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RESEARCH ARTICLE

Infectivity and symbiotic efficiency of native arbuscular mycorrhizal fungi from high-input arable soils

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Abstract

Background Arbuscular mycorrhizal (AM) fungi are ubiquitous plant symbionts and an important biotic component of natural and agricultural soils. Yet we have only limited knowledge about the symbiotic functioning of native AM fungal communities in soils from high-input agricultural systems, where mycorrhiza can be suppressed by over-fertilization, tillage and other practices.

Aims and Methods We therefore conducted a greenhouse bioassay to examine the functioning of mycorrhizas established by native AM fungal communities from 28 conventionally managed arable soils. Their infectivity and potential to promote plant growth and nutrient uptake were evaluated in comparison to non-mycorrhizal controls and to a highly infective reference isolate, using leek (*Allium porrum*) as indicator plant. Mycorrhizal effects on soil water-stable aggregation (WSA) were determined as a proxy for an ecosystem benefit of mycorrhizas.

Results Root colonization by AM fungi as well as their effect on plant performance were negatively related to P availability as the most influential factor across the analysed gradients of soil conditions. Significant positive plant growth response to mycorrhiza was found only in a small subset of the soils, while positive effects on P uptake were more frequent and more pronounced. Root colonization and mycorrhizal growth response were higher after inoculation with the reference isolate than with the native AM fungal communities. Mycorrhiza-induced changes in WSA were significantly related to the plant mycorrhizal growth response.

Conclusions The results suggest that native AM fungal communities may improve plant growth only in a small subset of conventionally managed arable soils, whereby their effect can be limited by suboptimal colonization potential.

Keywords Arable soil · Native arbuscular mycorrhiza · Benefit · Leek · Phosphorus · Bioassay

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Introduction

Arbuscular mycorrhizal (AM) fungi (phylum *Mucoromycota,* subphylum *Glomeromycotina*) are root-associated symbionts of most terrestrial plant species (Spatafora et al. 2016) including almost all important crops (Verbruggen and Kiers 2010). In addition to improving plant nutrition and stress resistance (Smith and Read 2008) in exchange for photosynthetically fixed carbon (C), they contribute to a range of soil-related ecosystem services such as soil aggregate stabilization or prevention of nutrient losses (Cavagnaro et al. 2015; Lazcano et al. 2014; Wu et al. 2015). For this reason, they are regarded as an important component of agroecosystems and may play an important role in their transformation towards higher sustainability.

Despite the generally mutualistic character of arbuscular mycorrhiza, very diverse plant responses to colonization with AM fungi have been reported from specific conditions, ranging from highly positive to negative (Johnson et al. 1997; Klironomos 2003; Smith and Smith 2012; Tawaraya 2003). The performance of a single isolate or an AM fungal community can be described by their root colonization rate (i.e., ability to colonize the root system of the host plant) and by their symbiotic efficiency (i.e., the capacity to promote plant growth via improved mineral nutrition and tolerance to environmental stresses) (Avio et al. 2006; Jakobsen et al. 2002). Soil fertility is considered a major determinant of the symbiotic efficiency of AM fungi, and the trade balance model, which considers the interactive effects of C, phosphorus (P) and nitrogen (N) availability, predicts the exchange between plants and fungi under specific soil conditions (Johnson 2010; Johnson et al. 1997). Given that P-limited conditions are the most favourable for mutualistic mycorrhiza function and high P and N availability in soil detrimental (Johnson et al. 2015), the importance of AM fungal communities in intensively managed arable soils (from now on "arable soils") is disputable. Many studies in agricultural soils suggest that mycorrhizas contribute to growth and yield (Baum et al. 2015; Köhl et al. 2016; Pellegrino et al. 2015), enhance pathogen resistance (Wehner et al. 2010) and protect against herbivory (Bennett et al. 2009) or drought (Augé 2001). Many others, however, showed little effect of arbuscular mycorrhiza on crop productivity (Farmer et al. 2007; Köhl et al. 2014; Verbruggen et al. 2012a) or even revealed negative effects on plant growth (Ryan et al. 2005). A recent review by Ryan and Graham (2018) concluded that there is not enough evidence to specifically focus management of mycorrhizas in arable soils since the benefits of the symbiosis in crop production may be negligible as compared to other agronomic practices. Yet, the contribution of AM fungi to important ecosystem functions may be another motivation to promote them in arable soils (Kohler et al. 2017; Powell and Rillig 2018; Rillig et al. 2019), eventhough not agronomically relevant. Soil aggregation tends to increase with the density of AM fungal extraradical mycelium (ERM) (Haynes and Beare 1997) because AM fungi mediate the stabilization of aggregate structure (Daynes et al. 2013; Tisdall and Oades 1982).

AM fungi are usually present in arable soils, but they can be expected to benefit host plants in the most P-deficient soils only (Johnson et al. 1997; Johnson 2010). Agronomic practices negatively affect local AM fungal communities, decrease their abundances and diversity compared with undisturbed ecosystems (de Graaff et al. 2019; Gosling et al. 2006; Johnson 1993; Oehl et al. 2003). Overfertilization, for instance, increases P availability and makes mycorrhiza superfluous to crops, the host plant reduces the pool of C available to the fungi and their development in soil and roots (Lekberg et al. 2008; Liu et al. 2012). Tillage, on the other hand, decreases the infective potential of AM fungi in soils by disturbing the networks of ERM, the main source of inoculum in most soils (Sylvia 1992). Because root colonization by AM fungi is an important factor for mycorrhizal benefits (Lekberg and Koide 2005; Treseder 2004), lower infectivity of AM fungi in arable soils may decrease them regardless of soil conditions. Additionally, the symbiotic efficiency of AM fungi in arable soils has been suggested to decrease through selection of less mutualistic phenotypes, which can persist in root systems and soils even if not contributing to plant nutrition (Johnson 1993; Johnson and Gibson 2021; Verbruggen and Kiers 2010). Along these lines, agronomic practices can also indirectly affect soil aggregate formation by changes in the development and functioning of AM fungal communities (Bronick and Lal 2005).

While the infectivity and taxonomic composition of native AM fungal communities of arable soils have been systematically explored (e.g., Jansa et al. 2014; Oehl et al. 2003; Verbruggen et al. 2010, 2012b), their symbiotic efficiency has been much less targeted. Some

inoculation experiments, which explored the effect of external additions of AM fungal propagules into arable soils, suggest limitation of mycorrhizal benefits to crops by suboptimal colonization potential of native AM fungi (Cely et al. 2016; Köhl et al. 2016; Pellegrino et al. 2015). Absence of inoculation effects (e.g., Bender et al. 2019; Farmer et al. 2007; Li et al. 2021), on the other hand, can be explained either by high symbiotic efficiency of native AM fungal communities or by non-functional mycorrhiza in the given soil due to the soil nutritional characteristics or a range of other factors (Ryan and Graham 2002, 2018). Our knowledge on the symbiotic efficiency of native AM fungal communities of arable soils is, however, limited, because it has been directly focused only by a few studies, usually based on a low number of soils (Johnson 1993; Johnson et al. 2015; Martinez and Johnson 2010; Verbruggen et al. 2012a).

The main goal of our study was therefore to evaluate the potential of native AM fungal communities in arable soils to benefit their host plants in terms of nutrition and growth, as well as the soil environment, in terms of soil aggregation. In order to identify influential factors, we screened, in a greenhouse bioassay, AM fungal communities in their respective arable soils using leek as an indicator plant. Its growth and nutritional responses to inoculation with the native AM fungi were determined in relation to non-mycorrhizal controls and compared to responses to inoculation with a highly infective reference AM fungal isolate. We hypothesized that: 1) positive mycorrhizal effects on plant performance will increase with decreasing P availability in soil; 2) the ability of the native AM fungal communities to confer the benefits will be limited by their lower colonization potential, as compared to the reference; 3) soil aggregation will be improved in the mycorrhizal treatments and related to the density of ERM in soil.

Materials and methods

Experimental design

Soils collected from 28 maize fields were sterilized and used to establish three treatments differing in inoculation with AM fungi: 1) inoculated with the native AM fungal community of the given field (NAT); 2) inoculated with a reference isolate from a culture collection (REF); and 3) without AM fungal inoculation (NM). Each treatment was replicated 5 times, summing up to 15 pots per field and a total of 420 pots. Leek (*Allium porrum* L., var. Elefant) was selected as a host plant for the bioassay based on its high mycorrhizal responsiveness (Hepper et al. 1988; Jansa et al. 2008), small size enabling unrestricted growth in feasible pot size and compatibility with the conditions of agricultural systems.

Selection of the soils and sampling

The twenty-eight fields were selected to represent the most widespread soil type and the dominant agricultural management practices in the region. About 120 fields were pre-selected in three departments of Bohemia (Czech Republic) based on the public Land-Parcel Identification System (LPIS, http://eagri.cz/public/app/lpisext/lpis/verejny2/plpis/) and soil monitoring data from the Central Institute for Supervising and Testing in Agriculture (UKZUZ). The criteria were: 1) Cambisols as the regionally dominant Reference Soil Group (WRB 2015), at least 30 cm deep, with less than 25% gravel/stone content; 2) flat land or slight slope of less than 7º. The larger set was subsequently narrowed down to the investigated fields by selecting only fields with maize as crop in the sampling season: All the fields were selected in a potato agricultural growing area where silage maize is sown at the end of April and harvested around mid-September. The common crop rotation is as follows: red clover, winter wheat, silage maize, spring barley, winter rape, winter wheat, potatoes and spring barley under-sown with red clover. The most frequent preceding crop, based on communication with the farmers, was winter wheat (15 fields), followed by maize (10 fields), potato (2 fields) and red clover (1 field). Tillage in autumn 2018 was conventional, i.e., stubble cultivation followed by ploughing to a depth of 20–30 cm either with manure application (19 fields) or without any fertiliser application. Presowing tillage (e.g., harrowing, rolling) was carried out in April 2019 with application of different mineral fertilizers (N, NP, NPK, possibly with addition of Mg, Ca, S and Zn) or mineral fertilizers in combination with organic fertilizers (digestate and liquid phase of digestate). In order to increase the likelihood of including fields with functional AM fungal

communities, preference was given to fields with available-P (Mehlich III) lower than 80 mg kg^{-1}, according to the UKZUZ soil monitoring data (all fields except No. 17 and 51). This corresponds to categories "Low" and "Satisfactory" as delimited for Czech arable soils by Smatanová (2020). The main physico-chemical soil characteristics of the 28 selected fields as determined directly from the soil collected samples are shown in Table 1 and further details in Supplementary Table S1. The actual soil characteristics expectedly differed from the UKZUZ monitoring data (see Supplementary Fig. S1 for P), which are based on a different sampling approach and several years old for some of the fields.

The soils for the experiment were collected in May 2019 from the depth of 0–20 cm, at least 5 weeks after

Table 1 Main soil characteristics of the 28 arable soils under study

Field ID	P_{avail} [1] mg.kg^{-1}	N_{tot} [2] %	C_{org} [2] %	pH [3]	Mg_{avail} [4] mg.kg^{-1}	K_{avail} [4] mg.kg^{-1}	Ca_{avail} [4] mg.kg^{-1}	Des[5]
1	144	0.270	2.365	6.87	249	370	2526.0	2.1827
2	128	0.264	1.513	7.03	295	576	2236.5	2.0940
3	208	0.171	1.652	5.83	130	206	1179.0	2.2212
6	22	0.152	0.758	5.79	188	90	1594.0	0.5943
8	62	0.228	0.878	5.87	164	202	1505.0	2.4829
9	41	0.254	1.538	6.49	249	301	2103.0	1.9325
10	40	0.200	1.358	6.49	221	165	2589.0	0.3345
11	90	0.263	1.161	6.72	264	384	2490.0	1.0725
13	49	0.172	1.257	5.95	138	169	1383.0	0.1559
14	31	0.163	1.108	6.31	113	124	1842.0	1.8974
15	162	0.243	1.462	6.86	241	231	3315.0	1.4385
16	221	0.202	1.279	6.23	121	212	1517.0	1.2206
17	79	0.232	1.572	6.26	199	183	2269.5	0.4157
19	128	0.305	1.828	6.78	200	506	1580.0	2.5158
28	57	0.128	0.717	5.73	107	354	1277.0	1.1748
29	110	0.254	1.586	5.64	133	394	1234.0	1.8632
31	113	0.165	0.989	6.91	205	333	2130.0	0.9628
32	62	0.184	1.206	6.14	155	333	1450.0	1.0423
34	44	0.157	1.059	5.89	148	268	1448.0	1.2277
37	27	0.148	1.493	6.76	249	273	1995.0	1.3162
38	52	0.230	1.782	5.93	197	423	1471.0	1.4379
39	51	0.207	1.604	6.74	201	358	1845.0	1.4804
42	60	0.200	1.397	6.26	186	135	1797.0	3.1367
46	85	0.165	0.948	6.32	163	112	2001.0	1.2615
51	167	0.234	1.877	7.22	231	1802	1096.0	1.7525
53	136	0.270	2.014	5.85	207	359	1328.0	3.0250
58	78	0.168	0.858	6.64	223	186	2132.0	1.6923
59	126	0.249	1.498	5.75	257	459	1183.0	1.8589

[1] Plant-available phosphorus (Pavail) was extracted from the soil samples using the Mehlich 3 method (1:10 w/v sample/extraction agent ratio) and measured spectrophotometrically at 750 nm (Unicam UV-400) as phosphomolybdenum blue; [2] Total nitrogen (Ntot) and total carbon were analysed on a Flash 2000 analyzer (Thermo Scientific, USA). Organic carbon (Corg) was determined as difference to carbon values obtained after sample digestion with hydrochloric acid; [3] Soil pH was measured in deionized H2O (1:5 v/v sample/liquid ratio) using WTW Multilab 540 pH/mV meter; [4] Plant-available magnesium (Mgavail), potassium (Kavail) and calcium (Cavail) were extracted using Mehlich 3 (1:10 w/v sample/extraction agent ratio) and analysed by atomic absorption spectrometry (ContrAA 700, Analytik Jena, Germany); [5] Desiccation index is the ratio % sand / (% clay + % silt). Particle size fractions (% of clay, silt and sand) were determined by pipette method according to ISO 11277 (2009) as mass of three particle size fractions (clay < 0.002 mm, silt 0.002–0.05 mm, sand 0.05–2.00 mm)

sowing. Maize plants were emerging by the coleoptile (VE stage) or had a maximum of four leaves with fully developed leaf collar (V4 stage) (Ritchie et al. 1992). The final volume of soil per field (ca. 40 L) was a composite obtained from 5 points separated by 10 m on a transect orthogonal to the field margin, starting 20 m away from it. The collected soils were homogenized, and 3 L of each field soil were stored in a fridge (5 ºC) for later use as inoculum and for the preparation of bacterial filtrates. Subsequently, each soil sample was air-dried and sieved through a 4-mm sieve, a subsample was sieved through a 2-mm sieve for the determination of the physico-chemical characteristics. The remaining soils were sterilized by γ-irradiation (> 25 kGy) and stored at room temperature until the experimental set-up.

Experiment establishment and cultivation

Plastic pots (1 L, 11 cm diameter, 13 cm height) were first filled with 300 ml of sterile soil, then with a treatment-specific "inoculum layer" (as specified below), and with 200 ml of soil on the top.

To introduce the original soil microorganisms other than AM fungi into the sterilized soils in the two treatments, which did not receive the native microbial inocula, bacterial filtrates were prepared from each soil (Ames et al. 1987): the stored non-sterile soil was mixed with deionized water in 1:4 ratio (v:v), shaken for 1 h at 250 rpm and decanted through 150, 100 and 32 µm sieves. The final suspension was immediately mixed with the corresponding sterilised soil in the amount of 50 ml suspension per 1 L of soil, and the soils were incubated for 14 days at room temperature until the potting.

The inoculum for the REF treatments was prepared from 6-month-old cultures of *Rhizophagus irregularis* isolate PH5 with *Desmodium* sp. as host plant, grown in 2 L pots in a sand-zeolite mixture (1:1, v:v). *R. irregularis* is abundant in agricultural soils (Oehl et al. 2010) and a fast root colonizer (Pellegrino et al. 2011). Fast root colonization and high symbiotic efficiency has also been confirmed for the particular PH5 isolate (Blažková et al. 2021). For the preparation of the inoculum, the substrate of several cultures was wet-sieved and decanted, roots were cut to fragments of about 5 mm. The resulting suspension of mycelia, spores and chopped roots was checked under binocular microscope to verify the purity of the inoculum and a sufficient number of propagules (i.e., abundant mycelia, intraradical and extraradical sporulation). Later, 10 ml of the suspension was mixed with 400 ml of the incubated soil to prepare the inoculum layer of the REF treatment.

The inoculum layer of the NAT treatment was prepared by mixing 200 ml of the stored non-sterile field soil with 200 ml of sterile soil. Additionally, to compensate for the organic-matter amendment to the REF treatment with the inoculum suspension, 10 ml of autoclaved (twice 121 ºC for 30 min) "blank inoculum" suspension was added, which had been prepared in the same way as the inoculum suspension for the REF treatment. The inoculum layer of the NM treatment was prepared by adding 10 ml of the "blank inoculum" suspension to 400 ml of the incubated substrate.

Three leek seedlings were planted into each pot after 15 days of pre-cultivation in trays with autoclaved sand. The experiment was established at the end of September and cultivated for 7 weeks in standardized greenhouse conditions: heated greenhouse (temperature 18–30 °C) equipped with LED panels (EuledK 200HS, Euled s.r.o., Czech Republic) that provided supplementary lighting in broad spectrum of wavelengths resembling sunlight from 6:00 to 20:00 (14-h photoperiod). Photosynthetic photon flux density detected at plant level started and ended at ca. 250 µmol m^{-2} s^{-1} (supplementary light in mornings and evenings with no contribution of ambient light) and typically reached up to ca. 750 µmol m^{-2} s^{-1} past midday. Plants were watered daily according to their needs.

Harvest and data collection

At the harvest, shoots were separated from roots, dried at 65 ºC for 5 days and weighed to determine shoot and root dry weights per pot. Small portions of the dried shoots (0.5–1 g) were randomly subsampled and milled using a Retsch MM200 mill (Retsch GmbH, Haan, Germany) to determine the P and N concentrations in the shoots of the experimental plants. P concentration was evaluated by quantification of orthophosphate in a solution according to the malachite green method (Ohno and Zibilske 1991). N concentration was measured using a Flash EA 2000 elemental analyser

(Thermo Fisher Scientific, Waltham, MA, USA). P and N contents in shoots were then calculated (as a proxy of P and N uptake) by multiplying the concentrations by the shoot dry weight. Due to small biomass amounts in some treatments, the N shoot concentration was determined in the biomass of plants from a subset of 22 fields only, where three independent replicate samples were available per treatment, and only two replicates in the NM treatment of field No. 38.

To determine root colonization by AM fungi, roots were carefully washed with tap water, cut in fragments and conserved in 50% ethanol. Later, the roots were rinsed, covered by 10% KOH and stained with 0.05% Trypan Blue in lactoglycerol (Koske and Gemma 1989). The percentage of root colonization by hyphae, arbuscules and vesicles was microscopically estimated using the magnified intersection method (McGonigle et al. 1990), scoring 100 intersections per sample within 30 root segments of about 1.2 cm at 100 × magnification (Olympus BX60). A homogenised subsample of soil from each pot was extracted to determine the total length of extraradical mycelium (ERMt) using the modified membrane filtration technique (Jakobsen et al. 1992). Newly formed extraradical mycelium (ERMn) was calculated for each pot of the mycorrhizal treatments (NAT and REF) by subtracting from the ERMt value the mean value of the same parameter in the corresponding non-mycorrhizal treatment. Analysis of water-stable aggregates (WSA) was chosen as an indicator for the effect of the different treatments on soil quality (Amézketa 1999; Rillig and Mummey 2006). Soil samples with undisturbed soil structure were collected with a core sampler from each pot, air-dried and sieved to a fraction of 1–2 mm (Retch—ISO 3310–1). Pre-sieved aggregates were placed on a 0.25 mm WSA sieve device (Kemper and Rosenau 1986) and wet sieved in two solutions: (1) in demi H_2O for 3 min., gaining a water unstable fraction (m_u) and (2) in dispersion solution (3 mM sodium hexametaphosphate) for 6 min., gaining a water-stable fraction (m_s). The rest of the undisturbed aggregates and the soluble fraction were oven-dried (60 °C) for 24 h and weighted. The WSA was then calculated as means of $m_s/(m_s + m_u)$ of three independent sample replicates.

Statistical analyses

Percentage of root colonization by hyphae (RC) and by arbuscules (Arb) were rank transformed, percentage of vesicles (Ves) was ln transformed. Ratio of vesicles to arbuscules (Ves:Arb) was calculated as (Ves + 1) / (Arb + 1) due to the presence of 0 values in both parameters, and rank transformed. Mycorrhizal growth response (MGR) was calculated by the formula log(M/NM), where M is the shoot dry weight of a replicate mycorrhizal plant and NM is the mean shoot dry weight in the corresponding non-mycorrhizal treatment. This calculation of response conveniently renders positive values for increase and negative values for decrease. Analogously, mycorrhizal phosphorus response (MPR), mycorrhizal nitrogen response (MNR) and mycorrhiza-induced change in WSA (MAR) were calculated based on P shoot concentrations, N shoot concentrations and WSA.

The subsequently described analyses were all based on mean values per treatment obtained from the replicates per inoculation treatment × field. To provide an overview on the effects of inoculation treatment in the experiment, their overall effects were evaluated for all the parameters analysed. In case of plant performance (i.e., the plant parameters shoot dry weight, P and N shoot concentration, the N:P ratio in shoots), one-way ANOVA was used with inoculation treatment as a factor with 3 levels (NAT, REF and NM). Significant differences among the treatments were determined by Tukey's test at $p < 0.05$. Root colonization parameters (RC, Arb, Ves, Ves:Arb) and the mycorrhizal responses (MGR, MPR, MNR and MAR) were also analysed by one-way ANOVA, whereby the factor inoculation treatment had two levels (NAT, REF).

To provide a more differentiated view on plant performance including soil characteristics, pairwise Spearman's correlations were performed. Conveniently, the correlation matrix (Fig. 1) also provides information on the relationship of the different soil parameters among each other. For the responses to mycorrhiza (MGR, MPR, MNR) and fungal parameters (RC and ERMn), the role of soil parameters was addressed by general linear models (GLM). This approach has been selected because GLM account also for the relationship of the predictors, and mycorrhizal responses are more suitable to address the main questions of the

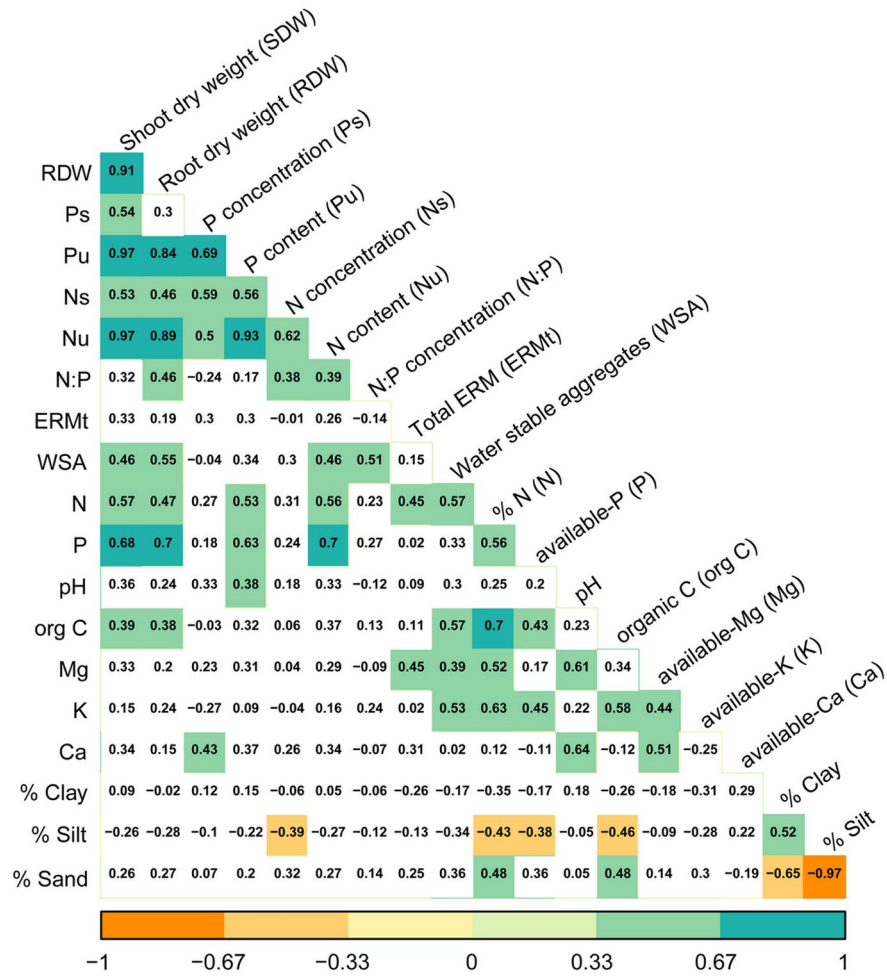

Fig. 1 Correlation matrix of plant parameters, soil characteristics, density of extraradical mycelium and water- stable aggregate formation in the treatment inoculated with native communities of arbuscular mycorrhizal fungi from the arable soils. For details on the determination of the soil characteristics see Table 1. Values show r values for individual pairwise Spearman's correlations. Dark/light green gradient highlight significant positive correlations while dark/light orange gradient highlight significant negative correlations. If not highlighted by colours, the correlation is not statistically significant (at $p = 0.05$)

experiment as compared to the basic plant parameters. The GLM included the main soil characteristics (as listed in Table 1) and inoculation treatment as categorical predictor with 2 levels (NAT, REF). The initial models included the interaction of inoculation treatment with each of the soil parameters. Complementarily, a general linear model was constructed to evaluate the effect of relevant mycorrhiza-related parameters (i.e., inoculation treatment, MGR and ERMn) on MAR. To obtain the final models, the Akaike Information Criterion (AIC) was used to select the most parsimonious model by stepAIC() function in R package "MASS" (Zhao et al. 2005).

All statistical analyses were conducted using the software R 1.4.1106 (R Development Core Team 2011).

Results

Main patterns of plant growth and nutrition

To provide an overview of the studied system across all the arable soils, a correlation matrix in Fig. 1 shows relationships between the plant parameters, as determined in plants inoculated with the native communities, and the characteristics of the 28 field soils. Shoot biomass was tightly positively correlated with root biomass and the P and N contents in shoots. Nutrient contents and concentrations of both nutrients in shoots were also positively correlated with each other. Regarding the soil parameters, main (positive) correlations were recorded for total soil N, available-P, organic C, Mg and K. Plant biomass and nutrient

contents in shoots, but not the nutrient concentrations, were correlated with total soil N and available-P.

Inoculation had no overall effect on plant biomass across all fields (Table 2). However, P concentration in shoots was significantly higher and the N to P ratio in shoots significantly lower after inoculation with the native communities (NAT) and the reference isolate (REF) as compared to the non-mycorrhizal plants. On the other hand, N concentration in shoots was higher in NAT-inoculated plants as compared to REF-inoculated and non-mycorrhizal plants. Mean values of the plant parameters per field and inoculation treatment are listed in Supplementary Table S2.

Fungal development in the inoculated treatments

The percentage of root colonization by hyphae ranged between 0.2 and 84% in NAT-inoculated plants and between 10.6 and 89.2% in REF-inoculated plants (for mean values per inoculation treatment and field see Supplementary Table S2). Hyphal root colonization was directly correlated with the frequency of arbuscules ($R^2=0.99$, $p<0.001$; 0.2 to 82.6% in NAT and 9.4 to 82.6% in REF) and with the frequency of vesicles ($R^2=0.29$, $p<0.001$; 0 to 12% in NAT and 1.8 to 21.2% in REF). No mycorrhizal structures were found in the non-inoculated plants, and all colonization parameters were significantly lower in NAT plants than in REF plants across all the soils (Table 3). As percentage of vesicles was six-fold higher in REF-inoculated plants than in NAT-inoculated plants, the REF isolate had a significantly higher ratio of vesicles to arbuscules compared to the fungal communities colonizing the roots of the NAT-inoculated plants (Table 3). The newly formed ERM did not significantly differ between pots with the NAT communities and with the REF isolate (Table 3), and no correlation was found between newly formed ERM and root colonization (analysis not shown).

Root colonization by hyphae was influenced mainly by available-P and also by inoculation treatment and pH (Table 4). The root colonization decreased with increasing available-P despite high

Table 3 Summary of arbuscular mycorrhizal (AM) fungal parameters per inoculation treatment across all the studied soils. The parameters are given only for the two treatments, which were inoculated with AM fungi: NAT (inoculated with the native AMF communities from the arable soils) and REF (inoculated with a reference isolate)

	df	F	p	NAT	REF
Hyphae (%)	1	6.171	0.016	45.20 ± 2.50	61.20 ± 2.10
Arbuscules (%)	1	4.317	0.043	43.70 ± 2.40	56.80 ± 2.00
Vesicles (%)	1	67.743	< 0.001	2.40 ± 0.30	12.60 ± 0.70
Ves:Arb	1	33.878	< 0.001	0.14 ± 0.02	0.26 ± 0.02
ERMn ($m.g^{-1}$)	1	1.242	0.270	1.07 ± 0.08	0.91 ± 0.08

The parameters are root colonization by hyphae, arbuscules and vesicles; ratio of vesicles to arbuscules (Ves:Arb) and newly formed extraradical mycelium in soil (ERMn). Values are means ± SE, F and p-values are given according to one-way ANOVA

Table 2 Summary of selected plant and soil parameters per inoculation treatment across all the studied soils. The inoculation treatments are NAT (inoculated with the native arbuscular mycorrhizal fungal communities from the arable soils), REF (inoculated with a reference isolate) and NM (non-inoculated control)

	df	F	*p*-value	NAT		REF		NM	
SDW (g)	2	2.654	0.077	0.39 ± 0.02	a	0.46 ± 0.02	a	0.35 ± 0.02	a
RDW (g)	2	1.478	0.234	0.06 ± 0.00	a	0.08 ± 0.01	a	0.08 ± 0.01	a
Ps ($mg.g^{-1}$)	2	16.198	< 0.001	3.14 ± 0.07	a	2.99 ± 0.08	a	1.99 ± 0.09	b
Ns ($mg.g^{-1}$)	2	9.004	< 0.001	45.70 ± 0.62	a	42.52 ± 0.76	b	40.87 ± 0.71	b
N:P	2	9.385	< 0.001	14.68 ± 0.38	b	14.58 ± 0.59	b	20.62 ± 0.83	a
ERMt ($m.g^{-1}$)	2	23.891	< 0.001	2.43 ± 0.09	a	2.23 ± 0.09	a	1.39 ± 0.06	b
WSA	2	0.99	0.376	0.18 ± 0.00	a	0.19 ± 0.00	a	0.17 ± 0.00	a

The parameters are shoot dry weight (SDW), root dry weight (RDW), P and N concentrations in shoots (Ps, Ns), N to P ratio in shoots (N:P), total extraradical mycelium (ERMt) and proportion of water-stable aggregates (WSA). Values are means ± SE, F and *p*-values are given according to one-way ANOVA. Significant differences between the treatments at $p=0.05$ according to Tukey's test are indicated by letters beside the values. Values within row which share the same letter are not significantly different

variability in the data particularly at intermediate P values. Interestingly, the difference between REF and NAT (i.e., "infectivity gap") increased at higher P-levels (Fig. 2a). In fact, when available-P and inoculation treatment were tested as the only two predictors of root colonization, available-P had a significant effect ($F=68.87$, $p<0.001$) together with the interaction of the factors ($F=4.71$, $p=0.031$). Consistently with the significant effect of available-P and non-significant effect of soil N, root colonization was differentiated according to P availability, while no pattern was apparent at the N availability gradient (Fig. 3a).

Newly formed ERM was significantly, but weakly affected by total N and available Mg, the latter also in interaction with inoculation treatment (Table 4). The length of newly formed ERM significantly increased with soil N in the NAT treatment, but the relationship was weaker than for those of hyphal root colonization and available P, and no relationship was observed in the REF treatment (Fig. 2b).

Plant mycorrhizal responses to inoculation

An overview of specific mycorrhizal responses within the set of 28 arable soils is shown in Supplementary Fig. S2. In NAT inoculated plants, growth response ranged between -0.36 and 0.78 (mean values per treatment), and was significantly positive (i.e., the NAT-inoculated plants had significantly higher biomass than non-mycorrhizal plants) in less than half of the soils (11 out of 28). Response to NAT inoculation in N shoot concentration (between -0.12 and 0.27) was significantly positive only in 4 out of 22 soils, while response in P shoot concentration was overall higher (between -0.07 and 1.19), and significantly positive in more than half of the soils (18 out of 28).

Across all the analysed soils, REF inoculation induced a significantly higher growth response than NAT inoculation, while NAT-inoculated plants led to a significantly higher change in N concentration than REF inoculation. No difference between the inoculation treatments was found for the change in P concentration (Table 5).

Multiple linear regression models revealed that mycorrhizal growth response was affected by P availability in soil (as the most influential factor), organic C, total N and inoculation treatment (Table 4). The growth response decreased along with increasing available-P, whereby higher variability in responses is apparent at low P availability (Fig. 2c). The difference between NAT and REF plants (i.e., "benefit gap") was higher at lower P availability. The mycorrhizal response of P concentration was affected by P availability only, while that of N concentration was significantly, but weakly affected by pH and Inoculation (Table 4). Mycorrhizal growth response was

Table 4 Effect of inoculation treatment (Inoculum: native communities and the reference isolate), selected soil characteristics and their interactions on plant responses to mycorrhiza and on main arbuscular mycorrhizal fungal parameters

Factors		MGR		MPR		MNR		Hyphae		ERMn	
	df	F	p	F	p	F	p	F	p	F	p
Inoculum	1	5.38	0.025			4.84	0.034	6.45	0.014	1.21	0.276
N	1	4.39	0.041							5.43	0.024
P	1	32.59	< 0.001	42.15	< 0.001			30.90	< 0.001		
Organic C	1	5.57	0.022			1.99	0.167			2.94	0.093
Mg	1					2.17	0.149			6.04	0.018
pH	1					5.10	0.030	5.44	0.024	3.56	0.065
Desiccation index (*)	1			3.31	0.074	1.94	0.171				
Inoculum × Organic C	1	2.31	0.134								
Inoculum × Mg	1									6.36	0.015
Inoculum × pH	1									2.48	0.122
Total df		55		55		43		55		55	

The analysed parameters are mycorrhizal growth response (MGR), mycorrhizal response of phosphorus and nitrogen concentration in shoots (MPR, MNR), root colonization by hyphae (Hyphae) and newly formed extraradical mycelium in soil (ERMn). The soil parameters are detailed in Table 1. F and *p*-values are given according to the most parsimonious general linear model, based on Akaike information criterion (AIC)

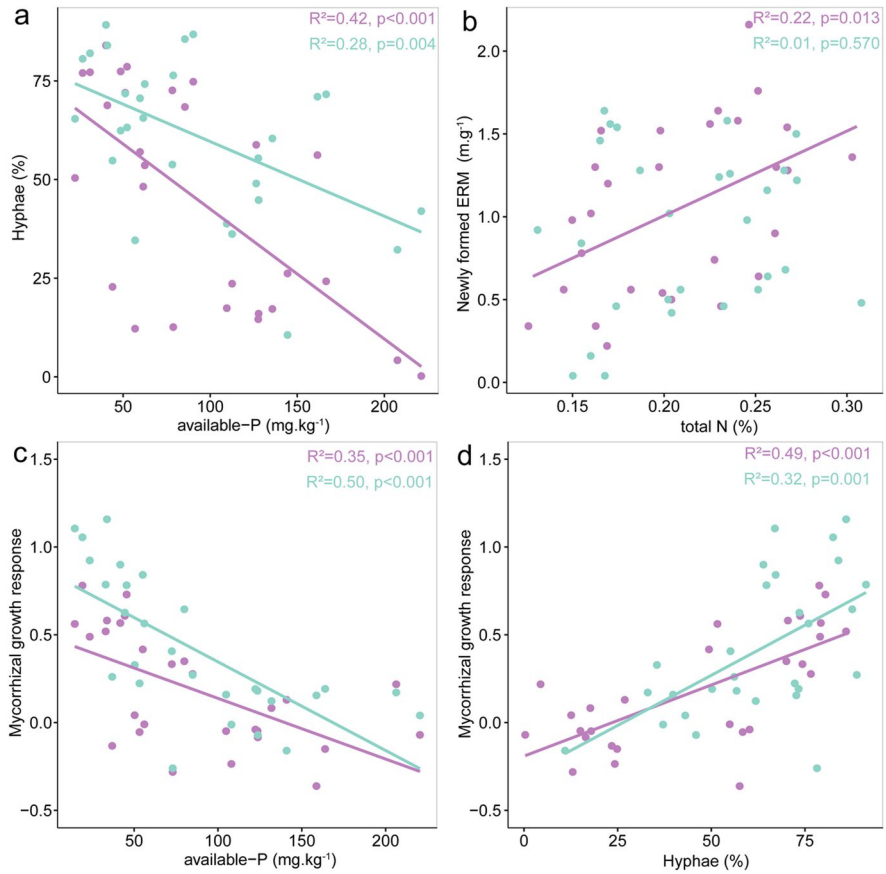

Fig. 2 Relationships between root colonization by hyphae and soil available-P (**a**), between newly formed extraradical mycelium and total N in soil (**b**), between mycorrhizal growth response and available-P (**c**) as well as between mycorrhizal growth response and root colonization by hyphae (**d**). The relationships are given separately for the treatments inoculated with native communities of arbuscular mycorrhizal fungi from the arable soils (NAT, purple dots) and the treatments inoculated with the reference isolate (REF, light-blue dots). Dots are mean values per soil ($n = 5$)

significantly related to root colonization by hyphae ($F = 117.72$, $p < 0.001$) and the relationship was similar in both inoculation treatments (Fig. 2d).

In general, mycorrhizal growth response was high at low P availability across the whole gradient of N (Fig. 3b) which is consistent with the more pronounced effect of available-P than of soil N on mycorrhizal growth response and in accordance with the correlation of the mycorrhizal growth response and root colonization. Also, high mycorrhizal growth response was more strictly limited to low P availability than high levels of root colonization (compare with Fig. 3a).

Soil aggregation

The proportion of water-stable aggregates in the soil directly correlated with several soil parameters (total N, organic C, Mg and K) as well as with plant growth (Fig. 1). Across all the fields, soils of the different inoculation treatments did not differ in the proportion of WSA (Table 2; for values per field and inoculation treatment see Supplementary Table S2).

The mycorrhiza-induced changes in WSA were relatively small as compared to plant mycorrhizal growth responses or responses in P concentrations (ranging between -0.22 and 0.62 in NAT and between -0.18 and 0.51 in REF, mean value per treatment), and did not significantly differ between both inoculation treatments across all the fields (Table 5). The proportion of WSA was significantly increased by NAT-inoculation only in 4 out of the 28 arable soils (Supplementary Fig. S2). A regression model testing the effect of inoculation treatment, newly formed ERM and mycorrhizal growth response on the mycorrhiza-induced change in WSA revealed only a significant effect of mycorrhizal growth response ($F = 6.508$, $p = 0.014$), while the other factors were removed by the reduction of the model.

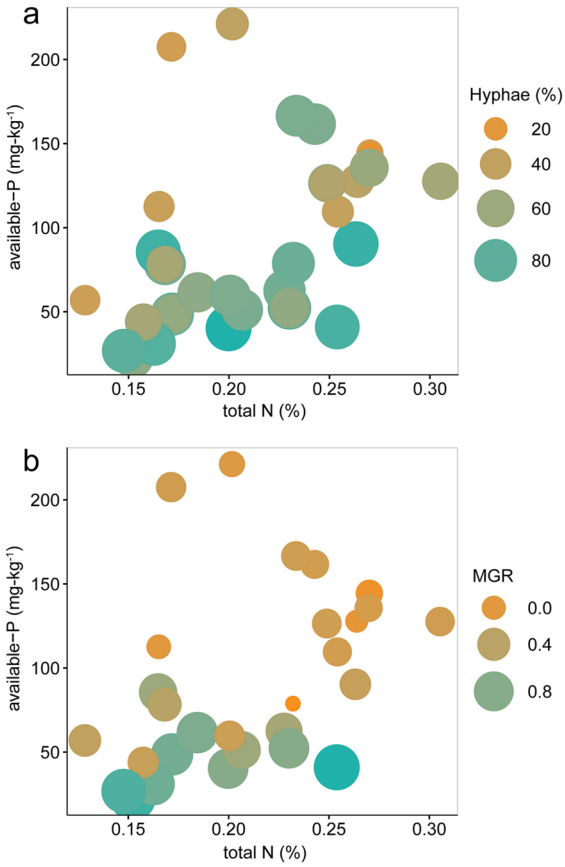

Fig. 3 Distribution of mycorrhizal growth responses (MGR) (**a**) and root colonization by hyphae (**b**) along gradients of available-P and total N present in the studied soils. The sizes and colours of the points indicate mean values of the corresponding parameter (MGR or hyphae) per soil (both mycorrhizal treatments pooled together, $n = 10$)

Table 5 Summary of responses to mycorrhiza per inoculation treatment across all the studied soils. The inoculation treatments are NAT (inoculated with the native arbuscular mycorrhizal fungal communities from the arable soils) and REF (inoculated with the reference isolate)

	df	F	p	NAT	REF
MGR	1	5.447	0.023	0.18 ± 0.03	0.41 ± 0.04
MPR	1	0.519	0.475	0.52 ± 0.03	0.45 ± 0.03
MNR	1	4.317	0.044	0.11 ± 0.02	0.03 ± 0.02
MAR	1	0.593	0.445	0.08 ± 0.02	0.11 ± 0.02

The responses are mycorrhizal growth response (MGR), mycorrhizal responses of phosphorus and nitrogen concentration in shoots (MPR, MNR) and mycorrhiza-induced change in water-stable aggregates (MAR). Values are means ± SE, F and p-values are given according to one-way ANOVA

Discussion

Our bioassay shows that some conventionally managed arable soils enable the establishment of mutualistic mycorrhiza and host AM fungal communities, which benefit a highly mycorrhiza-responsive host plant by improving its nutrition and growth. In that, our findings are in line with earlier studies, which reported positive effects of inoculation with AM fungi on crop growth in arable soils (Bender et al. 2019; Köhl et al. 2016; Lekberg and Koide 2005; McGonigle 1988; Pellegrino et al. 2011, 2015). P availability has been confirmed as the most important soil factor for the infectivity of the native AM fungal communities as well as for the growth benefits by mycorrhiza (Bender et al. 2019; Lekberg and Koide 2005). In addition, the functional screening of a relatively large set of soils indicates how frequent mycorrhizal effects on plant nutrition and growth may be in arable soils and links them to mycorrhizal effects on soil aggregation.

How beneficial can mycorrhiza be in arable soils?

Mycorrhiza most frequently increased P concentration in shoots, followed by plant growth and N concentration in shoots across all the analysed fields. This agrees with the principal mechanism of mycorrhiza functioning via improved uptake of the low-available macronutrient P (Bender and van der Heijden 2015; Clark and Zeto 2000; Treseder 2004), and also with previous reports on mycorrhizal effects on crops (Jansa et al. 2005; Miller et al. 2002; Rillig et al. 2019; Sanders and Tinker 1973; Smith et al. 2003).

Mycorrhizal phenotype (Johnson et al. 2015) was suggested to range between mutualism and parasitism depending on gradients of P and N availability in soil (Johnson et al. 2010). More and less mutualistic phenotypes can be clearly distinguished along the gradient of soil P availability in our set of soils, while no trend is apparent along the soil N gradient (Fig. 3a). Possibly, the selected soils do not cover a broad-enough range of N availability to induce functional differentiation of mycorrhizas. Also, higher temporal and spatial variation of N in soils, as compared to P (Mamo et al. 2003; van Es et al. 2005), may preclude differentiation along an N gradient unless N availability is extremely high or low. In the low-P soils, positive mycorrhizal growth responses were mostly coupled with increased

shoot P concentrations and relatively high root colonization (over 50%), the latter in a range that is consistent with previous reports for leek in experimental conditions designed to support functional mycorrhizas (Jansa et al. 2008; Konvalinková et al. 2017). In that, it seems that mycorrhizas follow the "strong mutualism" scenario in these soils, which assumes that the fungus supplies P to a P-limited host plant in exchange for C, with none of the two partners limited by N (Johnson et al. 2010). The N:P ratios in the shoots of mycorrhizal plants, however, indicate co-limitation by both nutrients and even limitation by N (see Supplementary Fig. S3). Consequently, the size of the mycorrhizal benefits may be restricted by low N availability at least in some of the soils, consistently with the "limited mutualism" scenario. The more pronounced effects of mycorrhiza on P concentrations than on growth are in line with this assumption. In high-P soils, we did not find negative growth effects of mycorrhiza, and therefore no indication for parasitism, which had been predicted for conditions of high availability of both N and P (Johnson et al. 2010). Together with the observed reduction of colonization rates, it seems that the fungi acted as commensals, their development and C demand was restricted by N limitation (Grman and Robinson 2013; Püschel et al. 2016) or by combined high availability of P and N (e.g., Blanke et al. 2005; Jiang et al. 2018).

The a priori selection of the studied arable soils was confined to conditions of low to intermediate P availability, which represent ca. 50% of arable soils in the region (Smatanová and Sušil 2018). Our selection also accords with the European assessment of soil P status in European arable lands by Tóth et al. (2013, 2014) which estimated that around a half of the croplands in Europe have low to intermediate available-P. The encountered strong negative relationship between P availability and mycorrhizal growth response (Fig. 2c) suggests that mycorrhiza would have not enhanced leek growth or P uptake (see Supplemental Figures S2a and S2b) in soils with higher P availability. Furthermore, leek is a highly mycorrhiza-responsive plant species, so that less mycorrhiza-responsive host plants, such as C3 grasses (Hoeksema et al. 2010; Köhl and van der Heijden 2016) or modern crop varieties (Sawers et al. 2008; Zhu et al. 2001), would most probably profit less from mycorrhiza than leek in the tested arable soils. In that, the bioassay, even though highly simplified, suggests that AM fungi contribute to crop growth only in a small subset of conventionally managed arable soils in the Central-European geographical context, if at all. This conclusion is reinforced by the fact that beneficial effects of mycorrhiza are overall smaller in more complex field conditions than in controlled greenhouse systems (Lekberg and Koide 2005). On the other hand, our short-term greenhouse bioassay quantified only basic nutritional parameters and growth, while the contribution of arable-soil AM fungi to stress resistance of crops (Augé 2001; Hohmann and Messmer 2017) or yield has to be adressed in more realistic experimental conditions.

How beneficial are the native AM fungal communities of arable soils?

Across all the screened arable soils, native AM fungal communities had lower root colonization and induced lower mycorrhizal growth response than the reference isolate, whereby AM fungal root colonization was significantly correlated with mycorrhizal growth response. This supports our hypothesis that the ability of native AM fungal communities to improve plant growth was decreased by suboptimal infectivity. In contradiction to the meta-analysis of Lekberg and Koide (2005), however, we found no relationship between the "infectivity gap" (i.e., difference in root colonization between the reference isolate and the native AM fungi) and the "benefit gap" (i.e., difference in mycorrhizal growth response), because each of the two "gaps" was differently correlated with soil P availability.

The "infectivity gap" was largest at highest P availability (Fig. 2a). While colonization by the REF isolate is an immediate reflection of the suitability of soil conditions for the formation of mycorrhiza (because high propagule numbers were applied), colonization by the native AM fungal communities also reflects the long-term impact of the soil and site conditions on their abundance. The "infectivity gap" therefore suggests that low root colonization by native AM fungi in arable soils (Gosling et al. 2013; Lekberg and Koide 2005; Liu et al. 2014; Smith and Smith 2011) is not only due to the immediate unsuitability of the nutritional conditions for mycorrhiza formation, but also has a legacy component. When crops obtain sufficient nutrients via roots, they reduce C flow to the associated fungi, which gradually decreases the fungal

biomass and the abundance of infective propagules in soil (Deng et al. 2017; Hoeksema et al. 2010; Ji and Bever 2016; Johnson and Graham 2013; Verbruggen and Kiers 2010). In that, our results theoretically corroborate earlier studies that encourage inoculation of crops with AM fungi (e.g. Hijri, 2016; Köhl et al., 2016; Lekberg and Koide, 2005; Pellegrino et al., 2015, 2011; Zhang et al. 2019), be it only for the small subset of soils, where AM fungi have the potential to benefit their host plants. However, given the costs of inoculation and potential risks (Schwartz et al. 2006), increasing the carrying capacity for AM fungi in these soils by management changes would be a more sustainable solution. This will require to specifically identify the factors that decrease the AM fungal abundance of these soils below a functional optimum.

In contrast, the "benefit gap" was most pronounced at the lowest P availability, i.e., the most favourable soil conditions for mutualistic mycorrhizas (Fig. 2c). Possibly, the reference isolate colonized roots faster than the native communities, which provided the plants with higher benefits due to earlier supply of nutrients (Blažková et al. 2021). AM fungal isolates and communities may also differ in the initial speed of root colonization and reach comparable plateau levels after some time (Jansa et al. 2008; Voříškova et al. 2016), whereby the initial speed of root colonization can be decisive for the plant benefits in P uptake and growth (Blažková et al. 2021). Another explanation could be decreased mutualistic quality of the native AM fungi in arable soils due to selection pressures towards highly competitive "selfish" genotypes, which supply less nutrients and act as stronger C sinks (Verbruggen and Kiers 2010). To conclude on this, however, more physiological evidence would be needed, e.g. in terms of C flow into the fungi or P supply directly via fungal hyphae, as well as evaluation of plant fitness based on the whole plant life cycle. Ultimately, the relevance for crop production would have to be tested in a realistic agronomic context.

The lower ratio of vesicles/spores to arbuscules in the roots of NAT-inoculated plants (Table 3) does not indicate less mutualistic symbiosis by the NAT communities as compared to the REF isolate. Contrarily, less mutualistic AM fungi were proposed to develop higher ratio of storage and reproductive structures (i.e., vesicles and spores) to nutrient absorptive structures (i.e., arbuscules and extraradical mycelia) (Johnson et al. 1997; Nijjer et al. 2010). On the other hand, *R. irregularis*, the AM fungal species inoculated in the REF treatment, is known to produce abundant intraradical spores, so that morphology of monospecific root colonization by this species is not directly comparable to root colonization by AM fungal communities. It is also possible that the root-colonizing NAT communities contained a significant proportion of arbuscule-forming Mucoromycotina (M-AMF), termed also fine root endophytes, which do not form classical large vesicles (Orchard et al. 2017a, b). Recently, these fungi were shown to be more abundant in arable soils than in other land-use systems in Australia (Albornoz et al. 2022). Though we did not specifically look for the fine-root-endophyte morphotype of root colonization in our experimental plants, it is probable that they were part of the arbuscule-forming fungal community, because of their global distribution (Orchard et al. 2017b).

The two inoculated treatments, NAT and REF, possibly differed from each other in the community composition of other soil microorganisms than AM fungi, as these cannot be added into the treatments in exactly the same manner and quantity. While this may potentially impact on plant performance, the study of Gryndler et al. (2018) suggests that plant mycorrhizal responses are relatively robust against changes in soil microbiome, possibly due to functional redundancy within microbial communities. In a previous study by Duffková et al. (2019), we reported differences in N transformation and N availability between sterilised soils with differently restored original microbiomes, leading to lower N uptake in plants inoculated with native soil as compared to those inoculated with greenhouse-grown cultures. In this study, however, the difference was exactly opposite, so we assume that the more careful procedure (i.e., the use of fine sieves instead of filter paper for the filtrate preparation, in combination with an incubation period of the soil) enabled an efficient restoration of the soil microbial communities (Shaw et al. 1999; Veresoglou et al. 2012).

How does mycorrhiza affect soil aggregation in arable soils?

No significant enhancement in soil aggregation was detected in the mycorrhizal treatments (see Table 2) which contrasts with previous reports on the pivotal

role of AM fungi in aggregate formation and stabilization (Kohler et al. 2017; Leifheit et al. 2014; Wilson et al. 2009). It is important to distinguish the direct contribution of AM fungi to soil aggregation due to hyphal growth and hyphal products, such as e.g., some components of the glomalin-related soil protein pool (Holátko et al. 2021; Rillig 2004), from their indirect effect via plant growth promotion, given that plants themselves and their productivity are crucial factors in the formation of soil aggregates (Chaudhary et al. 2009; Hallett et al. 2009; Rillig et al. 2002). In our experiment, the significant relationship of mycorrhiza-induced change of WSA with mycorrhizal growth response, but not with the newly formed ERM, indicates indirect, plant-mediated mechanisms rather than direct effects of the mycelia or their products. Hallett et al. (2009) showed similar results and concluded that plants greatly contribute to soil aggregate stability regardless of their mycorrhizal status. Similarly, reduction of nutrient losses from soils, another important ecosystem benefit of mycorrhizas, has been proposed to be conditioned by mycorrhizal effects on plant growth (Duffková et al. 2019; Köhl et al. 2014; Tran et al. 2021).

However, having on mind that mycorrhizal effects on soil aggregation are highly context-dependent in experimental conditions (Leifheit et al. 2014; Piotrowski et al. 2004), we should be cautious in concluding absence of direct effects by AM fungi. For instance, the overall absence of inoculation effect on WSA can certainly be related to the short duration of our experiment (Leifheit et al. 2014). On the other hand, potential direct effects of AM fungi on soil aggregation also need to be related to the effects of other factors, such as management practices in agroecosystems, in order to determine their relative importance.

Conclusions

Our study suggests that mycorrhiza may improve crop nutrition and growth only in a small subset of conventionally managed arable soils in the Central European geographical context, which have low or intermediate P availability. While the results of the bioassay cannot be directly extrapolated to field-grown crops, the highly mycotrophic host plant grown in controlled greenhouse conditions indicated a potential maximum of effects, unlikely to be surpassed in common crops in field conditions.

The bioassay also revealed factors, which may limit mycorrhizal benefits in arable soils: The more pronounced positive effects of mycorrhiza on P shoot concentration than on growth indicate that growth benefits in host plants may be limited by low N availability in low-fertile arable soils. The lower infectivity and mycorrhizal effects of the native AM fungal communities, as compared to the reference isolate, suggest that the infectivity of native AM fungi is suboptimal with respect to potential nutritional benefits of mycorrhiza. The parallel screening of mycorrhizal effects on plant growth, nutrition and soil aggregation suggests that effects on soil aggregation may be largely plant-mediated, meaning that positive effects of mycorrhiza on soil quality may be partly conditioned by mycorrhizal effects on crops (Rillig et al. 2019; Ryan and Graham 2002).

Based on these results, our screening suggests subsequent future research steps for a better understanding of the role of AM fungi in arable soils: 1) "Potential" benefits, as explored in our screening, should be linked to mycorrhizal benefits in relevant crops, in order to estimate how frequently AM fungi contribute to crop growth in arable soils. 2) It is important to explore whether ecosystem benefits of arbuscular mycorrhiza (effect on soil aggregation as example) are directly related to the presence or quantity of AM fungi or whether they are mediated by mycorrhizal effects on crop growth. This will clarify to which extent AM fungal communities in soils are important independently of their effect on plant productivity. 3) We need to address the effect of mycorrhiza on stress resistance specifically in crops, in accordance with the assumption of mycorrhiza as a bet-hedging strategy (Lekberg and Koide 2014; Veresoglou et al. 2022).

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Author contribution MJ, JJ and RD designed the study. Material preparation and data collection were performed by PAB, AB, DP, MR, OH and MK, data were analysed by PAB, JJ, OH and RD. The first draft of the manuscript was prepared by PAB and MJ, while JJ, RD, OH and DP commented on its later versions. All authors read and approved the final manuscript.

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Declarations

Competing interests The authors have no competing interests to declare that are relevant to the content of this article.

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