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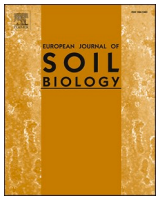

Original article

Multifunctional endophytic bacteria intimately associated within spores of arbuscular mycorrhizal fungi in a chernozem soil in Central Europe

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ABSTRACT

Chernozems are counted among the most fertile soils worldwide. Unexpectedly high spore density and species richness of arbuscular mycorrhizal fungi (AMF) were found in a long-term field trial established on such a soil. The purpose of the present study was to estimate bacterial communities associated within spores of selected AMF species from a long-term field trial on a highly fertile Calcic Chernozem to unravel their diversity belonging to different genera and species. We hypothized that high AMF species richness found in the Chernozem soil is reflected in a bacterial diversity with multifunctional traits mediated by indigenous bacterial compositions. The AMF species *Funneliformis mosseae*, *Scutellospora calospora* and *Septoglomus nigrum* were selected, since they occurred abundantly both in reduced and conventional tillage systems. The pure cultures of isolated bacterial strains were tested for ecological functions (traits) such as phosphorus solubilization, siderophore production, indole-3-acetic acid production and 1-aminocyclopropane-1-carboxylate deaminase activity. In addition, antimicrobial activity against both hemibiotrophic and necrotrophic fungi and oomycetes was evaluated. The majority of bacterial strains was exclusively associated with only one of the three AMF species, thus, giving evidence that each AMF species may harbor its own bacterial community. A large number of bacterial communities was shown to exert multifunctional activities ranging from plant growth promotion traits to antimicrobial activity. These findings suggest that the multifunctionality of bacteria intimately associated with AMF could markedly expand the ecological function of an autochthonous AMF population and empower host plants to explore robust ways to cope with changing environmental conditions.

1. Introduction

Arbuscular mycorrhizal fungi (AMF) display a key role in maintaining plant productivity in natural and agricultural habitats by transferring minerals such as phosphorus (P) and micronutrients to their host plants and receiving carbohydrates, in particular fatty acids in exchange [1–5]. The function of AMF includes improved resistance of host plants to drought, cold, and saline–alkali stress, as well as various diseases, including soil-borne diseases and promoting soil aggregate's structure [6–10].

The obligate biotrophy of AMF is an ancient feature that reflects the long-term co-evolution with plants dating back to the Devonian period approx. 500 million years ago [2,11–13]. During this long co-evolution they have developed intimate associations also with other microorganisms which evidently enhanced plant growth and the capability of plants to alleviate biotic and abiotic stresses. AMF also harbor endobacteria which modulate not only the fungal gene expression, but also the plant metabolism [12,14]. The endobacterium '*Candidatus* Glomeribacter gigasporarum' living inside *Gigaspora margarita* was recorded to be unculturable without the presence of AMF, supporting the idea that some endobacteria could be even obligate mutualistic biotrophs of AMF [15–18]. A wide diversity of bacterial species was shown to be closely associated with extraradical hyphae and spore walls [19–21]. Spore walls are considered the preferred habitat for endophytic bacteria since

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they may provide ecological advantage over the other microbes in that they are protected from adverse external abiotic stress of temperature, salinity or drought [22,23]. A few works reported the isolation and characterization of AMF spore associated bacteria from a small number of AMF giving first evidence that some bacteria exhibit antagonistic activity against plant pathogens [20,24], solubilization of P such as phytate which is not accessible for AMF and phytohormone production [22]. Despite this findings, little information is currently available on the functional significance of culturable bacterial communities associated with AMF spores in particular from field sites with different soil types. Most of the studies conducted so far were focusing on glasshouse studies with AMF isolates, belonging to different genera and species and maintained for several generations in pot or axenic root cultures with the same host plant and under the same environmental conditions [21,22,25].

The conclusion may be drawn that bacteria intimately associated with AMF spores brings another level of complexity to diversity and function of the mycorrhizal symbiosis [26–28]. Thus, AMF and bacteria can be considered as tripartite associations resulting in a consortium with plant growth promotion (PGP) activities.

AMF are naturally found in almost all terrestrial ecosystems and all soils with flowering plants [29], ranging from shallow Leptosols in coldest climates [30,31], acidic, infertile, young to old Andosols [32]. Highly fertile soils are considered to harbor low diversity of AMF. Especially intensively used, nutrient-rich croplands harbor a particularly low diversity of AMF, since plants under those conditions might not depend on the mycorrhizal symbiosis to efficiently acquire P and other soil nutrients and the transfer of these nutrients to the host plant [33,34].

Chernozems in Central to Eastern Europe are counted among the soil types as the most fertile soils worldwide [35,36]. However, information on AMF diversity from highly productive Chernozems used as croplands are extremely rare [37]. Unexpectedly high spore density and species richness of AMF (36 AMF species of 17 different genera) were found in the highly productive Calcic Chernozem cropland under study, even under high-input conditions, which were, however, higher in reduced tillage than in regularly ploughed plots [38]. AMF spore density and species richness in the Calcic Chernozem soil were higher than usually found in Central European Luvisols and Cambisols with similar land use and soil texture [33,39]. More recently a set of studies was performed in different types of Chernozems, according to the Canadian soil classification system, where high AMF species richness was found in cereal-cropped soils [40]. Interestingly, out of the four different Chernozem types, 'Black' Chernozems (most probably corresponding to typical Calcic Chernozems according to the IUSS/FAO classification) and 'Dark Brown' Chernozems harbored the highest species richness, while 'Brown' and 'Grey' Chernozems had lowest AMF richness as compared to the chemically more fertile 'Black' and 'Dark Brown' Chernozems [41]. According to these findings it is likely that rich AMF-species communities are a general characteristic for very fertile and productive 'Black' Chernozems in Germany and Canada.

The objective of the present study was to estimate the occurrence of bacterial communities intimately associated within spores of AMF species from a long-term field trial established on a highly fertile Calcic Chernozem soil under study and to assess whether diverse bacterial communities are associated with AMF spores belonging to different genera and species. The question behind this is whether high AMF species richness found in the Chernozem soil is reflected in a bacterial diversity with multifunctional ecological traits mediated by indigenous bacterial compositions. This would lead to another aspect of biodiversity beyond AMF species richness, and to focus more on functional diversity of AMF [4]. For our study we selected three AMF species: *Funneliformis mosseae*, *Scutellospora calospora* and *Septoglomus nigrum*. In addition, a consortium of various AMF species was evaluated consisting of *Acaulospora* sp., *Archaeospora* sp., *Entrophospora etunicata*, *Pacispora* sp., *Rhizoglomus irregulare* and *R. clarum*.

Bacteria isolated from AMF spores were *in vitro* investigated for two main ecological functions: biocontrol effects and plant growth promotion effects (PGPE), traits that are partly also attributed to AMF after colonizing roots [42–46]. Screenings of bacteria for ecological functions are, in a first step, commonly carried out *in vitro* [22,47,48]. For antagonistic biocontrol effects of isolated bacteria from AMF spores we used representative hemibiotrophic and necrotrophic soil and root pathogenic fungi of the genera *Sclerotinia, Botrytis, Alternaria, Rhizoctonia, Fusarium* and *Phytophthora* (Oomycete), as there are some reports that indicate that AMF colonized roots are more tolerant or resistant to soil, root and stem pathogens [10,46,49,50]. The question was whether the isolated bacteria are able to act against these pathogenic fungi, and so in theory, whether the bacteria can be a supportive part of AMF efficacy for plant health.

Plant growth promoting bacteria (PGPB) are known to produce various phytohormones that influence plant growth and development. Auxins, especially indole-3-acetic acid (IAA) synthesis are the most commonly reported mechanism, and lower concentrations promote root elongation and overall plant growth [51–53]. Over 80 % of rhizosphere microbes can synthesize IAA [54]. The modulation of ethylene levels through the production of the enzyme ACC deaminase is also important, as this breaks down the ethylene precursor ACC, thereby reducing ethylene levels, which improves root growth [55] and stress tolerance in plants [56,57]. PGPB convert insoluble forms of phosphorus in the soil into phosphates that are available to plants [58]. Primarily, this happens through the release of organic acids and phosphatase enzymes such as phytases [59,60]). PGPB produce siderophores, small iron-binding molecules that chelate iron (Fe^{3+}), which is often inaccessible in the soil, and make it available to plants. This not only promotes iron uptake by plants, but also acts as an indirect biocontrol mechanism. Siderophores deprive phytopathogenic microorganisms of iron, which inhibits their growth [61].

Different combinations of AMF and bacterial activities may represent the basis of a differential symbiotic performance of AMF isolates [22]. Thus, it is crucial to gain knowledge on the functional significance of bacteria associated with AMF spores. We hypothesized that high AMF species richness found under the conditions of high natural fertility and productivity of a Chernozem soil would offer novel information of the composition of bacterial populations intimately associated within different AMF species and genera.

2. Material and methods

2.1. AMF spore collection and identification from a long-term field experiment

AMF-spores were collected from a long-term tillage trial, laid out in 1992 on the experimental station of the Anhalt University of Applied Sciences, in Bernburg-Strenzfeld, Germany. In this field trial the effect of tillage practices on crop yield, plant availability of P and K, as well as other plant nutrients, is being investigated [62]. The trial location is situated in the South of the fertile Chernozem (="Schwarzerde") plain of the Magdeburger Börde. 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).

Soil 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 (approx. 1.5 kg samples) and homogenized by passing through a sieve (1 cm mesh size) for the identification of AMF.

AMF spores were extracted from the collected field samples by wet sieving and decanting technique, down to a mesh size of 45 μm, followed by water and sucrose centrifugation [63]. AMF spores were identified according to all original and emended AMF genus and species descriptions available [64–68].

2.2. Bacterial isolation from AMF spores and identification

Out of 36 AMF species identified at the study site [38] three AMF species were selected for further studies: *Funneliformis mosseae*, *Scutellospora calospora* and *Septoglomus nigrum*. In addition, a randomized collection of various AMF species was evaluated consisting of *Acaulospora* sp., *Archaeospora* sp., *Entrophospora etunicata*, *Pacispora* sp., *Rhizoglomus irregulare* and *R. clarum*. 100 to 200 intact and healthy spores of each AMF species were used for bacterial isolation as described in Ref. [22]. Before the spores are crushed aseptically with pistil (spores dispersed in 1 mL sterile physiological solution (9 g L^{-1} NaCl)), a surface sterilization was carried out, first with fresh Chloramine T solution (20 mg mL^{-1}, amended with 25 μL polyether trisiloxane Break-Thru S240 (Evonik Industries AG, Essen, DE)) and then with Ampicillin solution (100 μg L^{-1}; filter sterilized, incubation for 1 h at 4 °C), interposed with wash steps with sterile physiological solution. 100 μL spore suspension for each sample were plated in triplicate onto different culture media (7 days of incubation at 28 °C). As control served 100 μL suspension of the aseptic solution prior to crushing the AMF spores to ensure that the AMF containing solution was free of any bacterial or fungal contaminants.

For bacterial isolation from AMF spores, selective culture media were used to isolate specific functionally bacterial groups: Waksman agar medium for *Actinomycetes*, Ashby's mannitol agar for bacterial species able to grow on N-free medium and *Pseudomonas* agar for cultivation of *Pseudomonads*. Luria Broth (LB) culture agar was used as a non-selective nutrient culture medium for the majority of gram-negative and gram-positive bacteria. All media were supplemented with 100 mg L^{-1} of cycloheximide and 500 UI L^{-1} of nystatin to inhibit fungal growth.

2.3. Identification of bacterial strains

Bacterial strains intended for identification were cultivated on LB agar plates at 24 °C until first colonies were grown. With sterile toothpicks cell material of one colony forming unit were transferred to 6 μL nuclease-free water and heated up to 99 °C for 5 min for cell disruption. 1 μL of the suspension was used for amplification of the 16S rDNA. The PCR was performed in a final volume of 20 μL with 2 μL forward primer Eub338f (5′-GCTGCCTCCCGTAGGAGT-3′ [69], and 2 μL reverse primer Eub1387r (5′-GCCCGGGAACGTATTCACCG-3′ [70], as well as with appropriate voluminal of Taq (10 μL TAQ PCR Master Mix) or Phire polymerase (10 μL reaction buffer, 0,6 μL polymerase; Plant Direct PCR Kit). The PCR protocol starts with initial denaturation at 94 °C for 2 min, followed by 30 cycles of denaturation at 94 °C for 30 s, annealing at 55 °C for 30 s and extension at 72 °C for 1 min, ending with a final extension at 72 °C for 5 min. To examine the quality and size of PCR products, electrophorese was carried out with DNA loading dye and 1 kb DNA ladder in 1.5 % agarose gel, containing gel stain Roti®-Safe in TAE-buffer. The bands were visualized by UV light and photographed (Gene Genius Bio Imaging Systems Synoptics Ltd, Cambridge, GB). The clean-up of the PCR products and the subsequent sequencing was performed by the company MICROSYNTH SEQLAB GMBH, Göttingen. Sequences were analyzed using BLAST on the National Center for Biotechnology Information (NCBI) web page (https://blast.ncbi.nlm.nih.gov/Blast.cgi) using the database (nr/nt) and the closed related sequences were downloaded. Alignments of the sequences and the closed related sequences were done with the SILVA Web aligner [71], and phylogenetic trees were constructed with the ARB software package [72], using the maximum likelihood algorithm. The partial sequences of 16S rRNA genes were submitted to GenBank at NCBI under the accession numbers PQ187282-PQ187394 and PQ327562-PQ327564.

2.4. Antagonistic activity of bacteria from AMF spores

In vitro tests were performed to evaluate the antagonistic effects of bacteria from AMF spores against necrotrophic and hemibiotrophic fungi and oomycetes. The tests were conducted with the fungal pathogens *Sclerotinia sclerotiorum* (Lib.) de Bary, *Botrytis cinerea* PERS., *Alternaria brassicicola* (Schwein.) Wiltshire, *Rhizoctonia solani* (AG 2), *Fusarium culmorum* (Wm. G. Smith) Sacc., *Fusarium graminearum* (Schwabe), *Fusarium oxysporum* Schlechtendahl and the Oomycete *Phytophthora capsici* (Leonian isolates) Sarej. LT123. The fungal isolates were cultivated on potato dextrose agar (PDA) and the Oomycete *Phytophthora capsici* on V8 juice agar (Campbell V8 juice; Gourmondo Food GmbH, München, DE).

A dual-culture *in vitro* assay was performed on PDA with standardized bacterial suspensions (OD_{600} of 0.1) from bacterial cultures growing on LB-Agar for 7 days at 28 °C. A volume of 50 μL of each culture was added symmetrically at four positions of the agar, 3 cm away from a mycelium agar disk (0.28 cm^2) of a pathogen species placed centrally on the PDA plate. After incubation at 22 °C for 1–3 weeks, the diameter of the grown mycelium was measured crosswise and compared with the control without the bacterial suspension (three biological or technical replicates). Growth inhibition (GI) was calculated using the formula:

$$GI = (P \cdot 100) / C \quad (1)$$

where C is the mycelial growth (in mm) of the pathogen in the control plates (medium only), an P is the mycelial growth (in mm) of the pathogen in the dual culture. An activity-severity index (-, +, ++ and +++) was calculated. The leasion index of +++ indicates ≥80 % inhibition of fungal growth and the index of – indicates <25 % inhibition of fungal growth on test plate.

2.5. Ecological functions of bacteria

Within all ecological function test systems, the concentration of bacterial solutions was adjusted to 10^7 cells per mL before incubation, whereby 50 μL bacterial suspension were used for inoculation in each experiment.

2.5.1. Phosphorus solubilization from mineral phosphate and phytate

The ability of isolated bacteria to solubilize phosphate was assayed on Pikovskayas agar (recipe per L: 0.5 g yeast extract, 10 g glucose, 0.5 g $(NH_4)_2SO_4$, 0.2 g KCl, 0.1 g $MgSO_4$, 0.1 mg $MnSO_4 \cdot H_2O$ and $FeSO_4 \cdot 7H_2O$, each, 15 g Bacto™ agar (Becton Dickinson, Heidelberg, DE)), according to Subba Rao [73]. Two different phosphorus sources (either 5 g L^{-1} $CaHPO_4$ or phytate) were added to the agar before autoclaving. The strains were spot inoculated on each agar plate and incubated at 28 °C for 7 days. The formation of halo zones around bacterial colonies indicated mineral phosphate solubilization and phytate capacity of the strains. After incubation, colony diameter and halo zones (in mm) were recorded. The Phosphate Solubilization Index (PSI) was calculated with following formula:

$$PSI = diameter\ (halo\ zone) / diameter\ (colony) - 1 \quad (2)$$

An activity index of >0.5 was recorded as high activity (+++), an index of >0.25 but <0.5 as medium activity (++), an index of >0 but <0.25 as low activity (+) and an index of 0 as not active (−).

2.5.2. Siderophore production

Siderophore producing strains were detected using the over-lay Chrome Azurol S assay (CAS) according to Pérez-Miranda *et al.* [74] and further modification by Louden *et al.* [75]. For preparing CAS agar 100 mL sterilized Blue Dye solution (50 mL Chromazurol S solution (c = 1.21 mg mL^{-1}), 10 mL acidic $FeCl_3 \cdot 6H_2O$ solution (c = 0.27 mg mL^{-1} in 0.01 N HCL), 40 mL hexadecyltrimethylammonium bromide solution (c = 1.82 mg mL^{-1})), 100 mL 0.5 M morpholinopropanesulfonic acid (MOPS) buffer (pH 6.8) and 2 mL 0.1 g mL^{-1} $MgSO_4$ and 0.01 g mL^{-1} $CaCl_2$ solution, each, were added to sterilized CAS medium (0.3 g KH_2PO_4, 0.2 g K_2HPO_4, 0.5 g NH_4Cl, 0.1 g NaCl, 2 g fructose, 2 g glucose, 15 g agar) The bacterial strains were incubated on LB agar at 25 °C for 3

days. After incubation, 10 mL of CAS agar was spread as an overlay on the microorganisms and incubated at room temperature. Siderophore-producing strains showed a change in color (from blue to yellow or orange) in the overlaid medium around the colonies. After 7 days the radius of the halo was measured (mm) from the colony edge to the edge of the colored halo. The calculation of the activity index based on decolorized halos as described in formula (2), P solubilization section.

2.5.3. ACC deaminase activity

1-Aminocyclopropane-1-carboxylate (ACC) deaminase activity was evaluated by using three different modifications of a minimal medium (MM) according to Brown and Dilworth [76]. The basic MM was prepared according the following recipe: 12 g agarose and 950 mL Aq. dest. were heated till the solution was clear. Then, 10 mL solution 1 (36 g L^{-1} KH_2PO_4 and 140 g L^{-1} K_2HPO_4, sterile filtered), 10 mL solution 2 (25 g L^{-1} $MgSO_4$, 2 g L^{-1} $CaCl_2$ and 20 g L^{-1} NaCl, sterile filtered), 1 mL solution 3 (11 g L^{-1} $FeCl_3$ and 0.15 g L^{-1} EDTA, sterile filtered), 1 mL solution 4 (1 g L^{-1} thiamine HCl, 2 g L^{-1} Ca-pantothenate, 200 mL 0.01 % [w/v] biotin, sterile filtered) and 20 mL 10 % [w/v] glucose solution were added. The basic MM were split into three parts. One part remained untreated (negative control). The other two parts were added with ammonium chloride (positive control) and ACC solution (ACC test plate for the determination of bacteria capable of using ACC as nitrogen source), 2.1 mL 10 % [w/v] each (ACC purchased at Flurochem Ltd, Derbyshire, GB). Each bacterial strain was plated onto the 3 test plates, sealed with parafilm and incubated at 25 °C for 7 days (three technical and three biological replicates). The evaluation of the test plates was visually performed according to the intensity of bacterial growth. An activity index of 6 was recorded as high activity (+++; growth on 100 % of the plate) and an index of 1 as not active (-, no visible growth).

2.5.4. Indole-3-acetic acid production

Indole-3-acetic acid (IAA) production was evaluated modified as it is descripted in Bharadwaj *et al.* [24] using absorption measurement at 530 nm. The quantification of IAA production was carried out with an external calibration (concentration levels: 1, 2, 2.5, 4, 5, 8, 10, 12.5, 20, 25, 40 and 50 μg mL^{-1}; calibration function: $y = 0.029x + 0.0529$, $R^2 = 0.9915$).

2.6. Statistical analyses

Statistical analyses, data manipulation and generation of charts were performed by using R version 4.3.3 [77], along multiple packages [78–88]. Using the vegan R package [89], a Bray-Curtis distance matrix was first created, which was used to calculate the PCoA. SHAPRIO-WILK test ($\alpha = 0.05$) was performed to check for normal distribution, to verify the homogeneity of variance LEVENE test was used. The significance of growth rate was proofed with ANOVA analyses and post-hoc TUCKEY test with confidence interval of 95 %.

3. Results

3.1. Phylogenetic identification of bacteria and association of the strains with spores of Scutellospora calospora, Funneliformis mosseae, Septoglomus nigrum and others

A total of 90 strains were isolated from the spores of the different AMFs. Their 16S rRNA gene was partially sequenced and the sequences blast against the nr/nt NCBI Genbank database (Supplement Table 1) and phylogeny verified with phylogenetic trees calculated with maximum likelihood (Figs. 1–3, Supplement Fig. 1). The results show that the majority of isolates belong to the *Bacillaceae* family, followed by *Paenibacillaceae* and *Planococcaceae*. The most abundant genus was *Bacillus*, followed by *Paenibacillus* and *Priestia* (Supplement Table 1, Figs. 1–3, Supplement Fig. 1). Of the *Bacillus*, most isolates fall into the Cerus clade and only a few into the Subtilis clade (e.g. BLB 744 (PQ187340)). Of the other isolates, many belonged to genera that were recently unnamed and formerly also belonged to the genus *Bacillus*, such as *Neobacillus, Metabacillus* or *Domibacillus* (Figs. 1–3, Supplement Fig. 1).

In total, 45 bacterial species were shown to be differently distributed in *Scutellospora calospora*, *Funneliformis mosseae* or *Septoglomus nigrum* (Supplement Table 1, Fig. 4, Supplement Fig. 2). Interestingly the vast majority of isolated bacteria was exclusively associated with only one of the three AMF species. Thus, 9 bacterial species were exclusively associated with spores of *Scutellospora calospora*, one of the predominant species of the study site. Exclusively associated with spores of *Funneliformis mosseae* were 5 bacterial species and with *Septoglomus nigrum* 13 bacterial species, respectively. Although members of *Bacillaceae* and *Paenibacillaceae* were found in all three AMF species, the taxonomic affiliation of these bacteria was different in each AMF species. In addition, *Microbacterium* sp. BLB 712 (PQ187311) was found exclusively in *Scutellospora calospora* spores. Putative cold tolerant *Psychrobacillus* sp. BLB 760 (PQ187353) and BLB 772 (PQ187363) were only associated with *Funneliformis mosseae* and, however, *Sporosarcina* sp. BLB 752 (PQ187348), frequently isolated from extreme environments such as ant-arctic soils and the actinomycete *Streptomyces* sp. BLB 790 (PQ187376) appeared only in *Septoglomus nigrum* spores.

It was evident that only a low degree of consistency was achieved between the bacterial species identified in 2 or even all 3 AMF species. Thus, the number of taxonomically identical bacterial species found in both *Scutellospora calospora* and *Funneliformis mosseae* spores was limited to 6 and in both *Scutellospora calospora* and *Septoglomus nigrum spores* to 6 as well. In spores of both *Septoglomus nigrum* and *Funneliformis mosseae*, 1 remaining identical bacterial species was observed. Bacterial strains close related to *Priestia megaterium, Peribacillus* sp. and *Brevibacterium* sp. were the only bacterial species isolated from spores of all three AMF species under investigation. On the other hand, 15 bacterial endophytes were detected in the AMF consortium that were not found in any of the three AMF species under study (Supplement Table 1). The relatively high number of various *Paenibacillus* species in the consortium was striking. BLB 801 (PQ187386) is related to *Microvirga ossetica* sp. nov., a species of the N-fixing *Rhizobiales* (Supplement Table 1).

3.2. Screening for antimicrobial activity against hemibiotrophic and necrotrophic fungi and oomycetes

Antimicrobial activity against the hemibiotrophic and necrotrophic fungi and oomycetes were screened *in vitro*. These plant pathogens were selected in view of their great economic importance and their different life styles, so that reliable results could be achieved about the potential of the selected bacteria to control important plant diseases.

Twenty-one bacterial isolates were shown to display antimicrobial activity (Supplement Table 2). The high number of active isolates against the oomycete *Phytophthora capsici* (19) was striking, followed by antifungal performance against *Alternaria brassicicola* (11). The antifungal effect against *Fusarium* species (*Fusarium culmorum*, *F. graminearum*) and *Botrytis cinerea* also received some attention (12, 11 and 8, respectively). Conversely, the effect against *Sclerotinia sclerotiorum* and *Rhizoctonia solani* AG2 was much less pronounced (4 each).

Interestingly, most of the bacterial isolates displaying antimicrobial activity were shown to control a broad spectrum of diseases (Supplement Table 2, Figs. 5 and 6). Accordingly, 8 isolates exhibited a markedly broad spectrum of activity covering five to six out oven seven antimicrobial traits under study. BLB 706 (PQ187306), BLB 748 (PQ187344) and BLB 791 (PQ187377) were related to *Bacillus hominis.* The strains BLB 735 (PQ187332) and BLB 749 (PQ187345) were related to *Paenibacillus* sp. The other highly active bacterial isolates were BLB 762 (PQ187355) related to *Bacillus velezensis,* BLB 710 (PQ187310) related to the Bacterium strain BS0961 and BLB 783 (PQ187370) related to *Peribacillus frigoritolerans*. Worth mentioning is that BLB 710 and BLB

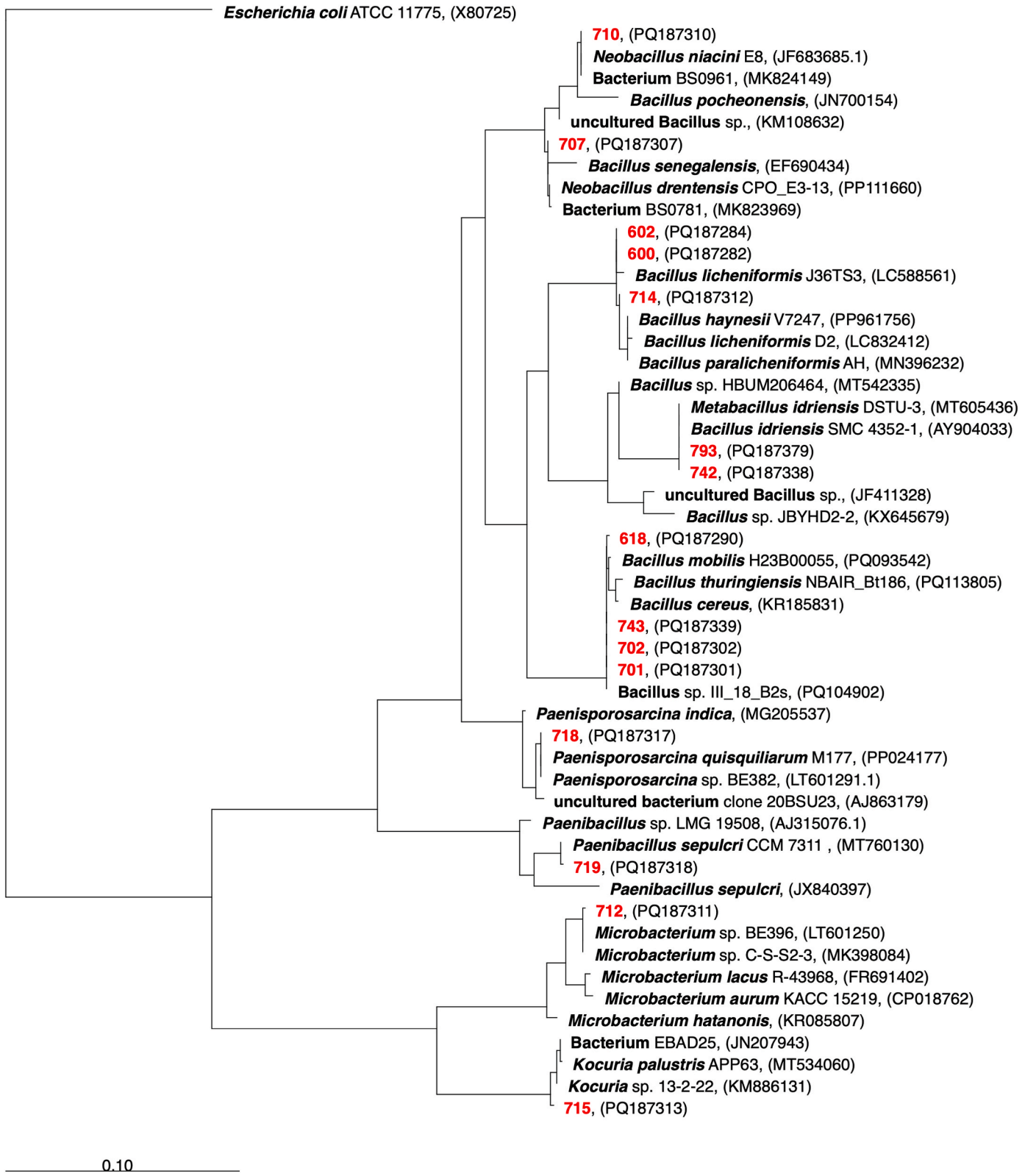

Fig. 1. Affiliation of the partial 16S rRNA sequences (red) of the isolates from spores of *Scutellospora calospora* to close related sequences, using a Maximum Likelihood tree. GenBank accession numbers are in parentheses. *Escherichia coli* ATCC 11775 was used as an outgroup. Bar, 0.1 substitutions per nucleotide position. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

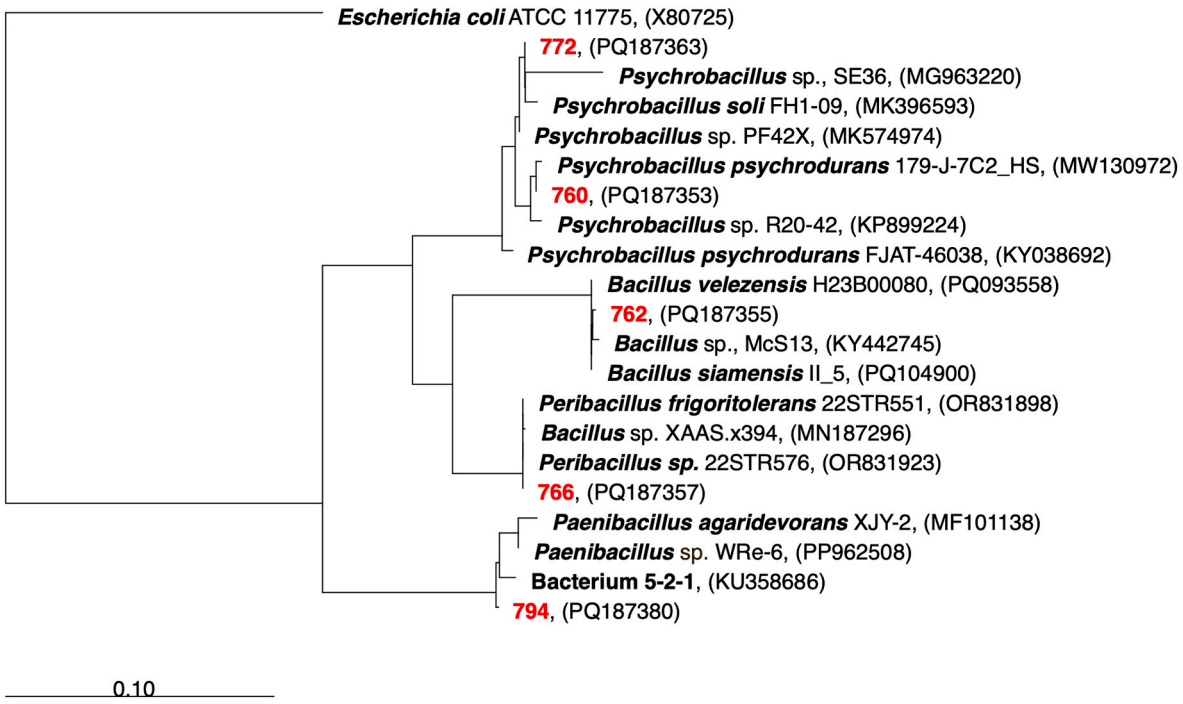

Fig. 2. Affiliation of the partial 16S rRNA sequences (red) of the isolates from spores of *Funneliformis mosseae* to close related sequences, using a Maximum Likelihood tree. GenBank accession numbers are in parentheses. *Escherichia coli* ATCC 11775 was used as an outgroup. Bar, 0.1 substitutions per nucleotide position. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

735 were the only isolates exhibiting markedly pronounced control of *Rhizoctonia solani* (AG 2).

3.3. Screening for PGPE

The *in vitro* screening of PGPE, included the ability to produce IAA and siderophores, to enhance ACC deaminase activity and to solubilize mineral phosphate (calcium phosphate) and phytate (Supplement Table 3). The majority of bacterial species displayed ACC deaminase activity (26), followed by siderophore production (21), mineral phosphate solubilization and IAA-production (4 each). Phytate solubilization was not observed with any of the bacterial isolates.

Pronounced ACC deaminase activity was in particular observed with BLB 738 (PQ187334) related to *Brevibacterium* sp., BLB 746 (PQ187342), BLB 761 (PQ187354) and BLB 770 (PQ187361) related to *Priestia aryabhattai*, and BLB 782 (PQ187369), BLB 784 (PQ187371), BLB 792 (PQ187378) and BLB 796 (PQ187382) related to various strains of *Priestia megaterium.* (Supplement Table 3; Fig. 7). BLB 796 (PQ187382) showed also remarkably high IAA production (Supplement Table 3). In addition, strains related to *Priestia megaterium* (BLB 780 (PQ187368), BLB 784 (PQ187371) and BLB 792 (PQ187378)) and one strain related to *Peribacillus frigoritolerans* (BLB 783 (PQ187370)) increased IAA production.

Siderophore production was common and very pronounced for most of the bacterial strains with strains mainly related to *Bacillus* sp., *Brevibacterium* sp., *Paenibacillus* sp., *Peribacillus* sp., *Priesta* sp. and *Sporosarcina* sp. (Supplement Table 3; Fig. 8). Unexpectedly the number of P-solubilizing bacteria was relatively small and, however, confined to not further identified *Bacillus* species (BLB 715 (PQ187313)), *Microbacterium* sp. (BLB 712 (PQ187311)), *Peribacillus* sp. (BLB 747 (PQ187343)) and *Streptomyces* sp. (BLB 790 (PQ187376)).

Interestingly, a considerable number of strains were able to exert multiple PGP traits. 13 bacterial strains fulfilled at least two such characteristics. However, the most promising isolates were represented by BLB 796 (PQ187382) because of its remarkably high IAA activity (40.12 ± 2.23 µg mL^{-1}) and BLB 738 (PQ187334). Last isolate shows a high siderophorores solubility (SPI = 0.69) and a nearly high ACC deaminase activity index of 5.33 (dataset: [90]).

Comparing the results of antimicrobial traits with those of PGPE, there is evidence for only few similarities between selected bacterial species with both PGPE and antimicrobial traits. Strains related to *Priestia aryabhattai, Priestia megaterium* and *Streptomyces* sp. that had shown remarkably high PGPE were, however, ineffective against pathogens. Conversely, the performance of most strains with significant antimicrobial activity was not positively correlated with PGPE. This holds true particularly for strains related to *Bacillus hominis*. However, notable exceptions included isolate BLB 762 (PQ187355), which was related to *Bacillus velezensis*, as well as BLB 783 (PQ187370) and BLB 705 (PQ187305), which were related to *Peribacillus* sp. These isolates exhibited both pronounced antimicrobial activity (at least against two pathogens) and one strong PGPE.

4. Discussion

4.1. Spore-associated bacterial isolates

Out of approximately 36 AMF species identified in the chernozem soil at the study site [38], three AMF species were selected for the isolation of spore associated bacteria: *Funneliformis mosseae*, *Scutellospora calospora* and *Septoglomus nigrum*. In total 45 bacterial species were identified based on 16S rDNA sequencing from spores of either *Scutellospora calospora*, *Funneliformis mosseae* or *Septoglomus nigrum* (Supplement Table 1). As a result of the diverse bacterial communities living closely associated with spores of AMF, a considerably large number of bacteria were shown to exert multifunctional activities ranging from PGPE to antimicrobial activity against both hemibiotrophic and necrotrophic fungi and oomycetes. Since AMF are obligate symbionts which grow and sporulate in the soil surrounding the roots, the composition of the bacterial populations living strictly associated with their spores may vary depending on environmental variables such as soil types and host plants [91]. However, the question as to whether specific bacterial populations are associated to specific AMF

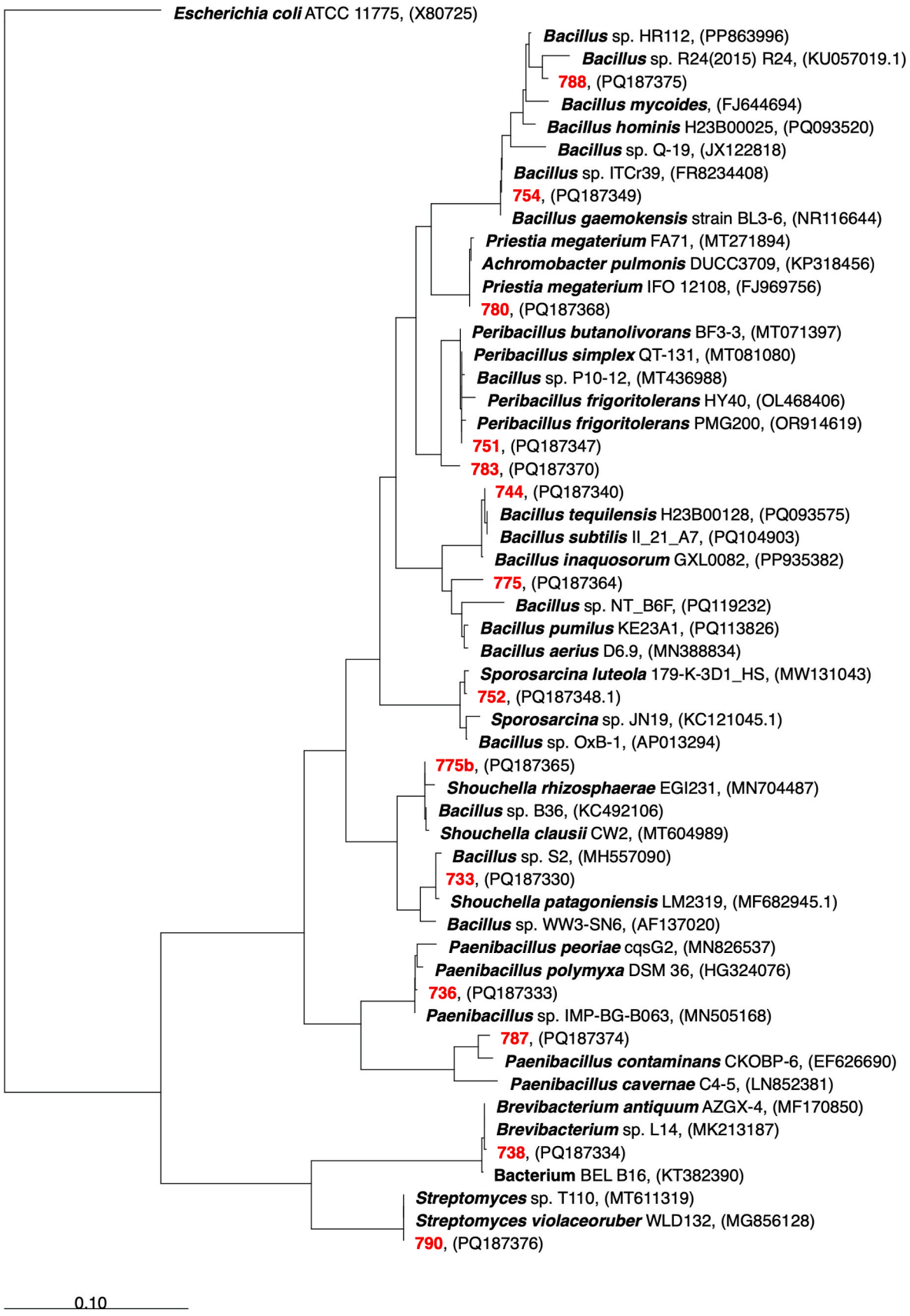

Fig. 3. Affiliation of the partial 16S rRNA sequences (red) of the isolates from spores of *Septoglomus nigrum* to close related sequences, using a Maximum Likelihood tree. GenBank accession numbers are in parentheses. *Escherichia coli* ATCC 11775 was used as an outgroup. Bar, 0.1 substitutions per nucleotide position. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

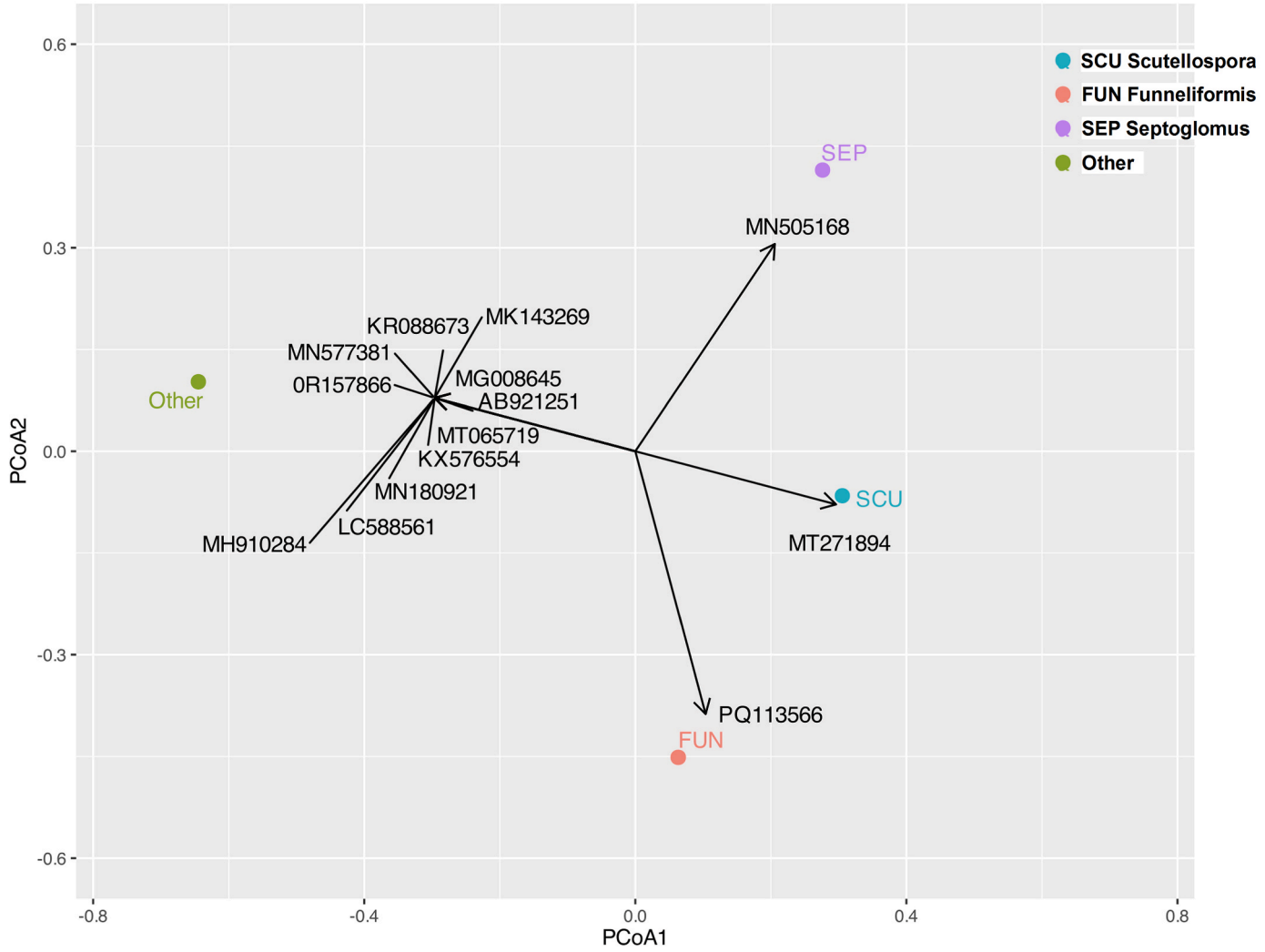

Fig. 4. Principal axis coordinate analysis (PCoA) calculated based on the Bray-Curtis community dissimilarity distance matrix of bacterial isolates from spores of AMF FUN (*Funneliformis mosseae*), SCU (*Scutellospora calospora*), SEP (*Septoglomus nigrum*) and Other (*Archeospora* sp., *Claroideoglomus etunicatum*, *Pacispora* sp. and *Rhizoglomus irregulare*). Arrows indicate the 13 isolates that had the greatest influence on the matrix. The numbers on the arrows are the accession numbers of the next relative sequence of the isolates (Supplement Table 1). Isolates with the same closest related sequence were grouped together.

taxa has so far only been the subject of a few studies [23,91,92].

We provide clear evidence that the majority of bacterial species were exclusively associated with only one of the three AMF species. *Priestia aryabhattai*, *Priestia megaterium,* and two strains of *Peribacillus* sp. were the only bacterial strains isolated from spores of all three AMF species under investigation. There is increasing evidence that each AMF species may harbor its own bacterial community. This finding is also supported by the results of a mixture of randomly collected AMF species. 14 bacterial species were detected in the AMF consortium that were not found in any of the three AMF species under study. Somehow surprising is the detection of *Microvirga ossetica* (BLB 801 (PQ187386)) from the AMF consortium. *Microvirga ossetica* is a more recently described species of the N-fixing *Rhizobiales* isolated from root nodules of the legume species *Vicia alpestris* [93].

Recent reports on mycorrhizal interactions suggest a complex tripartite interplay of the host plant with AMF and fungus-associated bacteria [94–96] and in many cases these associations show a certain type of specificity [27,94,97]. In a similar approach Agnolucci *et al.* [91] conducted a glasshouse study with AMF isolates, belonging to different genera and species and maintained for several generations in pot cultures with the same host plant, under the same environmental conditions. Six AMF isolates were shown to display diverse bacterial community profiles unrelated with their taxonomic position, suggesting that each AMF isolate recruits on its spores and different microbiota. Bianciotto *et al.* [16] recently demonstrated for the AMF *Gigaspora margarita* a continuous vertical transmission of its endobacteria from one generation to another, ensuring the enduring nature of the association.

Interestingly Liu *et al.* [98] were able to prove that microorganisms in soil have a weak impact on the distribution of endophytic bacteria in plant tissues of non-mycorrhizal Tartary buckwheat (*Fagopyrum tataricum*). Accordingly, the endophytic microbiome of the leaf, stem, root and next-generation seeds was comparable between treated (grown in sterile soil) and control plants (grown in non-sterile soil), indicating that the plants had alternative robust ways to shape their microbiome. In case that endophytic bacterial communities in AMF spores are well preserved and transmitted to the next generation independent from soil, this could be of great ecological importance for plants. Those closely associated endophytic compositions could significantly improve the capability for the AMF symbiosis to cope with abiotic or biotic stress under changing environmental conditions.

AMF-species communities are likely to be a general charcteristic for very fertile and productive black chernozems characterized by a deep, rich humus horizon and therefore rich in organic matter [38,40,41]. In

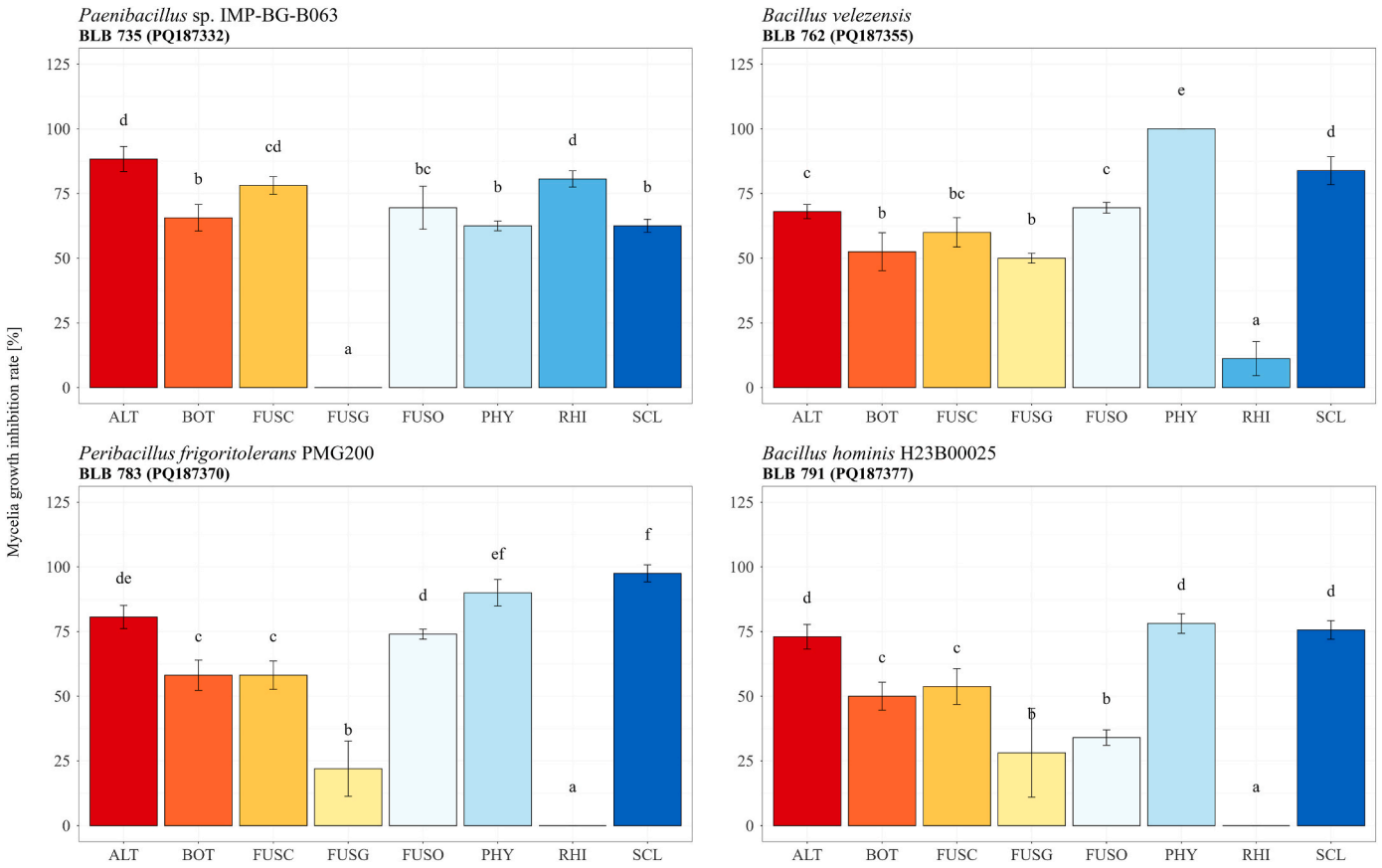

Fig. 5. *In vitro* tests to evaluate antagonistic effects of bacteria strictly associated within AMF spores against necrotrophic and hemibiotrophic fungi and oomycetes. Graph bars represent values of three replications, error bars represent standard error of the median. Significant differences in mycelial growth inhibition assessed using ANOVA with subsequent post-hoc TUCKEY Test ($P \geq 0{,}05$) are marked with compact letter display.

this context it could be interesting, that the fertility of chernozem is not solely based on the properties of the loess. The strong bioturbation is also an important factor in chernozems and involves processes such as mixing soil constituents, redistributing organic compounds, and creating channels for water and gas transport, which help in maintaining soil structure and fertility [35]. Earthworms are a primary bioturbating agent in chernozems and through their normal ecological functions they are likely to influence microbial communities including those of AMF [99]. Studies have demonstrated close interaction between diverse species of earthworms with AMF in terms of population density and facilitation of nutrient uptake by plant roots. Thus, the phenomenon of "functional synergism" between earthworms and AMF may be a significant mechanism in soil improvement, and plant growth [100]. One could speculate that the complex interaction between AMF and earthworms has contributed to the formation and stability of the rich humus horizon of chernozems and may therefore be a reason for the high AMF abundance in these soils, challenging the common assumption that high fertility limits AMF prevalence.

Although the mechanisms by which the symbiosis is established and by which the plant benefits from AMF root colonization are well understood, the role of fungus-associated bacteria in the symbiosis remains to be still unclear. However, more recently Glaeser *et al.* [101] proved that the *Alphaproteobacterium Rhizobium radiobacter*, which is strictly associated with its fungal host *Piriformospora indica*, exerts plant beneficial activity independently from the host. Thus, the data generated support the possibility that the beneficial biological activity assigned so far to *Piriformospora indica* can be at least partly attributed to the strictly associated bacterium *Rhizobium radiobacter*. *Piriformospora indica* is a symbiotic model fungus of the *Serendipitaceae* of the *Sebacinales* [102]. Since its discovery in the Indian Thar dessert in 1996 [103], *Piriformospora indica* and related *Sebacina vermifera* strains were shown to promote biomass, yield and health of a broad spectrum of plants [104] and to reprogram plants to salt-stress tolerance and disease resistance [105–107].

High AMF species richness and diversity were found in the highly productive Chernozem cropland under study, even under high-input conditions [38]. The observed high biodiversity and multifunctionality of the spore-associated bacteria might indicate a higher level of ecological resilience or adaptability in this specific soil system, compared to less diverse AMF/bacterial communities found in other fertile agricultural soils. The question may be raised, as to whether AMF species have found their specific ecological niches for reproduction under specific environments. One could perhaps shift attention to bacterial populations living strictly associated with AMF spores. Considering the evidence that each AMF species appears to harbor its own distinct bacterial community, we assume that the specific, diverse, and multifunctional traits provided by these associated bacteria could be a primary driver enabling the persistence of AMF in this environment. This could mean that AMF species richness goes hand in hand with multifunctional traits mediated by indigenous bacterial compositions. The multifunctionality of bacteria closely associated with AMF spores could markedly expand the ecological function of an autochthonous AMF population and empower host plants to cope with changing environmental conditions, may be also in future in response to major global change factors [108].

4.2. Antimicrobial activity of bacterial isolates

The use of AMF as a biocontrol method to antagonize soil-borne pathogens has received considerable attention [109]. It has been

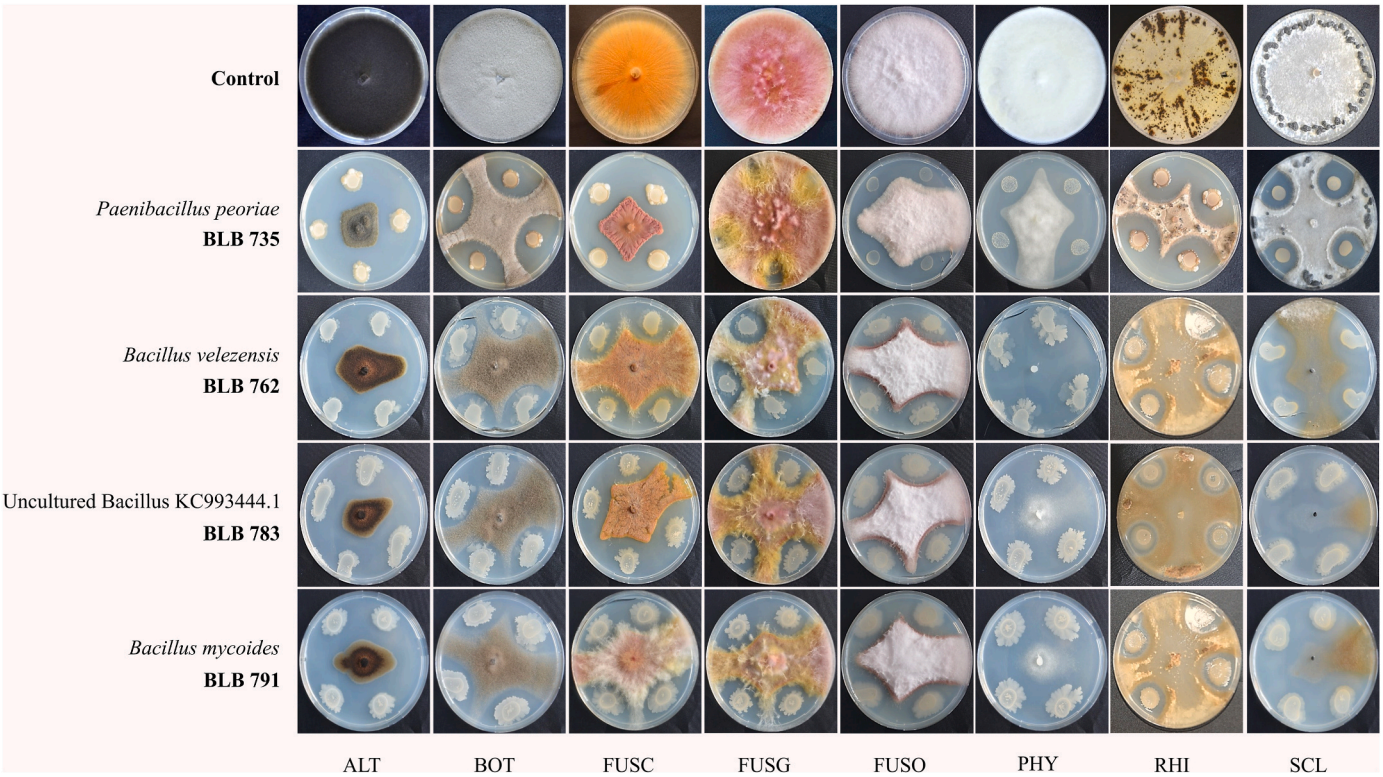

Fig. 6. Photo documentation of mycelial growth inhibition rates of *Alternaria brassicicola* (ALT), *Botrytis cinerea* (BOT), *Fusarium culmorum* (FUSC), *F. graminearum* (FUSG), *F. oxysporum* (FUSO), *Phytophthora capsici* (PHY), *Rhizoctonia solani* AG2 (RHI), *Sclerotinia sclerotiorum* (SCL) after 1 week of inoculation with bacteria isolated from AMF spores (BLB).

shown in a number of pathosystems that AMF confer resistance against root pathogens [8,46,109–111]. There are somehow interesting interactions reported between AMF and soil bacteria, including the binding of soil bacteria to the fungal spores by bacteria [112]. The interactions of AMF with spore associated bacteria that antagonize soil-borne pathogens can have important implications in the ecological functionality of AMF.

The data displayed that out of 90 bacterial strains tested, about 23 % showed antimicrobial activity against at least one of the pathogens tested (Supplement Table 2, dataset [90]). *Bacillus hominis* (BLB 706 (PQ187306), BLB 791 (PQ187377)), *Bacillus velezensis* (BLB 762 (PQ187355)), Bacterium strain BS0961 (BLB 710 (PQ187310)), *Paenibacillus* sp. (BLB 735 (PQ187332)) and *Peribacillus frigoritolerans* (BLB 783 (PQ187370)) appeared to have a broad spectrum of antimicrobial activity against fungal pathogens (min. 5) and the oomycete *Phytophthora capsici*. This study is the first report on AMF spore associated bacteria exhibiting broad-spectrum antimicrobial control collected from a field soil sample. It has only recently been recognized that bacterial endophytes play an important role in resistance to diseases [113–115] and those signals exist to mediate crosstalk between the endophyte and its host [116,117]. In recent years, endophytic microorganisms of *Bacillus* spp. and *Paenibacillus* spp., both of which exerted outstanding antimicrobial activity in the present study, have shown promise for the control of phytopathogens because of their strong effects, broad-spectrum antimicrobial properties and strong safety profile [118–120]. It is known that *Bacillus* spp. act through multiple mechanisms, such as direct antagonistic action against target organisms, producing various secondary metabolites, hydrolytic enzymes, and inducing plant defense responses via systemic resistance to pathogens [121,122]. BLB 735 (PQ187332) related to *Paenibacillus* sp. with antimicrobial activity against *Yersinia ruckeri* (unpublished) is also related (99.78 %) to *Panibacillus peoriae* that is a beneficial bacterium reported to have biocontrol effects being considered to have great potential for agricultural applications [123,124].

4.3. Functional diversity of bacterial isolates

P solubilization from mineral phosphate and phytate was not the most common PGP trait, since out of 90 tested strains only 4 strains were able to solubilize mineral phosphate, and none of the strains was shown to solubilize phytate (Supplement Table 3). These results are somehow surprising since P-solubilizing bacteria (PSB) are frequently associated with AMF colonized roots [125–127] and ubiquitous in the rhizosphere of higher plants in different soils [128]. Battini *et al.* [22] recorded that a fairly high number of the tested bacteria associated with *Rhizoglomus intraradices* were involved in the solubilization of mineral phosphate and phytate.

The use of PSB as biofertilizers is considered a promising approach to improving food production and increasing crop yields [129–131]. Interestingly, bacteria with high P-solubilizing potential, completely failed to promote P acquisition in maize grown on a calcareous Loess sub-soil pH 7.6 with nitrate fertilization and rock phosphate as a sparingly soluble P source [132,133]. In this context it is worthwhile to be mentioned, that the soil at the study site is a Calcic Chernozem having developed on Loess sediments over limestone with a pH of 7.0–7.4 [62]. It remains to be established to what extent the fairly low number of PSB found to be associated with AMF spores at the study site may be attributed to the high natural fertility and high P content of the calcareous soil.

Siderophore-producing strains were found in various bacterial groups and represented 23 % of the total isolates tested. It was somehow striking that siderophore production was in particular evident with *Bacillus hominis* (BLB 755 (PQ187350)), *Bacillus velezensis* (BLB 762 (PQ187355)), *Paenibacillus* sp. (BLB 749 (PQ187345)) and *Peribacillus* sp. (BLB 705 (PQ187305)), which also exhibited high antimicrobial activity against both fungal and oomycete diseases. Such a trait may be

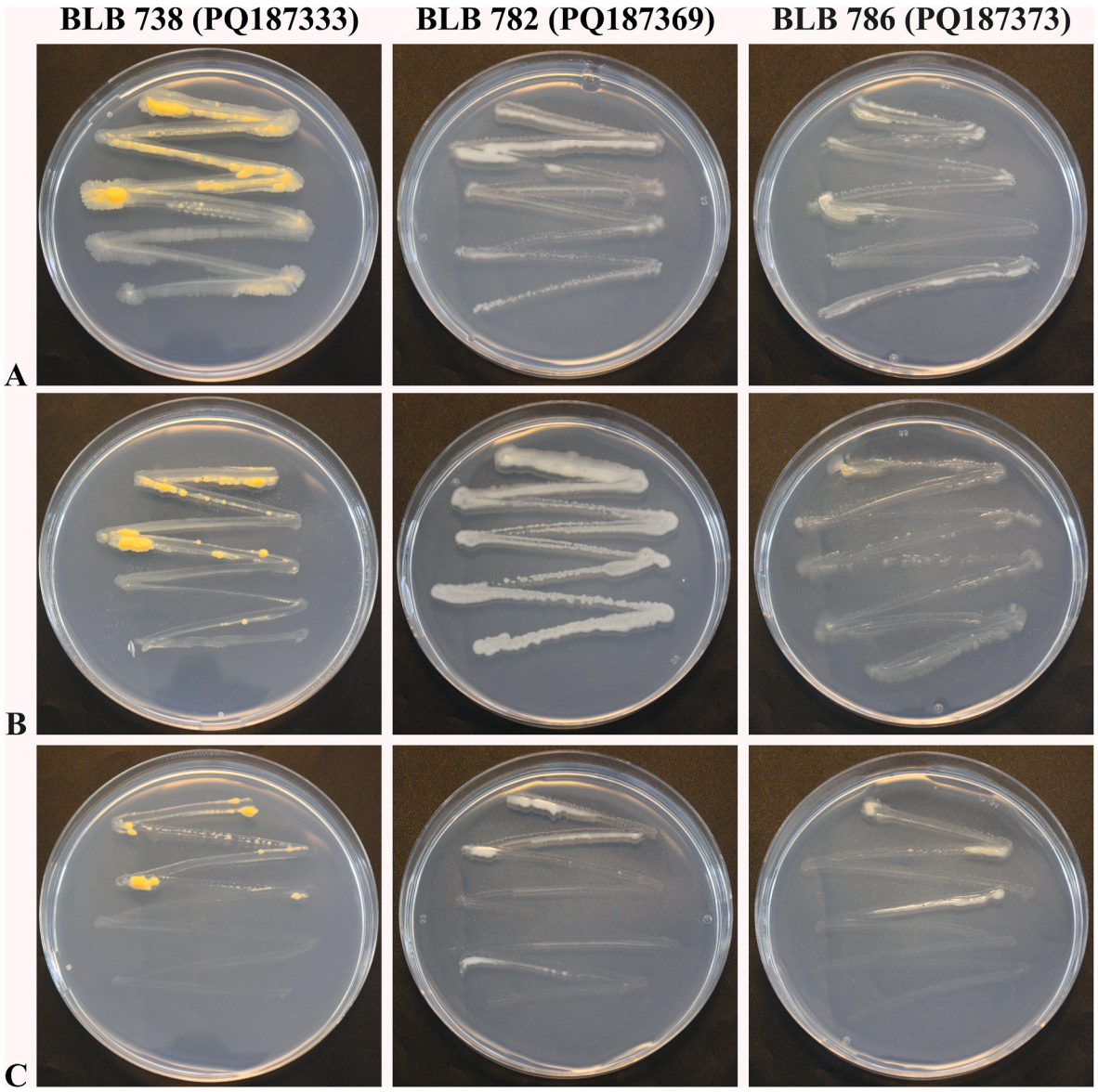

Fig. 7. ACC-Deaminase activity of bacteria isolated from AMF spores after 1 week of incubation. BLB 738 (PQ187334): *Brevibacterium* sp. L14, BLB 782 (PQ187369): *Priestia megaterium* FA71 and BLB 786 (PQ187373): *Peribacillus* sp. 22STR576. **A:** ACC as sole nitrogen source. **B:** positive control with ammonium chloride as sole nitrogen source; C: negative control without amended nitrogen.

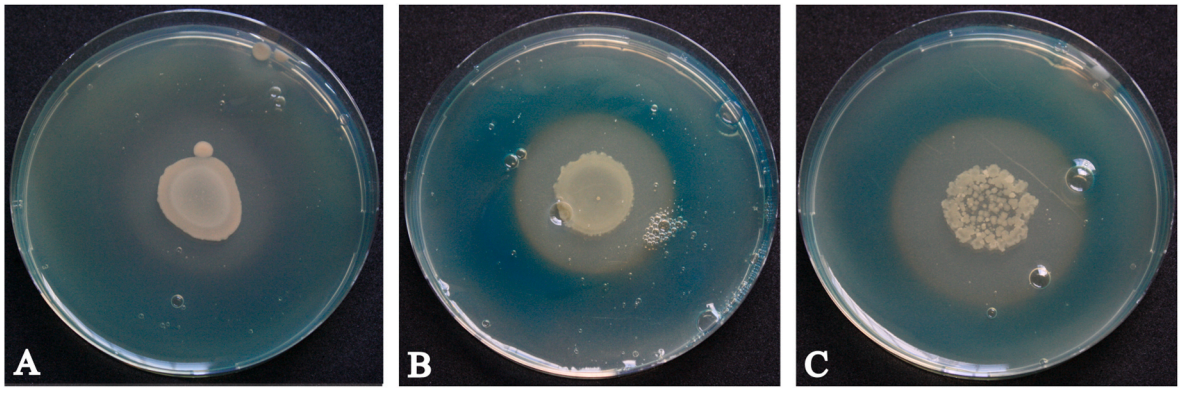

Fig. 8. Siderophore formation of bacteria isolated from AMF spores after 1 week of incubation. BLB 612 (PQ187288): *Bacillus hominis* H23B00025, BLB 762 (PQ187355): *Bacillus velezensis* and BLB 798 (PQ187384): *Paenibacillus* sp. SNH_M13.

functional for AMF to efficiently control soilborne diseases, by means of bacterial siderophore-mediated competition for iron [22,134,135], since siderophores deprive phytopathogens of iron by binding to the bioavailable forms of iron first [136,137]. More recently AM fungal species were found to encode rhizoferrin type siderophores such as glomuferrin which may be widespread in the AM symbiosis [138]. Overall, both AMF and plant growth-promoting rhizobacteria are able to produce siderophores [139].

ACC-deaminase activity was evident for 29 % of the bacterial strains tested and accordingly the most common trait. ACC deaminase is a bacterial enzyme associated with alleviation of plant stress [136,140]. ACC deaminase also supports colonization of plants by bacterial endophytes and may be functional for plant growth promotion [141,142]. Interaction of AMF and plant rhizosphere microbes are reported to enhance plant tolerance to abiotic stresses mediated by strongly enriched abundance of ACC deaminase and IAA genes [143]. Reflecting the ACC deaminase activity of a fairly high number of AMF associated bacteria in the chernozem soil, the conclusion may be drawn that bacteria-AMF interactions may play an important role in ACC deaminase mediated alleviation of abiotic and biotic stress in plants [144].

We obtained five IAA producing strains. In particular *Priestia megaterium* produced considerably high concentrations of IAA. IAA is able to stimulate the development of plant root systems [145,146]. Diverse bacterial species possess the ability to produce the auxin phytohormone IAA. In a previous study a strain of *Bacillus aryabhattai*, isolated from maize rhizosphere, had demonstrated promising PGP properties, including nitrogen fixation, P solubilization and IAA production [147]. The whole genome sequencing of *Bacillus aryabhattai* revealed many signature genes that are functionally associated with plant growth promotion and high concentration of IAA. However, the role of bacterial IAA in plant–microorganism interactions appears to be diverse, due to the diversity of IAA expression regulation across IAA biosynthesis pathways in plants and across bacteria [148].

Overall, there is much evidence, that diverse bacterial taxa are closely associated within spores, sporocarps, and extraradical mycelium of AMF showing different functional plant growth promotion activities [27]. Such specific and close physical relationships reflect complex interactions among AMF, bacteria, and host plants, suggesting that AMF might act as carriers of the endophytic microbiota to become established in roots.

5. Conclusions

This study was aimed at the identification and determination of multifunctionality of endophytic bacteria intimately associated with spores of AMF from a Calcic Chernozem soil in Central Europe. We provide clear evidence that the majority of bacterial strains were exclusively associated with only one of the AMF species under study, suggesting that each AMF species may harbor its own bacterial community. As a result of the diverse bacterial communities living closely associated with spores of AMF a considerably large number of bacteria were shown to exert multifunctional activities ranging from PGP traits to antimicrobial activity against hemibiotrophic and necrotrophic fungi and oomycetes. Given the high AMF species richness and diversity found in the highly productive Chernozem cropland, even under high-input conditions, the multifunctionality of bacteria closely associated with AMF could markedly expand the ecological function of an autochthonous AMF population and empower host plants to explore robust ways to cope with changing environmental conditions. We emphasize that the observed high biodiversity and multifunctionality of the spore-associated bacteria might indicate a higher level of ecological resilience or adaptability in this specific soil system, compared to less diverse AMF/bacterial communities found in other fertile agricultural soils.

Associated content

The dataset of research findings on the multifunctionality of endophytic bacteria, isolated from arbuscular mycorrhizal fungi, is available free of charge at doi: 10.6084/m9.figshare.29401706.

CRediT authorship contribution statement

Helmut Baltruschat: Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Johanna Hummel:** Writing – review & editing, Writing – original draft, Visualization, Data curation. **Marit Gillmeister:** Writing – review & editing. **Stefan Ratering:** Writing – original draft, Visualization. **Kathrin Kabrodt:** Writing – review & editing, Resources. **Ewald Sieverding:** Writing – review & editing, Writing – original draft, Methodology, Investigation. **Fritz Oehl:** Writing – review & editing, Writing – original draft.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ejsobi.2025.103760.

Data availability

Dataset of multifunctional endophytic bacteria, isolated from AMF-spores in chernozem soil (Original data) (Figshare)

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