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RESEARCH

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Diversity of root endophytic bacteria from maize seedling involved in biocontrol and plant growth promotion

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Abstract

Background: Native endophytes from maize could play a vital role in plant protection and growth promotion. The present study was undertaken to elucidate the effect of soil types and different maize varieties on culturable endophytic bacterial diversity and to use potential endophytes as biocontrol agents and plant growth promoters.

Results: Based on *rpoB* and 16S *rRNA* genes, one hundred seventy-four (174) endophytes distributed into twenty-five (25) genera were identified, in which the greatest number of isolates were classified into *Bacillus* (52.30%), followed by *Streptomyces* (13.22%), *Paenibacillus* (6.32%), and *Pseudomonas* (4.60%). Out of the total isolated strains, endophytic strains with total number thirteen (13), eighty-four (84), one hundred and five (105), and nine (9) were able to fix nitrogen, and solubilize calcium phosphate, calcium phytate, and potassium, respectively. Moreover, out of total endophytes; twenty-four (24), thirty-three (33) and twenty-one (21) endophytic strains displayed marked antagonistic effects against important fungal pathogens such as *Fusarium graminearum*, *Rhizoctonia solani* and *Exserohilum turcicum*, respectively.

Conclusions: Soil types play a functional role in culturable endophyte diversity and provide an isolation reference for endophytic reserves with multiple functions such as growth promoters and biocontrol agents.

Keywords: Maize endophytes, Biocontrol, Soil type, Phosphorus solubilizing, Potassium solubilizing, *Fusarium graminearum*

Background

Endophytes are important members of plant microbiome living asymptomatically in plant tissues and are found ubiquitously associated to kingdom planta. It is estimated that one or more endophytic bacteria are associated to every plant on planet earth (Ahmed et al. 2020). Endophytes are classified into bacteria, fungi, viruses, and protists (Murphy and Hodkinson 2018). Endophytic bacteria have been isolated and characterized from a diverse range of plants such as agronomic crops, prairie plants, plants inhabiting extreme environments, and wild and perennial plants (Afzal et al. 2019). Where most commonly isolated bacterial genera include *Bacillus*, *Burkholderia*, *Microbacterium*, *Micrococcus*, *Pantoea*, *Pseudomonas* and *Stenotrophomonas* (Liu et al. 2019). Endophytic bacteria develop intimate associations with plants and have greater capability to elicit beneficial effects within plants as compared to microbes isolated from plant surface, rhizosphere and soil (Selim et al. 2016). Potential endophytic bacteria act as plant growth promoters by improving nutrient uptake of plant through nitrogen fixation, siderophore production, phosphate and potassium solubilization. They can synthesize phytohormones

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such as indole 3-acetic acid (IAA), which are important indicators of plant growth. Endophytic bacteria are also known as biocontrol agents as they can efficiently defend plants from pathogen and pest attacks, by implying multiple mechanisms such as: competition, antibiosis and plant defense activation (Munir et al. 2020). Various studies have reported the ability of endophytic bacteria to antagonize phytopathogens such as *Verticillium longisporum, Rhizoctonia solani, Fusarium oxysporum* and *Pythium ultimum* (Long et al. 2010). With the intensification of agriculture, the inputs of chemical fertilizers and pesticides have also been increased which affect the agricultural sustainability, soil microbial diversity and food safety (Meena et al. 2020). Thus, it is very important to shift toward nature-based solutions such as endophytic bacteria exhibiting plant growth and biocontrol potential.

Maize is an intensively cultivated crop worldwide and considered as one of the most important cereal crop (Lobo et al. 2019). However, the production and yields are affected by pathogen attacks such as *Exserohilum turcicum, F. graminearum*, and *R. solani,* which cause northern corn leaf blight (Zhang et al. 2020), Gibberalla ear rot and stalk rot (Harris et al. 2016), and banded leaf and sheath blight (Singh et al. 2020), respectively. Finding an ideal bacterial endophyte with growth promoting and biocontrol attributes is not an easy task. Previous studies have reported the endophytic bacterial taxa associated to maize plants (Correa-Galeote et al. 2018). It is also known that several factors determine the endophytic diversity such as soil types and plant genotype (Afzal et al. 2019). Same plant cultivar growing in different soil type was reported to contain different endophytic bacterial diversity (Ding et al. 2013), as similar case was also reported for plant genotype being determinant of endophytic diversity (Rashid et al. 2012).

Exploring endophytic sources from important crop plants are gaining much attention to be used as alternatives to chemical fertilizers and pesticides. Thus, the aim of the present study was: (1) to assess the effect of soil and plant type on endophytic diversity, and (2) to isolate bacterial endophytes holding growth promoting and biocontrol ability against devastating fungal pathogens.

Methods

Sample collection

In the present study, the endophytic bacteria were isolated from the roots of maize varieties, Huidan-4, Diangu-166 and Diangu-1. The seedlings were cultivated in three replicated pots supplied with organic matter (Kunming Jinnin Woye Natural Fertilizer Company, China), red loam, and sandy loam, obtained from the Yunnan Diangu Agricultural Technology Co. Ltd. *Fusarium graminearum*, *Rhizoctonia solani* and *Exserohilum turcicum* strains were previously isolated and stored in the Molecular Plant Pathology Lab, Yunnan Agricultural University, Kunming, China, were used.

Different media used for checking endophytes characteristics

Different media (Luria Bertani (LB) medium: LB medium (10 g/l tryptone, 5 g/l yeast extract, 10 g/l NaCl, pH 7.0) and solid medium (solidified by adding 20 g/l agar on the basis of broth LB broth) were used for the separation and screening of endophytic bacteria; Ashyby medium: 10 g/l sucrose, 0.5 g/l $K_2HPO_4{\cdot}3H_2O$, 0.2 g/l NaCl, 1 g/l $CaCO_3$, 0.2 g/l $MgSO_4{\cdot}7H_2O$ and 20 g/l agar, pH 7.0–7.2 was used for endophytes to fix nitrogen, Pikovskaya medium: 10 g/l glucose, 0.5 g/l $(NH_4)_2SO_4$, 0.2 g/l NaCl, 5 g/l $Ca_3(PO_4)_2$, 0.2 g/l KCl, 0.1 g/l $MgSO_4{\cdot}7H_2O$, 2 mg/l $FeSO_4{\cdot}7H_2O$, 2 mg/l $MnSO_4{\cdot}4H_2O$, 20 g/l agar and 25 mg/l bromophenol blue were used to observe the phosphorus solubilization activity of endophytes. Aleksandrov medium: 5 g/l glucose, 0.5 g/l $MgSO_4{\cdot}7H_2O$, 5 mg/l $FeCl_3$, 0.1 g/l $CaCO_3$, 2 g/l $Ca_3(PO_4)_2$ and 2 g/l potassium aluminum silicate, 20 g/l agar and 25 mg/l, bromophenol blue were used to determine the potassium-resolving ability of endophytes (Liu et al. 2019). Moreover, calcium phytate medium: 10.0 g/l glucose, 0.2 g/l $(NH_4)_2SO_4$, 5.0 g/l $MgCl_2{\cdot}6H_2O$, 0.5 g/l $MgSO_4{\cdot}7H_2O$, 0.1 g/l KCl, 2.0 g/l calcium phytate, 20 g/l agar and the strain selected on this medium would be a phytate degrading bacteria (Li et al. 2016), minimal basal salts medium: 1. 0 g/l NaCl, 0.2 g/l $MgSO_4$, 1.0 g/l $(NH_4)_2$ SO_4, 0.5 g/l KH_2PO_4, 1.5 g/LK $2HPO_4$, 0.01 g/l $FeSO_4$, 0.01 g/l $CaCl_2$, agar 20 g/l. The pH value of the medium was adjusted to 7 with 1 mol/L HCl or NaOH, and sterilize with moist heat at 121 °C for 15 min (Singh et al. 2020; Baćmaga et al. 2015) were tested for growth condition of the microbes.

Isolation of endophytic bacteria

Surface-sterilized seeds of three maize varieties Huidan-4, Diangu-166 and Diangu-1, were planted in pots supplemented with organic matter, red loam and sandy loam. Three replicates of pots were used for each soil parameter. The roots were collected from potted plants after 15 days of plantation and washed with sterilized water to remove any attached soil particles. Root surface was sterilized with 70% ethanol for 30 s and then washed with sterilized distilled water. Subsequently, the roots were grinded, and homogenate was spread on LB agar plates. The plates were incubated at 37 °C for 24–48 h and regularly monitored for endophytic growth. All the bacterial endophytes were grouped based on their colony morphology. The total number of endophytes (CFU/g of roots) for each sample was also recorded. Also, pure culture of each endophyte was obtained by streaking on LB media and stored at − 80 °C in 20% glycerol for further study.

Molecular characterization of bacterial endophytes

Bacterial endophytes were selected based on their morphological traits and were identified from genomic DNA by using standard protocols (Sun et al. 2014b). The *rpoB* gene and 16S *rRNA* genes were amplified through PCR using specific primers as mentioned in earlier studies (Marín-Benito et al. 2014). The PCR amplified products were purified and subjected to sequencing at Shuoqing Biotechnology Company (China). Finally, the obtained sequences were aligned by the Basic Local Alignment Search Tool (BLAST) (http://www.ncbi.nlm.nih.gov/BLAST/Blast.cgi) and were compared to NCBI GenBank sequences.

Screening of nitrogen-fixing, phosphate and potassium-solubilizing isolates

The bacteria were simultaneously inoculated on Ashby's nitrogen-free medium, Pikovskaya, Aleksandrov (Liu et al. 2019) and calcium phytate agar plates to distinguish these bacteria for the required compounds (Sun et al. 2014a). The culture media for nitrogen-fixing and phosphate-solubilizing analysis were supplemented with 0.025 g/l bromophenol blue. The plates were incubated at 30 °C for 4–5 days. The ability of isolates for nitrogen-fixing, phosphate and potassium-solubilizing were identified by observing clear halo zones around the colonies.

In vitro antagonistic activity against pathogenic fungi

The filter papers with the pathogens; *F. graminearum*, *R. solani* and *E. turcicum* were separately placed on the center of each Petri dish containing 25 mL potato dextrose agar (PDA) medium and incubated for 3–5 days at 28 °C. A mycelial plug (0.5-cm in diameter) taken from five days old fungal plate was placed at the center of PDA dual culture plates. Single bacterial colony was streaked at about three centimeters from the fungi. The inhibition zone was observed after incubating the plates for 3–5 days at 28 °C.

Results

Isolation of endophytes

One hundred and seventy-four (174) culturable isolates were obtained from the roots of maize seedlings. These isolates were mostly similar among three maize varieties; however, the number and type of endophytic bacteria were dependent on soil type. While the number of bacterial endophytes recovered from maize planted in organic matter was ten (10) times higher than the number of bacteria in red loam and sandy loam. The total number of endophytes isolated from different types of soils were 10^4–10^5 CFU/g of roots, with non-significant differences among them (Table 1).

Identification of bacterial endophytes

In addition to morphological identification, the bacterial isolates were also confirmed and characterized using PCR-specific primers by targeting the *rpoB* and 16S *rRNA* genes. A total of one hundred and seventy-four (174) endophytes were recovered from the root of maize and assigned to twenty-five (25) bacterial genera. Out of these 25 genera, the majority of the endophytes belonged to *Bacillus*, *Streptomyces*, *Paenibacillus* and *Pseudomonas* genera. While *Bacillus* was the most dominant genera (52.30%) of the total isolates. However, *Streptomyces, Paenibacillus* and *Pseudomonas* accounted for 13.22, 6.32 and 4.60%, respectively, as compared to other genera, which had a low proportion as shown in Table 2. The greater bacterial diversity was recorded in organic matter (i.e., 18 genera) than the red loam and sandy loam which had ten bacterial genera each.

Table 1 The number of culturable endophytes from different varieties of maize seedling roots potted in the different soils

Type of soil	Variety of maize	Type of bacteria	Colony (CFUg^{-1} fresh root)	Proportion (%)
Organic matter	Huidan 4	26	1.40×10^5	24.60
	Diangu 166	26	1.87×10^5	32.98
	Diangu 1	26	1.10×10^5	19.33
Red loam	Huidan 4	18	4.15×10^4	7.31
	Diangu 166	16	3.90×10^4	6.87
	Diangu 1	16	1.01×10^4	1.78
Sandy loam	Huidan 4	16	1.56×10^4	2.75
	Diangu 166	16	1.00×10^4	1.77
	Diangu 1	14	1.49×10^4	2.62

Table 2 Isolation frequency of 174 endophytes from different maize seedling roots in different soils

Genus	Organic matter			Red loam			Sandy loam			Total
	H4*	D 166*	D1*	H4	D 166	D1	H4	D 166	D1	
Acinetobacter	0	0	1	1	0	0	0	0	0	2
Arthrobacter	1	0	0	0	0	0	0	0	0	1
Bacillus	13	12	6	11	9	13	11	7	9	91
Chryseobacterium	2	0	0	0	0	0	0	0	0	2
Enterobacter	2	0	0	0	0	0	0	1	1	4
Exiguobacterium	2	0	0	0	0	0	0	1	0	3
Jeotgalibacillus	1	0	0	0	0	0	0	0	0	1
Paenibacillus	1	3	1	1	2	1	1	1	0	11
Pseudomonas	1	1	2	0	1	0	0	0	3	8
Streptomyces	3	5	9	1	1	1	2	1	0	23
Burkholderia	0	1	2	0	0	0	0	0	0	3
Chitinophaga	0	2	0	0	0	0	0	0	0	2
Kurthia	0	1	0	0	0	0	0	1	0	2
Nocardia	0	1	0	0	0	0	0	0	0	1
Alicyclobacillus	0	0	1	0	0	0	0	0	0	1
Brevibacillus	0	0	1	1	2	0	0	0	0	4
Luteimicrobium	0	0	1	0	0	0	0	0	0	1
Rummeliibacillus	0	0	2	0	0	0	0	0	0	2
Agrobacterium	0	0	0	1	0	0	0	0	0	1
Microbacterium	0	0	0	1	0	0	0	0	0	1
Pantoea	0	0	0	1	1	0	0	0	0	2
Ensifer	0	0	0	0	0	1	0	0	0	1
Janthinobacterium	0	0	0	0	0	0	2	0	0	2
Fictibacillus	0	0	0	0	0	0	0	3	1	4
Isoptericola	0	0	0	0	0	0	0	1	0	1

*Huidan 4: H4, Diangu 166: D166, Diangu 1: D1

Functional characterization of endophytic isolates

The results of selected isolates showed that some endophytes could perform one or more functions such as nitrogen-fixing, phosphate and potassium-solubilizing. In total, 13 strains could efficiently fix nitrogen whereas, 84, 105 and 9 strains showed calcium phosphate, calcium phytate and potassium solubilization abilities, respectively. In dual culture assay, *F. graminearum*, *R. solani* and *E. turcicum* were antagonized by several endophytic bacteria accounting for total of 24, 33 and 21 isolates, respectively. In addition, some of these strains could inhibit two or more fungal pathogens (Fig. 1). The study highlighted that the highest number of endophytic bacteria were isolated from plants potted in organic matter as compared to other composts. In total, endophytic strains with 78, 50 and 46 isolates were obtained from organic matter, red loam, and sandy loam, respectively. The number of isolates was least, but the proportion of functional strains was highest from sandy loam (Table 3). The highest proportions of nitrogen-fixing and potassium-solubilizing strains were recorded from organic matter than other two soils. Moreover, high numbers of strains exhibiting phosphate-solubilizing and antagonizing abilities were recovered from sandy loam and the lowest from organic matter.

Functional properties in relation to bacterial genera

The bacterial isolates belonging to *Bacillus*, *Streptomyces*, *Burkholderia* and *Pseudomonas* were more functional in terms of the characteristics tested above (Table 4). Out of the total, more than 50% strains belong to *Bacillus* had the abilities of all seven functional groups. The present work revealed the dominance of *Bacillus* in all functional categories which are beneficial for plants. Also, the calcium phosphate and calcium phytate solubilizing activity was recorded for 64 and 70 isolates, belonging to *Bacillus.* The isolates from remaining genera exhibited low plant benefiting abilities, whereas no potential bacteria with these characteristics were found from the 8 genera.

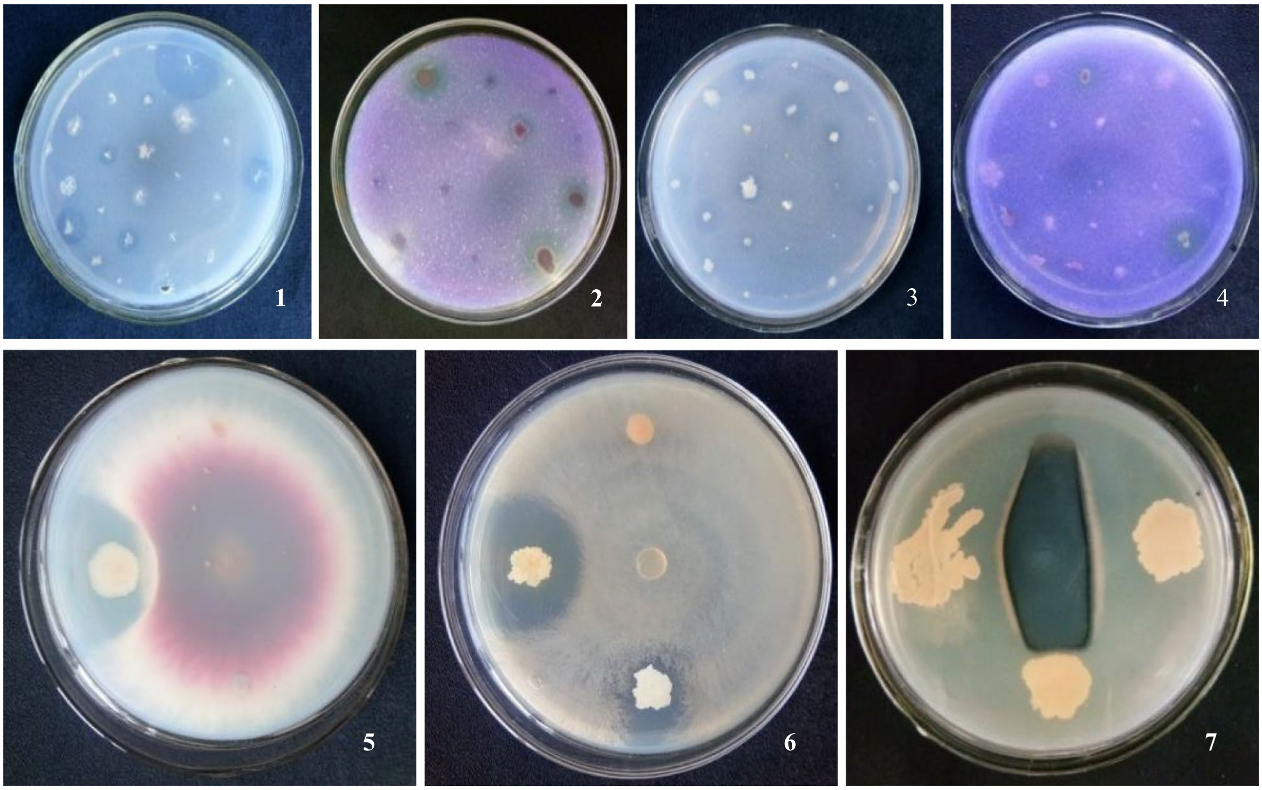

Fig. 1 Growth of endophytic bacteria on different culture media showing nitrogen fixing (1), calcium phosphate (2), calcium phytate (3) and potassium (4) solubilizing activities and the antagonistic activity against *Fusarium graminearum* (5), *Rhizoctonia solani* (6) and *Exserohilum turcicum* (7)

Abundance and proportion of endophytic genera in the roots of maize seedlings in different soil types

Significant differences in composition ratio of endophyte genera were recorded present in the three different soil types. The organic soil consists of maximum number of endophytic genera with 18, followed by 10 endophytic genera each from red loam and sandy loam. In terms of the number of genera in different soil types, the range is expressed as: organic soil > red loam = sandy loam, but in terms of the total number of genera of organic soil, red, and sandy loam, the overall expression is: organic soil > red > sandy loam. The number of genus isolated from organic soil accounted for more than 75% of the total, red loam accounted for more than 15%, and sandy loam accounted for less than 10%. Among the 25 genera, the most dominant genera recorded were *Bacillus, Streptomyces, Paenibacillus* and *Pseudomonas* in all soil types (Fig. 2).

Discussion

Endophytic bacteria are essential components of plant microbial system and known to perform countless beneficial jobs for plants. Bacterial endophytes act as both growth promoters and disease defenders for plants (Card et al. 2015). Endophytic bacteria are generally considered as subset of rhizospheric bacterial community, as they enter through roots and either localize at entry sites or spread systematically inside the whole plant (Compant et al. 2010). In addition to many abiotic factors, soil conditions are known to significantly influence the bacterial community structure in rhizosphere as well as in plant endosphere (Papik et al. 2020). Other important factor to be considered is plant genotype that can govern the endophytic bacterial communities (Ding and Melcher 2016).

The present study revealed the effects of soil type and plant genotype on bacterial endophytes and functional attributes of isolates. As soil type and physiochemical properties are important drivers of endophytic bacterial population in host plant. Obtained results showed that bacterial population and diversity were greater in

Table 3 The number of functional bacteria from roots of three maize varieties planted in three kinds of soils

Function	Variety	Organic soil		Red loam		Sandy loam	
		No	Ratio (%)	No	Ratio (%)	No	Ratio (%)
Nitrogen fixation	H4*	3	3.85	0	0.00	0	0.00
	D166*	1	1.28	1	2.00	1	2.17
	D1*	5	6.41	0	0.00	2	4.35
$Ca_3(PO_4)_2$-solubilization	H4	11	14.10	8	16.00	12	26.09
	D166	6	7.69	8	16.00	8	17.39
	D1	13	16.67	10	20.00	8	17.39
Calcium phytate-solubilization	H4	11	14.10	13	26.00	13	28.26
	D166	12	15.38	10	20.00	12	26.09
	D1	12	15.38	8	16.00	14	30.43
Potassium-solubilization	H4	3	3.85	1	2.00	0	0.00
	D166	1	1.28	0	0.00	0	0.00
	D1	3	3.85	0	0.00	1	2.17
Fusarium graminearum inhibition	H4	4	5.13	2	4.00	2	4.35
	D166	5	6.41	3	6.00	1	2.17
	D1	0	0.00	3	6.00	4	8.70
Rhizoctonia solani inhibition	H4	6	7.69	1	2.00	3	6.52
	D166	6	7.69	4	8.00	1	2.17
	D1	2	2.56	4	8.00	6	13.04
Exserohilum turcicum inhibition	H4	0	0.00	4	8.00	5	10.87
	D166	1	1.28	2	4.00	3	6.52
	D1	2	2.56	0	0.00	4	8.70

*Huidan 4: H4, Diangu 166: D166, Diangu 1: D1

organic soil than the red loam and sandy loam. The greatest diversity of endophytic bacteria could be related to the availability of surplus nutrients in organic matter. The application of organic matter is known to alter the microbial composition of soil systems as organic matter supports the microorganisms and increases their different activities related to mineral solubilization (Boehm et al. 1993). In total, 78 bacterial endophytes belonging to 18 genera were isolated from the maize roots, planted in organic matter. A study also reported the shift in bacterial diversity in response to availability of organic matter (Landa et al. 2013) which is in agreement with our results. In relation to functions, nitrogen fixing, and potassium solubilizing bacteria were higher from organic soil whereas phosphate solubilizing and fungal antagonistic were more in red loam and sandy loam. It can be speculated that availability of certain nutrients in soil enriched certain endophytic bacteria performing related functions for providing plant with maximum benefits.

The other important factor determining the culturable endophytic bacteria community is plants genotype. To study the effect of plant genotype on bacterial structural and functional diversity, three varieties of maize plant were used. Almost similar number of endophytic bacteria were recovered from three varieties grown in different soils. Thus, the results highlighted that maize varieties did not have much influence as compared to soil types. Whereas functional characteristics of endophytic isolates across soil types were more different than plant genotype. Phosphate solubilizing endophytic bacteria were the highest from all soil types and varieties as compared to other functional groups. While number of endophytic bacteria with nitrogen fixing ability was the highest in D1 grown in organic matter and sandy loam. Similarly, isolates antagonistic toward *F. graminearum* were abundant in H4 and D166 grown in organic matter, followed by D1 and H4 grown in sandy loam. In general, no correlation could be established in plant variety and soil type in terms of functional activities of endophytic bacteria.

Endophytic bacteria perform diverse functions for plant amelioration, and there is an increasing trend to integrate endophytes in biocontrol of plant diseases (Ahmed et al. 2020). As agriculture is completely dependent on the use of chemicals pesticides to obtain

Table 4 Number of bacterial isolates from different genera and functional groups

Genus	Function						
	a	b	c	d	e	f	g
Acinetobacter	1	1	2	0	0	0	0
Arthrobacter	0	1	0	0	0	0	0
Bacillus	1	64	70	1	25	29	19
Chryseobacterium	0	0	0	0	0	0	0
Enterobacter	2	2	3	3	0	0	0
Exiguobacterium	0	0	0	0	0	0	0
Jeotgalibacillus	0	0	1	0	0	0	0
Paenibacillus	0	0	6	0	1	1	0
Pseudomonas	4	4	8	2	0	3	1
Streptomyces	0	5	7	0	1	2	1
Burkholderia	3	2	1	2	0	0	1
Chitinophaga	0	0	1	0	0	0	0
Kurthia	0	0	0	0	0	0	0
Nocardia	0	0	0	0	0	0	0
Alicyclobacillus	0	1	0	1	0	0	0
Brevibacillus	0	1	1	0	0	0	0
Luteimicrobium	0	0	0	0	0	0	0
Rummeliibacillus	0	0	0	0	0	0	0
Agrobacterium	0	0	0	0	0	0	0
Microbacterium	0	0	0	0	0	0	0
Pantoea	1	2	2	0	0	0	0
Ensifer	0	0	0	0	0	0	0
Janthinobacterium	0	0	0	0	0	0	1
Fictibacillus	0	0	3	0	0	0	0
Isoptericola	0	1	0	0	0	0	0

a: growth in N-free media; b: $Ca_3(PO_4)_2$ solubilization; c: calcium phytate solubilization; d: potassium solubilization; e: *Fusarium graminearum* inhibition; f: *Rhizoctonia solani* inhibition; g: *Exserohilum turcicum* inhibition

maximum production. According to an estimate, the use of chemical pesticides is growing at an annual rate of 11%, but only 1–2% reaches to its target and 10–20% remains on the plant surface, whereas about 80–90% contaminate the environment (Ye et al. 2018). The unchecked inputs of agrochemicals pose negative effects on consumer's health as well as the environment like photo-toxicity and development of resistance in the pathogens (Meena et al. 2020). Thus, expanding endophytic source with biocontrol properties is crucial for sustainable agriculture. To screen isolated endophytic bacteria for pathogen antagonism, the biocontrol ability of isolates was tested by dual culture assay against three phytopathogenic fungi such as *F. graminearum*, *R. solani* and *E. turcicum*. The results revealed that maximum number of isolates belonged to *Bacillus,* followed by *Streptomyces, Burkholderia* and *Pseudomonas. Bacillus* is well known for its plant growth promoting and biocontrol activities (Kefi et al. 2015). Various members of *Bacillus* have been reported to show antagonistic activity against many fungal and bacterial pathogens. The inhibiting action of biocontrol bacteria is possibly due to production of antibiotics and other bioactive compounds (Long et al. 2010) and Bacilli are prime producers of plethora of secondary metabolites having antifungal activities (Bacon et al. 2015). Moreover, some isolates belonging to *Pseudomonas* and *Streptomyces* also exhibited inhibition zone against tested pathogens. As many members of these genera are well known for antagonizing several plant pathogens (Vurukonda et al. 2018).

Conclusions

In conclusion, the study reveals the diversity of culturable endophytic bacteria from three maize varieties and the effect of soil and plant genotype on endophytic bacterial diversity. The findings suggest that effect of soil type on endophytic bacterial diversity was greater than plant genotype. However, the culture-dependent isolation methods may have some bias or errors; therefore, future research will focus on culture-independent techniques to gain

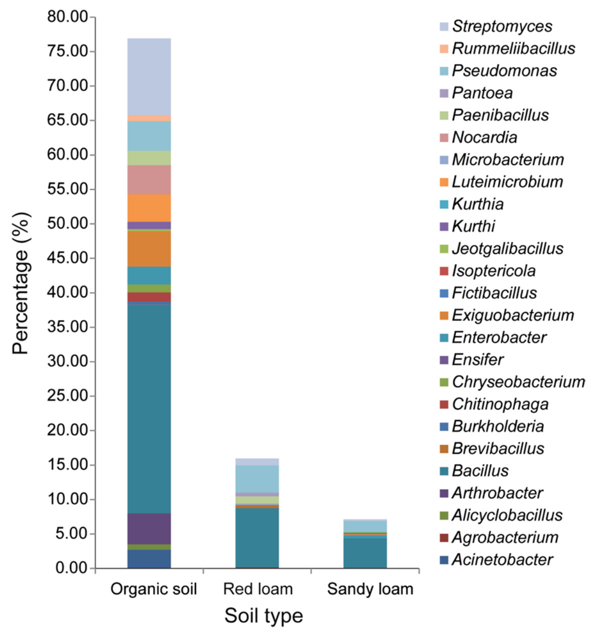

Fig. 2 Richness and percentage of endophytes of maize seedlings in different soils

more insight. Furthermore, endophytic bacteria harboring nutrient assimilation-related functions were found to be enriched in organic matter than other soil types; however, further research is required to find out exact correlation. Finally, endophytic bacteria belonging to genera well known for biocontrol attributes were also found. The present work provides an avenue to explore relationship among plant genotype, growing medium and functional properties of endophytic bacteria as well as the potential of isolates to be developed as plant growth promoters and biocontrol agents.

Abbreviations

IAA: Indole 3-acetic acid; LB: Luria bertani; CFU/g: Colony forming unit/gram; PCR: Polymerase chain reaction; BLAST: Basic local alignment search tool; PDA: Potato dextrose agar.

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Author contributions

HC, YW, and YH, conceived and designed the study and experiments; HC, SM, Pengfei He, Pengbo He, HC, and JL performed the experiments; HC, and Pengfei He analyzed the data; HC, SM, AA, and YH wrote the manuscript; and all authors contributed to the final draft of the manuscript.

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Availability of data and materials

This material is the author's own original work, which has not been previously published elsewhere and has no conflict of interest.

Declarations

Ethics approval and consent to participate

The paper reflects the author's own research and analysis in a truthful and complete manner. All authors have been personally and actively involved in substantial work leading to the paper and contributed to preparing the final draft of the manuscript and will take public responsibility for its content. This article does not contain any studies with human participants or animals performed by any of the authors.

Consent for publication

The manuscript has not been published in whole or in part elsewhere and is not currently being considered for publication in another journal. All the authors have seen the final version of the manuscript.

Competing interests

The authors declared that they have no conflict of interest.

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