP) in below-seed fertilization, respectively (Deubel et al., 2011). The basis fertilization with P and K is identical in all treatments (60 kg P and 75 kg K ha^{-1}). Fungicides were not applied in maize and weed control was conducted for all plots as appropriate.

Table 1
Soil cultivation, fertilization and plant protection characteristics in the long-term field experiment under study during 23 years of different farming.

Site code	Reduced tillage			Conventional tillage		
	Extensive	Moderate intensive	Intensive +P	Extensive	Moderate intensive	Intensive + P
	RE	RM	RI	CE	CM	CI
Soil cultivation	Conservation tillage			Mould-board plough		
Fertilization type	UAN	UAN	AHL + DAP	UAN	UAN	UAN + DAP
N fertilization (kg N ha^{-1})	60	120	102 + 18 kg	60	120	102 + 18
P-fertilization (kg P ha^{-1})	60					
K fertilization (kg K ha^{-1})	75					
Pesticide use	No fungicides; Coragen (with active ingredient Chlorantraniliprole) against European corn borer (*Ostrinia nubilalis*) except RE and CE					
Weed suppression strategy	Broad-leaf weed control as appropriate					

UAN denotes Urea Ammonium Nitrate; DAP denotes Diammonium phosphate.

2.2. Soil sampling at the field site

In October 2015, soil core samples were collected at 0–15 cm soil depth from the maize trial plots. Four replicates had been established before, from which each 12 subsamples were taken that were pooled to one per replicate (ca. 1.5 kg samples) and homogenized by passing through a sieve (1 cm mesh size) for AMF investigation.

2.3. AMF spore isolation and identification

AMF spores were extracted from 25 g field samples by wet sieving, followed by water and sucrose centrifugation (Sieverding, 1991). Spores were passed to a Petri dish, and their number was counted. For identification of the AMF species, the extracted spores were mounted on slides with polyvinyl alcohol lactic acid glycerol (PVLG) and PVLG + Melzer's reagent (1,1 v/v) and observed under a compound microscope. AMF species were identified according to the manuals of Schenck and Pérez (1990) and Błaszkowski (2012), considering also all original and emended AMF genus and species descriptions available. Glomeromycota classification was based on Oehl et al. (2011b), considering all updates on the higher taxa to species level since then (e.g. Sieverding et al., 2014; Błaszkowski et al., 2015, 2018; Castillo et al., 2016; Tedersoo et al., 2018). However, as number of AMF genera increased since 2011 from 29 to 45 genera, we are summarizing the current classification system in Table 2.

2.4. Estimation of AMF abundance and diversity parameters

To assess AMF community composition and structure, species richness, relative abundance, frequency, evenness and diversity were determined. Species richness was defined as the number of AMF species recorded in each study area. The relative abundance of AMF species (RAi) was calculated according to the equation: $RAi = A/\Sigma a \times 100$, where RAi is the relative abundance of a given species i, A = abundance of the species i, Σa = sum of abundances of all species. The ecological indices were evaluated according to the Shannon index: $H' = -\Sigma (Pi \ln [Pi])$, where Pi = ni/N, ni = number of individuals of the species i, and N = total number of individuals of all species (Shannon, 1948); Pielou's evenness index (J) = H′/Log (S), where H′ is the value obtained by the Shannon index and S is the total number of species (Pielou, 1975); Margalef's index, calculated based on: d = S-1/LogN, where S = number of species, N = total number of spores per sample (Margalef, 1958); and Sørensen's similarity index (Brower and Zar, 1984), which was used to compare AMF communities between different treatments. The analyses, including the Cluster dendrogram, were performed using the PRIMER 6.0 program (Clarke and Gorley, 2006).

2.5. Statistics and multivariate data analysis

The data of the different soil parameters, AMF spore density, species richness and the different AMF diversity and community parameters as well the harvest quantities were averaged for each of the four replicates of the treatments. The data were subjected to analysis of variance (ANOVA) in order to compare the six treatments. The means were additionally compared by Fisher's Least Significant Difference ($p < 0.05$). For testing the abundance of selected species at all sites, the non-parametric Kruskal–Wallis test was chosen with Bonferroni adjusted *p*-values using the 'package 'agricolae' (Mendiburu, 2017) in the R program (R Core Team, 2018). The data on the AMF communities (relative abundance) were used to perform redundancy analyses (RDA), to consider the ecological and soil parameters. We used Permutational Multivariate Analysis (PERMANOVA) to verify differences between reduced tillage and conventional treatments. (For the analyses of indicator species, the Monte Carlo test (Metropolis and Ulam, 1949) was used according to Dufrêne and Legendre (1997). The species with indication values > 30% and $p < 0.05$ were considered to be good indicators of the areas. Redundancy analyses (RDA) and indicator species analyses were performed using the program PC-ORD version 6.0 (McCune and Mefford, 2006).

3. Results

3.1. Soil parameters

The reduced tillage treatments RE, RM and RI had generally higher organic carbon (19.1–20.9 g kg^{-1}) and total nitrogen contents (1.8–1.9 g kg^{-1}) than the plough-tilled treatments CE, CM and CI (15.2–15.5 and 1.4–1.4 g kg^{-1}, respectively). Plant available potassium was also significantly increased in the reduced tillage plots (320–347 versus 199–218 mg kg^{-1}). Remarkably, available P and Mg was not affected either by soil tillage system or by different fertilization inputs ranging on high levels: Double-Lactate extracted P (P-DL): 74–104 mg kg^{-1}; Calcium-Ammonium-Lactate extracted P (P-CAL): 47–67 mg kg^{-1}; Mg: 234–275 mg kg^{-1} (Table 3).

3.2. AMF spore density

AMF spore density was highest in the two reduced tillage systems without DAP below-seed P fertilization (RE and RM) with 41 and 31 spores g^{-1} soil and lowest in the two conventional tillage systems subjected to moderate and intensive fertilization (CM and CI) with 17 and 15 spores g^{-1} soil, respectively (Fig. 1). In the reduced tillage system with high fertilization (RI) and the conventional tillage system with low fertilization (CE), the spore densities were intermediate (21 and 23 spores g^{-1} soil).

Table 2
Current classification of the phylum Glomeromycota (= AM fungi, within the subkingdom Mucoromyceta).

Class	Order	Family	Genus
Glomeromycetes	Glomerales	Glomeraceae	*Glomus*
			Dominikia
			Funneliformis
			Funneliglomus
			Kamienskia
			Microdominikia
			Microkamienskia
			Nanoglomus
			Oehlia
			Orientoglomus
			Rhizoglomus
			Septoglomus
			Sclerocarpum
			Sclerocystis
			Simiglomus
		Entrophosporaceae	*Entrophospora*
			Albahypha
			Claroideoglomus
			Viscospora
	Diversisporales	Diversisporaceae	*Diversispora*
			Desertispora
			Otospora
			Tricispora
			Redeckera
			Corymbiglomus
		Sacculosporaceae	*Sacculospora*
		Pacisporaceae	*Pacispora*
		Acaulosporaceae	*Acaulospora*
			Kuklospora
	Gigasporales	Gigasporaceae	*Gigaspora*
		Scutellosporaceae	*Scutellospora*
			Bulbospora
			Orbispora
		Racocetraceae	*Racocetra*
			Cetraspora
		Dentiscutataceae	*Dentiscutata*
			Fuscutata
			Quatunica
		Intraornatosporaceae	*Intraornatospora*
			Paradentiscutata
Archaeosporomycetes	Archaeosporales	Archaeosporaceae	*Archaeospora*
			Intraspora
			Palaeospora
		Ambisporaceae (= Appendicisporaceae)	*Ambispora (= Appendicispora)*
		Geosiphonaceae	*Geosiphon*
Paraglomeromycetes	Paraglomerales	Paraglomeraceae	*Paraglomus*
			Innospora
		Pervetustaceae	*Pervetustus*

Classification based on Castillo et al. (2016), updated here (July 2019).

Table 3
Selected chemical soil parameters in the long-term field experiment after 23 years of different farming in maize before harvest (October 2015).

Site code	Reduced tillage			Conventional tillage			*p*-Value	*LSD*
	Extensive	Moderate intensive	Intensive +P	Extensive	Moderate intensive	Intensive +P		
	RE	RM	RI	CE	CM	CI		
Organic carbon (C_{org}; g kg^{-1})	19.1 b	19.4 b	20.9 a	15.3 c	15.5 c	15.2 c	2.1×10^{-10}	0.973
Total N (N_t; g kg^{-1})	1.8 a	1.8 a	1.9 a	1.4 b	1.4 b	1.4 b	3.6×10^{-8}	0.134
pH (H_2O)	7.6 a	7.4 a	7.3 a	7.0 a	7.3 a	7.4 a	0.234	0.261
P_{avail} (DL; mg kg^{-1})	74.1 a	94.8 a	73.6 a	103.9 a	91.7 a	91.1 a	0.209	27.9
P_{avail} (CAL; mg kg^{-1})	47.1 a	65.3 a	50.5 a	67.4 a	60.7 a	50.7 a	0.135	18.1
K_{avail} (DL; mg kg^{-1})	320 a	347 a	341 a	217 b	218 b	199 b	1.6×10^{-5}	55.9
Mg_{avail} ($CaCl_2$; mg kg^{-1})	241 a	272 a	275 a	246 a	234 a	243 a	0.555	55.6

DL and CAL denote Double Lactate and Calcium Lactate soluble P, respectively. Available K was also determined by DL-method, while Mg was determined after 0.0125 M $CaCl_2$ extraction (VD-LUFA). Average and standard deviation of four field plot replicates per treatment. Non-significant differences between treatments are shown by identical miniscule letters within the rows and were determined with Fischer's Least Significant Difference (*LSD*) test at the $p < 0.05$ level after a one-way ANOVA.

Table 4
AMF species found in maize before harvest (October 2015) in the long-term field experiment under study, with their relative abundance per site and their frequency per 24 field plots analyzed. Numbers in brackets represent the absolute spore numbers identified per species.

AMF species	Species code	Reduced tillage			Conventional tillage			Fre-quency (%)
		Extensive	Moderate intensive	Intensive +P	Extensive	Moderate intensive	Intensive +P	
		RE	RM	RI	CE	CM	CI	
Funneliformis mosseae	Fu.mos	38.4 (435)	20.8 (123)	17.1 (70)	41.1 (234)	35.0 (176)	35.4 (134)	100.0
Rhizoglomus irregulare	Rh.irr	8.1 (92)	20.0 (118)	26.2 (107)	24.3 (138)	19.0 (96)	21.6 (82)	100.0
Fu. fragilistratus	Fu.fra	3.7 (42)	2.4 (14)	6.6 (27)	6.0 (34)	17.0 (89)	15.6 (59)	100.0
Oehlia diaphana	Oe.dia	1.9 (21)	2.4 (14)	2.0 (8)	2.6 (15)	6.5 (16)	3.4 (13)	100.0
Fu. geosporus	Fu.geo	5.6 (63)	4.6 (27)	5.9 (24)	1.6 (9)	2.7 (14)	2.6 (10)	100.0
Archaeospora trappei	Ar.tra	1.5 (17)	1.4 (8)	4.9 (20)	2.3 (13)	3.1 (16)	4.7 (18)	100.0
Paraglomus turpe	Pa.tur	3.5 (40)	6.6 (39)	5.6 (23)	2.6 (15)	1.8 (9)	2.4 (9)	100.0
Scutellospora calospora	Sc.cal	6.5 (74)	6.1 (36)	7.8 (32)	4.2 (24)	2.7 (14)	3.7 (14)	95.8
Palaeospora spainiae	Pa.spa	1.0 (11)	1.9 (11)	1.7 (7)	0.5 (3)	0.8 (4)	1.1 (4)	83.3
Dominikia compressa	Do,com	2.7 (30)	4.1 (24)	1.0 (4)	1.1 (6)	1.2 (6)	2.6 (10)	83.3
Pa. laccatum	Pa.lac	1.1 (12)	4.2 (25)	0.7 (3)	1.4 (8)	3.7 (19)	1.6 (6)	83.3
Claroideoglomus luteum	Cla.lut	1.8 (20)	1.9 (11)	1.5 (6)	0.9 (5)	0.4 (2)	1.1 (4)	79.2
Septoglomus nigrum	Se.con	4.4 (50)	6.4 (38)	6.4 (26)	0.4 (2)	1.0 (5)	0.8 (3)	79.2
Cl. claroideum	Cl.cla	2.4 (24)	3.7 (22)	1.5 (6)	3.7 (21)	0.4 (2)	1.6 (6)	75.0
Cl. etunicatum	Cl.etu	1.9 (21)	1.4 (8)	2.0 (8)	1.6 (9)	0.6 (3)	0.5 (2)	70.8
Fu. coronatus	Fu.cor	0.1 (1)	0.5 (3)	0.2 (1)	0.5 (3)	0.8 (4)	0.3 (1)	37.5
Rh. intraradices	Rh.int	0.6 (7)	1.4 (8)	1.0 (4)	1.9 (11)	0.2 (1)		50.0
Do. aurea	Do.aur	2.2 (25)	0.5 (3)	0.2 (1)	0.5 (3)	0.4 (2)		41.6
Tricispora sp.1	Tr.sp1	0.8 (9)	0.5 (3)	0.2 (1)		0.4 (1)	0.3 (1)	41.6
Ambispora sp.2	Am.sp2	0.4 (4)		0.5 (2)	0.2 (2)	0.8 (4)		37.5
Ambispora fennica	Am.fen	1.2 (13)	4.1 (24)	4.2 (17)		0.8 (4)		58.3
Diversispora epigaea	Di.*epi*	0.5 (6)	0.3 (2)	2.7 (11)	0.2 (1)			41.7
Archaeospora sp.3	Ar.sp3	1.0 (11)	0.7 (4)	0.2 (1)	0.2 (1)			33.3
Di. celata	Di.cel	1.5 (17)	1.0 (6)		0.2 (1)			33.3
Rh. fasciculatum	Rh.fas	0.5 (6)			0.7 (4)			25.0
Glomus microcarpum	Gl.mic	2.4 (27)	1.4 (8)					33.3
Do. bernensis	Do.ber	1.2 (13)	1.4 (8)					29.2
Gl. badium	Gl.bad	2.3 (26)	0.3 (2)					25.0
Paraglomus sp.4	Pa.sp4	0.2 (2)	0.2 (1)					8.3
Ar. myriocarpa	Ar.myr	0.1 (1)	0.2 (1)					8.3
Albahypha drummondii	Al.dru	0.3 (3)						8.3
Rh. invermaium	Rh.inv	0.1 (1)						4.2
Entrophospora infrequens	En.inf	0.1 (1)						4.2
Pacispora dominikii	Pa.dom				0.4 (2)	0.8 (4)		16.7
Ambispora sp.5	Am,sp5				0.7 (4)	0.2 (1)	0.8 (3)	16.7
Tricispora sp.6	Tr.sp6				0.2 (1)			4.2
Total spore numbers identified per treatment		1128	591	409	568	510	379	
Total species richness per treatment		33	29	23	26	23	19	
Total spore numbers identified		3585						
Total species richness		36						

3.3. AMF species richness at site and in the different farming systems

In this field experiment, 36 AMF species were found in maize (Table 4) belonging to all three classes, all five orders, eight families and 17 genera of AMF. Most species belonged to the family Glomeraceae (15 species, including *Dominikia*, *Funneliformis*, *Glomus*, *Oehlia*, *Rhizoglomus* and *Septoglomus* spp.), followed by the five Entrophosporaceae species (including *Albahypha*, *Claroideoglomus* and *Entrophospora*), four Diversisporaceae (including *Diversispora* and *Tricispora*), Archaeosporaceae (*Archaeospora* and *Palaeospora* spp.) and Paraglomeraceae species, two Ambisporaceae species, and one species each of the families Pacisporaceae and Scutellosporaceae (Table 4).

AMF species richness decreased in the order: RE > RM > RI ≥ CE ≥ CM > CI with 27, 24, 18, 17, 16 and 14 species as average of four field plot replicates per treatment (Table 5). Total species richness was highest in RE and RM (33 and 29 species) followed by CE (26), RI and CM (each 23 species), and lowest in CI (19; Table 4).

3.4. AMF diversity

The Margalef and the Simpson diversity calculations (Table 5) were higher in the reduced tillage systems RE, RM and RI (3.62–4.56 and 0.824–0.897, respectively) than in the conventional tillage systems CE, CM and CI (2.75–3.29 and 0.758–0.805). The Pielou index that considers the evenness between populations of different species was highest in RM and RI (both 0.829), intermediate in RE, CM and CI (0.723–0.741) and lowest in CE (0.666; Table 5). Finally, Shannon diversity, which considers both species richness and evenness, was higher in the three reduced tillage systems (2.38–2.61) than in the conventional tillage systems (1.89–1.98; Table 5).

3.5. Redundancy analysis (RDA)

Firstly, the RDA separated well the reduced tillage plots at the right from the conventionally tilled plots at the left and upper part of Fig. 2. The reduced tillage and conventional tilled plots differed in

Table 5
Shannon diversity, Margalef diversity, Pielou evenness, Simpson diversity in maize before harvest (October 2015) in the field experiment after 23 years of different soil cultivation and land use intensity.

Site code	Reduced tillage			Conventional tillage			p-Value	*LSD*
	Extensive	Moderate intensive	Intensive +P	Extensive	Moderate intensive	Intensive +P		
	RE	RM	RI	CE	CM	CI		
Species richness	26.8 a	23.5 b	17.8 cd	17.3 cd	15.5 cd	13.5 d	2.9×10^{-7}	3.117
Shannon diversity	2.43 a	2.61 a	2.38 ab	1.89 c	1.98 c	1.89 c	1.2×10^{-6}	0.214
Margalef index	4.56 a	4.51 a	3.62 ab	3.29 bc	3.01 c	2.75 c	5.6×10^{-6}	0.578
Pielou evenness	0.741 b	0.829 a	0.829 a	0.666 c	0.723 bc	0.730 bc	0.0004	0.068
Simpson diversity	0.824 ab	0.897 a	0.875 a	0.758 c	0.805 bc	0.783 bc	0.0003	0.054

Average of four field plot replicates per treatment. Non-significant differences between treatments are shown for each parameter by identical miniscule letters within the rows and were determined with Fischer's Least Significant Difference (*LSD*) test at the $p < 0.05$ level after a one-way ANOVA.

PERMANOVA analysis (F = 9.9541; $p < 0.0001$). They highlighted also again the homogenizing effect of soil tillage as the different tillage plots grouped quite close together, while the plots of the three different reduced tillage treatments grouped rather distant from each other. Secondly, the arrows for tillage, fertilization and land use intensity, but also for organic carbon, total nitrogen and available potassium are most indicative to explain the differences between the treatments (Fig. 2), while the arrows for pH and available P and Mg are shorter. The data strongly support that the effect of soil tillage was higher than the effect of fertilization and nutrient availability. Thirdly, many AMF species group together with the organic carbon, total nitrogen and available K vectors, opposite to the tillage vector, or at least on the same side, while only a few species, such as *Fu. fragilistratus* and *Pa. dominikii*, are directed together with cultivation intensity and thus with the tilled soils CE, CM and CI. None of the species clustered with fertilization land use intensity, but several species, such as *Do. bernensis*, *Do. aurea*, *Gl. badium* and *Rh. invermaium* cluster rather opposite to these latter vectors than to tillage intensity.

3.6. Indicator species analyses

AMF indicator species could be called those that are almost exclusively occurring under reduced-tillage or tillage, or those that are almost exclusively present under low or medium or high fertilization (Table 4; Figs. 3-4). The indicator species analysis according to Dufrêne and Legendre (1997), resulting in significant or non-significant indicator values and *p*-values for each species, gave additional strong hints. Several AMF species as those shown in Fig. 5 have similar spore abundances in all treatments and may not have any indicator value for tillage or fertilizer inputs. Other species, such as *Sc. calospora* and *Se. nigrum*, although also equally distributed, but unequally abundant in different tillage and fertilizer levels, had significant indicator value (IV) and *p*-values (Table 6) for tillage, fertilization or even both parameters. Sixteen AMF species were considered indicators of reduced tillage, while only one species was indicator of conventional tillage (*Fu. fragilistratus*); five species were indicator of low fertilization and one was indicator of medium fertilization, and no species was indicator of high fertilization (Table 6). Most of these species were negatively affected by conventional tillage, while only a few were affected by fertilization levels.

3.7. Maize grain yields

The maize grain yields did not differ significantly among treatments (*p*-

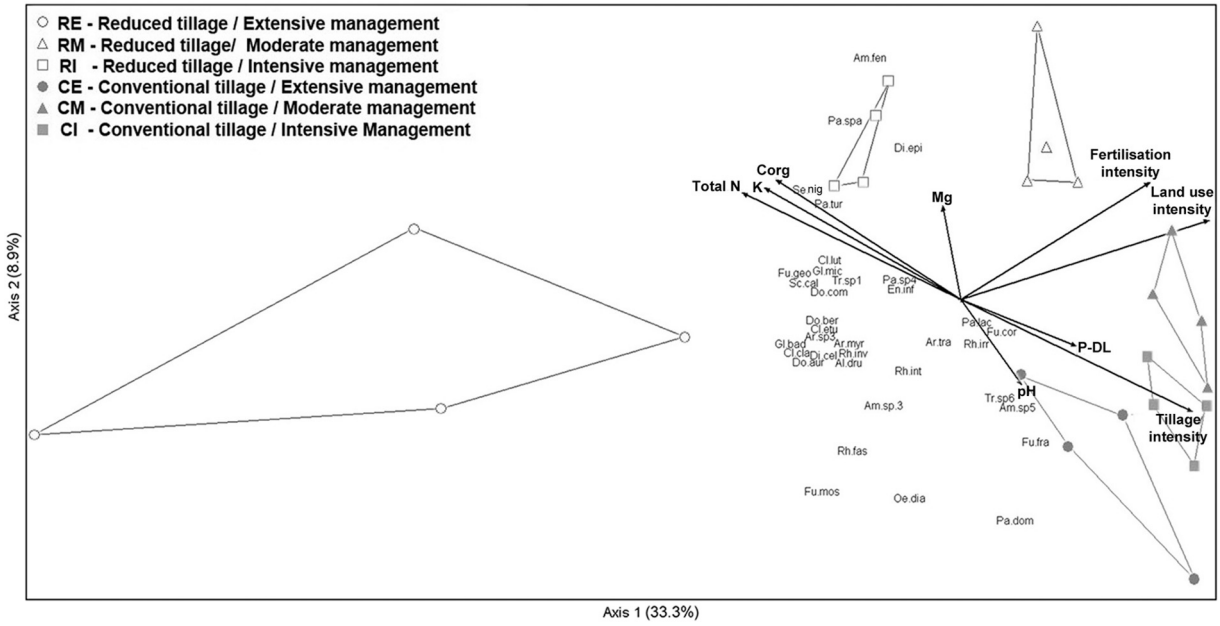

Fig. 2. Redundancy analysis (RDA) on the AMF species composition, considering the AMF spore populations in reduced till and conventionally tilled plots of different fertilization intensity in a 23-years field experiment (Table 1). Site codes of the treatments are given in Table 1, nutrient availability codes are given in Table 3, and species codes are given in Table 4.

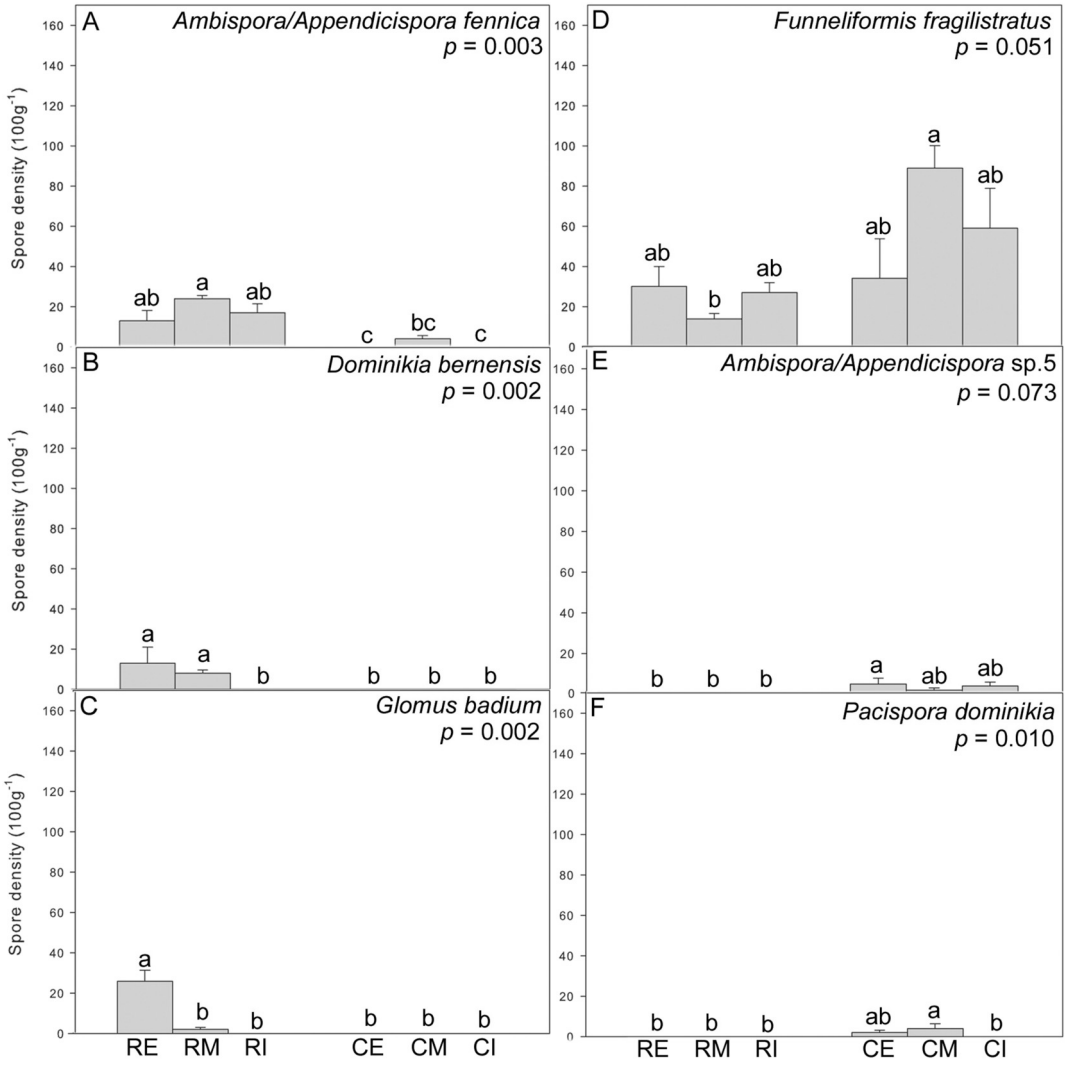

Fig. 3. Spore density (spores 100 g^{-1} soil) of AMF species negatively or positively affected by different tillage and fertilization practices. For testing the abundance of selected AMF species at all sites, the nonparametric Kruskal-Wallis test was chosen with Bonferroni adjusted *p*-values. Non-significant differences between differently managed plots are shown by identical miniscule letters above the corresponding columns.

value = 0.62), but presented the following order: RE (8.3 t ha^{-1}) < CE (9.1 t ha^{-1}) < CI (9.2 t ha^{-1}) < CM (9.3 t ha^{-1}) < RM (10.0 t ha^{-1}) < RI (10.2 t ha^{-1}).

4. Discussion

4.1. AMF in Chernozems

Up to 41 spores g^{-1} soil and 36 AMF species of 17 different genera were found in the long-term field experiment. These are unexpectedly high AMF spore and species numbers in this Calcic Chernozem soil under study, subjected to long-term agricultural cropping, higher than usually found in Central European Luvisols and Cambisols with similar land use and soil texture (e.g. in Regolsols, Luvisols and Cambisols; Oehl et al., 2003, 2010). Chernozems are counted to be the most fertile soils in Germany (Altermann et al., 2005), and it is likely that a high AMF spore density and species richness is a general characteristic for fertile European Chernozems, regardless of the former wide-spread assumption that such soils harbor only low AMF diversity. We know only one other recent set of studies performed in different types of Chernozems (according to the Canadian soil classification system), where up to 27 AMF species were found in cereal-cropped soils from Canada (Bainard et al., 2014). Of the four different Chernozem types, 'Black' Chernozems (most probably corresponding to typical Calcic Chernozems according to the IUSS/FAO classification) had the highest species richness, and 'Grey' Chernozems the lowest, although it was stated in that report that the diversity was not statistically different among soil types. In a similar study, 'Black' Chernozems from Canadian croplands hosted the largest numbers of AMF species (an average 29 AMF 'species' found in 23 croplands), identified as 'operational taxonomic units' (OTU, or so-called 'virtual taxa', derived from 'environmental soil sequencing' and subsequent molecular phylogenetic analyses) and almost twice the number of AMF sequences than obtained from 'Grey' Chernozems (an average 14 'species' from in total 7 fields; Dai et al., 2012). 'Brown' and 'Grey' Chernozems had lowest AMF richness as compared to the chemically more fertile two other soil types ('Black' and 'Dark Brown' Chernozems). The AM fungal communities of 'Black' and 'Dark Brown' Chernozem soils appeared to share some level of similarity. 'Grey' Chernozems differed most from the other Chernozem soils, indicating that soil types have distinct AM fungal community composition. Hence, indeed there are indications that very fertile and productive 'black' Chernozems in Germany and Canada have rich AMF species communities. It may well be that other soils like Vertisols, Cambisols or Luvisols (Bainard et al., 2014; Wetzel et al., 2014; Säle et al., 2015) may have similar or even higher AMF species richness and diversity, however, all AMF species richness depends on

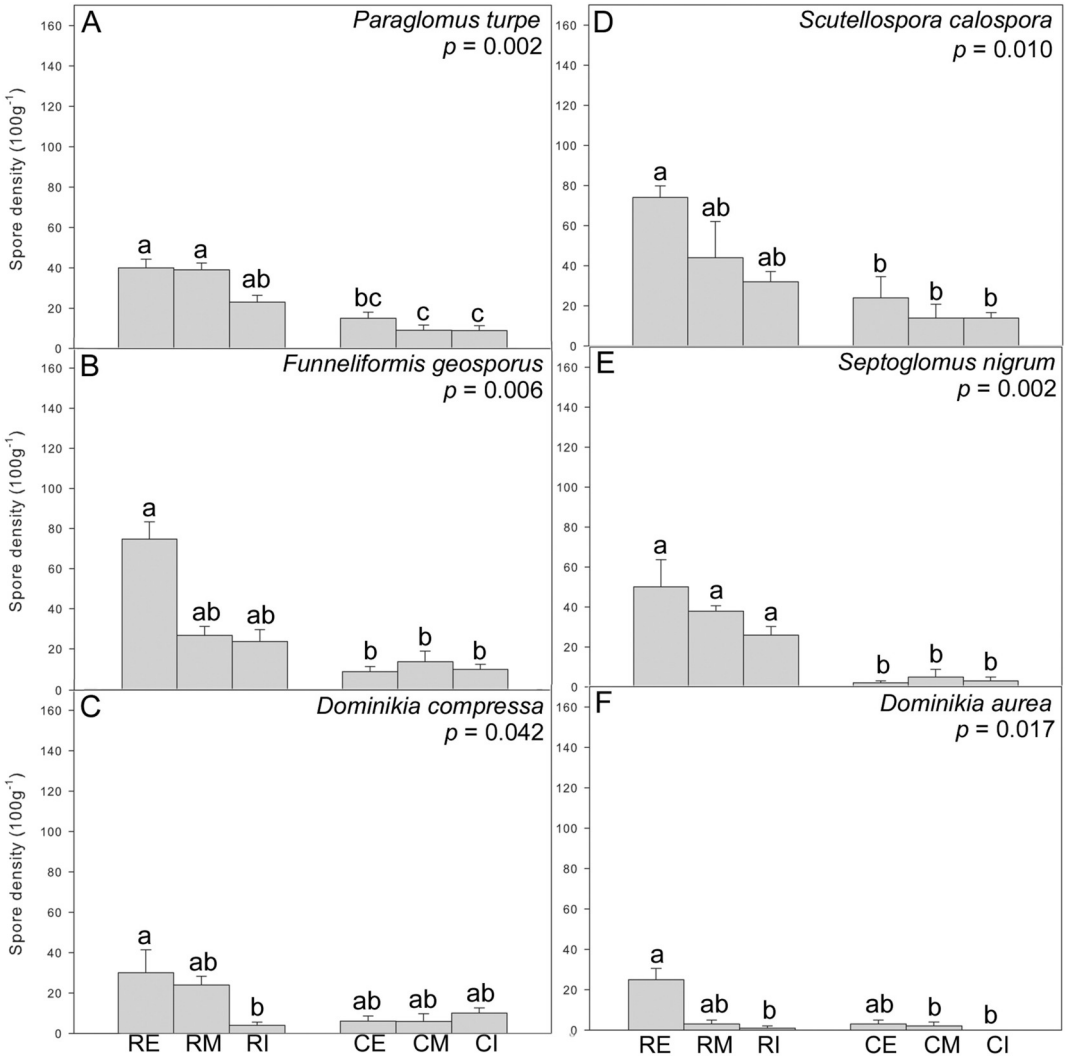

Fig. 4. Spore density (spores 100 g^{-1} soil) of AMF species affected by different tillage or fertilization practices, but present in all treatments tested. For testing the abundance of selected AMF species at all sites, the nonparametric Kruskal-Wallis test was chosen with Bonferroni adjusted *p*-values. Non-significant differences between differently managed plots are shown by identical miniscule letters above the corresponding columns.

the comparability of the ecosystems sampled. For example, differences in agronomic cropping can have a significant negative impact on the biodiversity of AMF as shown in our investigation, so that general conclusions on soil taxonomic classes, concerning AMF species richness, cannot be easily taken.

4.2. Soil tillage and N fertilization effects

Highest AMF spore density and AMF species richness were found in the reduced tillage systems with low and moderate, mainly N-fertilization in maize. This is in accordance with other studies from other soil types in Europe (Jansa et al., 2002; Alguacil et al., 2008, Brito et al., 2012; Maurer et al., 2014; Wetzel et al., 2014; Säle et al., 2015,). No-till appeared to contribute to higher root colonization by AMF and in consequence better crop nutrition, water relations and crops yield (Alguacil et al., 2011). The major contributing factor for the reduced spore abundance in conventional tillage systems tends to be the disruption of hyphal networks and dilution of AMF propagules through ploughing (Kabir and Koide, 2000).

Previous studies showed that intensifying the land use by monocropping and increasing the fertilization practice can also have a detrimental effect on AMF species diversity (e.g. Oehl et al., 2003, 2011a; Lumini et al., 2011; Walder et al., 2012). Remarkably, the differences between low-input and high-input systems were much lower in our Calcic Chernozem under investigation than in Central European Regosol, Luvisol and Cambisol soils under maize production and similar soil pH and texture (Oehl et al., 2003, 2010).

In our study, the three reduced tillage treatments grouped rather distant from each other thus explaining the variation of AMF community to a high extend, while the three ploughed treatments grouped close together. Furthermore the variation for soil tillage type, fertilization intensity, organic carbon, and total nitrogen was much higher than for available nutrients, and in particular for available P and Mg. These findings suggest that the effect of soil tillage by ploughing on the AMF community was much more pronounced than reduced tillage, fertilization and nutrient availability impacts. This finding is in accordance with Säle et al. (2015), who analyzed different tillage and fertilization systems in clayey Cambisol in Switzerland. In croplands, reduced or conventional tillage practices are linked with improved soil quality, carbon retention and higher microbial biomass (Anderson et al., 2017). Tillage distributes carbon and nitrogen throughout the soil profile and negatively affects microbial respiration and carbon content of the soil (Singh et al., 2010). Reduced tillage may favor stable aggregate structure and improve soil porosity and water conservation, too (Busari et al., 2015). There is increasing evidence that under reduced tillage practices also diversity of bacterial and overall fungal diversity is

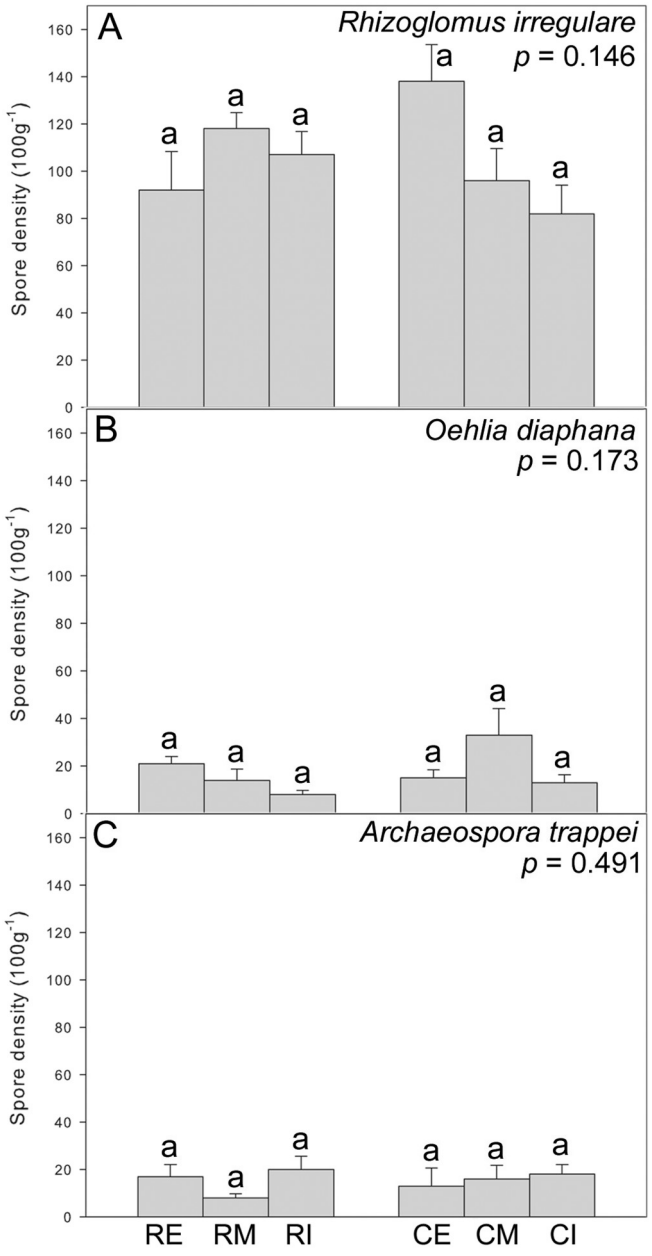

Fig. 5. Spore density (spores 100 g^{-1} soil) of three selected AMF species apparently not affected by tillage or fertilization level. For testing the abundance of selected AMF species at all sites, the nonparametric Kruskal-Wallis test was chosen with Bonferroni adjusted *p*-values. Non-significant differences between differently managed plots are shown by identical miniscule letters above the corresponding columns.

greater than in tillage cropping systems (Anderson et al., 2017).

4.3. "Dominant", "generalist" and "specialist" AMF species

Some AMF species were "generalists" (sensu the concept of Oehl et al., 2003, 2010), since they occurred abundantly both in the reduced and conventional tillage systems. These generalists (with > 70% frequency in different treatments) were represented by *Fu. mosseae, Rh. irregulare, Oe. diaphana, Ar. trappei, and Cl. claroideum. Funneliformis* spp., *Rh. irregulare* and *Claroideoglomus* spp. were also frequently found in fertile "Black" and "Dark Brown" Chernozem soils in Canada, although the method of AMF identification compared to that used by us differed (Dai et al., 2012; Bainard et al., 2014). Further, some of these

Table 6
Indicator species for different tillage systems and fertilization levels in the present study.

AMF species	Indicator value (IV)	*p*-Value
Reduced tillage		
Am. fennica	**85.3**	**0.0001**
Archaeospora sp.3	**54.9**	**0.0170**
Cl. claroideum	**60.0**	0.0560
Cl. luteum	**70.7**	**0.0111**
Cl. etunicatum	**66.5**	**0.0161**
Di. celata	**55.9**	**0.0112**
Di. epigaea	**67.9**	**0.0035**
Do. aurea	**49.8**	0.0569
Do. bernensis	**58.3**	**0.0049**
Do.compressa	**66.5**	**0.0404**
Fu. geosporus	**79.2**	**0.0002**
Gl. badium	**50.0**	**0.0139**
Gl. microcarpum	**75.0**	**0.0139**
Pa. spainiae	**72.5**	**0.0034**
Pa. turpe	**75.6**	**0.0001**
Sc. calospora	**73.2**	**0.0010**
Se. nigrum	**91.9**	**0.0001**
Tricispora sp.1	**47.4**	0.0582
Conventional tillage		
Fu. fragilistratum	**71.9**	**0.0056**
Pa. dominikii	**33.3**	0.0937
Ambispora sp.5	**33.3**	0.0987
Low fertilization		
Cl. claroideum	**57.1**	**0.0075**
Cl. etunicatum	**51.5**	**0.0396**
Di. celata	**46.9**	**0.0462**
Do. aurea	**61.8**	**0.0083**
Sc. calospora	**50.5**	**0.0244**
Medium fertilization		
Pa. laccatum	**60.3**	**0.0027**
High fertilization		
–		

Species with IV > 30% and significant *p*-value (< 0.05 in bold, < 0.10 in regular case) based on numbers of identified spores; Dufrêne and Legendre, 1997).

generalist species were also found in previous studies performed in Central Europe (Błaszkowski, 1993; Oehl et al., 2010, 2011a; Jansa et al., 2014), so generalists are not soil type or tillage dependent. However, dominant species, considering species with abundance higher than 20% of spore number within the community, were only *Fu. mosseae* and *Rh. irregulare* in our study. Because not identified on a species level, it is difficult to compare our results with those of Zhu et al. (2016) who identified three dominant OTU's ('virtual taxa') belonging to Glomerales in the maize rhizosphere of a typical 'black soil (Chernozem)' in northeast China, indicating that these OTUs likely occupied broad ecological niches in the maize rhizosphere (Zhu et al., 2016).

Some species, so-called AMF "specialists" (sensu Oehl et al., 2003, 2010) were exclusively found in reduced tillage, such as *Di. epigaea, Di. celata, Gl. microcarpum, Do. bernensis, Gl. badium,* and *En. infrequens*. Also *Se. nigrum* and *Sc. calospora* were more abundant under reduced tillage, which is in accordance with two studies in sandy-loamy respective clayey Cambisols from Switzerland (Maurer et al., 2014; Säle et al., 2015). Three other AMF "specialists" occurring at low frequency were well adapted to conventional tillage and even detected only under those conditions: *Pacispora dominikii, Ambispora* sp. 6 *and Tricispora* sp.6. To our knowledge, the latter two species have not been detected so far in Central Europe or elsewhere, while *P. dominikii* was already reported to be more frequent in croplands than in grasslands (e.g. Oehl et al., 2005). Furthermore, our data show that within this field trial the majority of the AMF species are responding more to reduced tillage management rather than to soil chemical properties, and only a few species, such as *Fu. fragilistratus* and *Pa. dominikii*, appear to be more

adapted to high cultivation intensity and tillage by ploughing.

4.4. AMF indicator species

The concept of indicator species is well known for plants growing on specific soils or in particular ecosystems or environments. General literature defines: “an indicator species is an organism whose presence, absence or abundance reflects a specific environmental condition”, or: “indicator species are plants and animals that, by their presence, abundance, lack of abundance, or chemical composition, demonstrate some distinctive aspect of the character or quality of an environment” (http://science.jrank.org/pages/3553/Indicator-Species.html#ixzz5LbNYgmKt; Heink and Kowarik, 2010). As far as we know, the concept of indicator species was first used in AM-research by Antoninka et al. (2011) in differently treated temperate grasslands and adopted e.g. by Silva et al. (2014, 2017) for arid to humid areas in tropical Brazil and for coastal mainlands and islands, respectively, that differed significantly in AMF species composition. For agricultural lands with reduced conservation tillage and with conventional tillage, Pontes et al. (2017b) identified indicator species from tropical savannas. AMF indicator species are not necessarily “specialists”, although there may be some overlap. In the Chernozem soil of the present study, we identified several indicator AMF species for reduced tillage (e.g. *Am. fennica*, *Do. bernensis* and *Se. nigrum*), reduced fertilizer inputs (e.g. *Do. aurea*) or for reduced tillage and low fertilizer intensity (e.g. *Cl. etunicatum*, *Di. celata* and *Sc. calospora*), but only a few for tillage by ploughing (e.g. *Fu. fragilistratus* and *Pa. dominikii*), and not any species clearly for highest fertilization level. Our Chernozem soil is not comparable with the Brazilian Ferralsols that, in addition to having different chemical and physical characteristics, have totally different AMF species compositions. Tropical and subtropical Ferralsols are rich in Acaulosporaceae and Gigasporales species that are not so frequent in Central European soils of slightly acidic to neutral soil pH (see also Wetzel et al., 2014, or Oehl and Koch, 2018). Hence, it appears that indicator species for tillage systems should be identified for each soil type and climatic condition separately.

Our results of maize yields may indicate that both is possible: i) high yields under lower AMF diversity with high relative abundance of effective species (*Fu. mosseae*, *Oe. diaphana* and *Rh. irregulare* are known to be physiologically very active (e.g. Säle, 2018) under conventional ploughing, ii) high fertilization can be compensated by broad AMF biodiversity and specific indicator species in extensive tilled systems. A first approach to estimate ecosystem functions of AMF communities was achieved by Köhl et al. (2014) showing that AMF communities from different tillage systems can change plant productivity, and AMF communities of non-tilled soils enhance plant P uptake.

5. Conclusions

Unexpectedly high AMF species richness and diversity were found in the highly productive Chernozem cropland under study, even under high-input conditions. This finding suggests a much higher significance of AM fungi in highly productive croplands than assumed so far. Several indicator AMF species were identified for reduced tillage, reduced fertilizer inputs or for both. Although such AMF indicator species have been identified, they should be verified for each soil type, climatic condition, land use intensity and cropping system separately, as those should be completely different for instance in nutrient-poor or in acidic soils, in soils of warmer or colder as well as of more humid or arid climates. Separate physiological studies could then identify which dominating or indicator AMF species are physiologically the most effective or whether there are also AMF species, which just found their specific ecological niches for reproduction under specific agronomic environments without any support of crop productivity.

Acknowledgements

F.O. acknowledges SNF for continuous support (projects 315230_130764, IZ73Z0_152740 and IZ76Z0_173895).

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