

"Metagenomic Identification of Candidate Iron-Acquisition Genes in the Cowpea Rhizosphere: Extension Implications for Sustainable Production"

Onaolapo A. A.^{1*}, Odelade K. A.², Olonisakin T. M.¹, Salami A. T.¹, Oriolowo M.³, Imoru A. S.¹, Adisa A.A.³

¹Department of Agricultural Extension Management, Federal Polytechnic Ayede, Oyo State, Nigeria.

²Science Laboratory Department, Federal Polytechnic Ayede, Oyo State, Nigeria.

³Department of Agricultural Technology, Federal Polytechnic Ayede, Oyo State, Nigeria.

*Corresponding Author

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ABSTRACT

Nutrient availability is critical to the growth, development, and productivity of cowpea (*Vigna unguiculata* L. Walp); however, iron — like several other essential elements — is often present in soil in forms poorly available for plant uptake. Farmers consequently rely heavily on synthetic fertilizers and other chemical inputs, whose continuous and inappropriate use may adversely affect soil health and the environment. Microbial-based nutrient mobilization offers a potentially sustainable alternative, while agricultural extension can facilitate farmers' awareness and adoption of such technologies. This study characterized rhizosphere microorganisms associated with cowpea grown at Iresa-pupa, Surulere Local Government Area, Ogbomoso, Oyo State, Nigeria, across the two local cropping seasons — the rain-fed ("winter", WS) and dry ("summer", SS) seasons — with emphasis on genes involved in iron acquisition, using a culture-independent shotgun high-throughput sequencing approach and *in-silico* functional annotation. Functional characterization identified several genes and open reading frames (ORFs) associated with iron acquisition and metabolism. The *fhuA* and ORF *AHA_1953* encoded putative ferrichrome-iron receptor proteins associated with siderophore uptake and iron homeostasis, while *fur* (ORFs *b0683*, *JW0669*, *PA4764*, *VAA_03429*, *VP0833*) was associated with ferric-uptake regulation, ferrous-iron binding, and siderophore biosynthesis. Iron-acquisition-related functional diversity and gene richness were both higher in the winter (rain-fed) sample than in the summer (dry) or bulk soil samples. The findings point to candidate rhizobacteria — including *Pseudomonas*, *Bacillus* and *Escherichia*-related taxa carrying these iron-acquisition genes — that could be evaluated as bio-inoculants, and they highlight opportunities for agricultural extension to promote microbial-based soil-fertility technologies through farmer education, demonstration plots, and participatory technology dissemination.

Keywords: Agricultural extension, cowpea rhizosphere, iron acquisition genes, shotgun metagenomics, sustainable agriculture.

INTRODUCTION

Iron is essential to nearly all forms of life, yet in aerobic, near-neutral-to-alkaline soils it exists mainly as poorly soluble Fe³⁺ oxides and hydroxides that are largely unavailable to plant roots (Saha *et al.*, 2016). Many rhizosphere

microbes overcome this by secreting low-molecular-weight iron chelators — siderophores — that solubilize Fe^{3+} and make it accessible for uptake, a process that simultaneously helps to suppress iron-dependent phytopathogens by starving them of the metal (Ahemad and Kibret, 2014). Because cowpea (*Vigna unguiculata* L. Walp) is widely grown on marginal, often iron-limited soils across Nigeria and the wider West African savanna, understanding which rhizosphere microbes carry iron-acquisition machinery — and how this varies with cropping season — is directly relevant to reducing farmers' reliance on synthetic iron and micronutrient fertilizers.

The rhizosphere — the soil zone directly influenced by root exudates — supports microbial densities and activities well above those of the surrounding bulk soil (Fan *et al.*, 2017; Uzoh and Babalola, 2018). Culture-dependent surveys under-sample this diversity because most rhizosphere microbes cannot be readily isolated. Shotgun metagenomic sequencing avoids this bias by sequencing total community DNA directly, allowing simultaneous taxonomic and functional characterization (Gkorezis *et al.*, 2016; Escobar-Zepeda *et al.*, 2015).

This study builds on a companion metagenomic survey of the same cowpea rhizosphere soils (winter/rain-fed, WS; summer/dry, SS; and bulk soil, BS), which characterized overall microbial community structure and broad functional-metabolism categories (nitrogen, phosphorus, potassium, sulphur and iron).

- (i) The present manuscript narrows the focus to the gene- and protein-level detail of the iron-acquisition subsystem specifically, using additional BLASTP annotation against UniProtKB, and asks which genes, ORFs and predicted source organisms carry iron-acquisition functions in this cowpea rhizosphere, and
- (ii) How does their abundance differ between the rain-fed and dry season. We then translate these molecular findings into concrete recommendations for agricultural-extension delivery of microbial-based iron-mobilization technologies to cowpea farmers.

MATERIALS AND METHODS

Study Site and Soil Sampling

Soil sampling was carried out at Iresa-pupa, Surulere Local Government Area, Ogbomoso, Oyo State, Nigeria. Samples were collected during the two locally recognized cropping seasons at this site: the rain-fed season (referred to throughout as “winter”, WS) and the dry season (referred to throughout as “summer”, SS); a soil sample taken from outside the cultivated cowpea field at the same site served as the bulk-soil control (BS). We use “winter” and “summer” here strictly as season labels carried over from the companion dataset (rain-fed vs. dry season, respectively) and not in the temperate-climate sense; exact sampling dates, rainfall and temperature records for the two collection events were not available to us at the time of this analysis.

Cowpea roots were gently shaken to remove loosely adhering soil, and the soil that remained firmly attached to the roots was collected as rhizospheric soil. All soil was passed through a 2-mm sieve and thoroughly homogenized in a single container per season to obtain one composite sample each for WS, SS and BS; approximately 2 kg of composite soil per sample was transported on ice (4 °C) to the Microbial Biotechnology Laboratory, Department of Science Laboratory Technology, Federal Polytechnic Ayede, and stored at –80 °C pending DNA extraction. Although there was no independent collection, spatially separated field replicates for either season — DNA extraction, not field sampling, was replicated (in triplicate) from each composite sample.

Selected soil physicochemical properties, determined according to Enagbonma and Babalola (2023) on the same composite samples, are summarized in Table 1 below provides the abiotic context for the microbial and functional data reported here.

Table 1. Physicochemical properties of the winter (WS), summer (SS) and bulk (BS) soil samples (source: Odelade *et al.*, 2025).

Parameter	WS	SS	BS
pH (H ₂ O)	7.62 ± 0.01	8.03 ± 0.01	7.67 ± 0.01
Organic carbon (%)	0.61	1.00	0.56
Organic matter (%)	0.69	1.14	0.72
Ammoniacal nitrogen, N-NH ₄ ⁺ (mg/kg)	11.74	10.20	13.30
Total carbon (mg/kg)	0.707	1.390	0.603
Total nitrogen (mg/kg)	0.081	0.096	0.062
Phosphorus (mg/kg)	112.38	21.88	83.31
Calcium (mg/kg)	796	3460	703
Potassium (mg/kg)	547	401	211

Genomic DNA Extraction and Sequencing

Metagenomic DNA was extracted in triplicate from 0.25 g of each composite soil sample using the PowerSoil DNA Isolation Kit (MOBIO, CA, USA) following the manufacturer's protocol. DNA concentration and purity were checked by UV spectrophotometry (NanoDrop 1000, Thermo Fisher Scientific, USA). Pooled DNA was used to prepare paired-end libraries (2 × 150 bp) with the Nextera DNA Flex Library Preparation Kit (Illumina) and sequenced on the Illumina NovaSeq 6000 platform.

Bioinformatics Annotation

Sequence reads for WS, SS and BS were submitted to the MG-RAST server (version 3.3.6; Meta Genome Rapid Annotation using Subsystem Technology), a widely used platform for taxonomic and functional annotation of metagenomes (Pal *et al.*, 2018). Reads were quality-filtered to remove sequences containing ambiguous nucleotides, length-filtered to remove sequences deviating by more than 2.0 standard deviations from the mean read length, and de-replicated to remove near-identical artefactual duplicates arising from shotgun library preparation. Hierarchical classification against the SEED subsystems database was used for taxonomic and functional annotation, with an identity cut-off of 60%, a maximum e-value of 1×10^{-5} , and a minimum alignment length of 60 bp for amino-acid sequences, consistent with the companion analysis of these same samples.

To resolve the iron-acquisition subsystem to the level of individual genes, ORFs, and predicted source organisms, the corresponding SEED-annotated reads from WS, SS and BS were further annotated by BLASTP against the UniProt Knowledgebase (UniProtKB) (The UniProt Consortium, 2015). UniProtKB entries were used to assign: gene/ORF identifiers and names; the taxonomic identity of the most likely source organism (via NCBI taxonomy as implemented in UniProt); molecular function and biological process terms (Gene Ontology); and, where available, KEGG pathway context. Relative richness/abundance of each annotated gene, ORF and protein product across WS, SS and BS was visualized as a heatmap using Morpheus (<https://software.broadinstitute.org/morpheus/>) (Xia *et al.*, 2019).

Throughout the Results and Discussion, gene/ORF name (e.g., *fhuA*, *AHA_1953*) was used to refer to the nucleotide-level annotation, protein product (e.g., “ferrichrome-iron receptor”) to refer to the predicted translated product, and predicted source organism to refer to the reference taxon in UniProtKB to which the sequence was

most similar — this is a similarity-based prediction, not a culture-confirmed identification of an organism actually present in the soil.

RESULTS

Genes, ORFs and predicted source organisms in the iron-acquisition subsystem

BLASTP annotation against UniProtKB identified a set of genes/ORFs encoding proteins with established roles in microbial iron acquisition and homeostasis (Table 2). These included: *hrtA* (heme efflux system ATPase, ATP binding/transport); *irpA* (iron-regulated protein A precursor, iron acquisition/uptake/storage); *etfB* (electron transfer flavoprotein beta subunit, electron transfer/nucleotide binding); *piuB* and *piuC* (iron-uptake factors); *fecA* (outer-membrane Fe-transport receptor); *hemR* and *hupA* (TonB-dependent hemin/ferrichrome receptors); and the yersiniabactin biosynthesis enzymes *Irp1* and *Irp2* together with *angR*. The ferric-uptake regulator gene *fur* (represented by ORFs *b0683*, *JW0669*, *PA4764*, *VAA_03429* and *VP0833*) was predicted from *Escherichia coli* (strain K12), *Pseudomonas aeruginosa* (strain ATCC 15692), *Vibrio anguillarum* (strain ATCC 68554), *Vibrio parahaemolyticus* serotype O3:K6 (strain RIMD 2210633) and *Bacillus subtilis* (strain 168), consistent with roles in zinc- and ferrous-iron binding, siderophore biosynthesis regulation, and positive regulation of peroxidase activity (Fillat, 2014). The ferrichrome-iron receptor gene *fhuA* and ORF *AHA_1953* were predicted from *Aeromonas hydrophila* subsp. *hydrophila* (strain ATCC 7966), *Synechocystis* sp. (strain PCC 6803/Kazusa) and *E. coli* (strain K12), consistent with siderophore-uptake transmembrane transporter activity and iron-ion homeostasis (Gresock and Postle, 2017). *Mycobacterium tuberculosis* (strain ATCC 25618) and *M. bovis* (strain ATCC BAA-935) carried *ideR*/ORF *MTCY05A6.32*, encoding the iron-dependent repressor IdeR/DtxR, linked to divalent-metal binding, oxidative-stress response and catechol-type siderophore biosynthesis (Wells *et al.*, 2013). *Synechococcus elongatus* (strain PCC 7942) carried *irpA*, linked to metal-ion binding and iron acquisition/uptake/storage (Kranzler *et al.*, 2013).

Additional ORFs identified without a named gene symbol included: *ETAE_1794* (putative heme-iron utilization protein), *PAS_chr2-1_0427* (putative high-affinity iron permease), *CTEST_08040* and *BN137_1358* (siderophore synthetase component/ligase), and *EGS71_07105*, *PROVRETT_07949*, *Avin_09350*, *HMPREF0010_01753* and *Sde_3611* (TonB-dependent siderophore receptors).

Table 2. Protein products, gene/ORF names and predicted source microbes involved in iron-acquisition metabolism (selected entries; full annotation set available on request).

Protein product	Gene / ORF name(s)	Predicted source organism(s)	Molecular function (GO)	Biological process (GO)
Electron transfer flavoprotein, beta subunit	<i>etfB</i>	<i>Methylophilus methylotrophus</i> (Bacterium W3A1)	Electron transfer activity (GO:0009055); nucleotide binding (GO:0000166)	Electron transport
Ferric uptake regulation protein Fur	<i>fur</i> (ORFs <i>b0683</i> , <i>JW0669</i> , <i>PA4764</i> , <i>VAA_03429</i> , <i>VP0833</i>)	<i>E. coli</i> K12; <i>P. aeruginosa</i> ATCC 15692; <i>V. anguillarum</i> ATCC 68554; <i>V. parahaemolyticus</i> RIMD 2210633; <i>B. subtilis</i> 168	DNA binding (GO:0003677); DNA-binding transcription activator/repressor activity (GO:0001216, GO:0001217); sequence-specific DNA binding (GO:0043565); zinc-ion	Regulation of siderophore biosynthetic process (GO:1900705); negative regulation of transcription (GO:0045892); regulation of secondary metabolite biosynthesis (GO:1900376); siderophore

Protein product	Gene / ORF name(s)	Predicted source organism(s)	Molecular function (GO)	Biological process (GO)
			binding (GO:0008270); ferrous-iron binding (GO:0008198)	biosynthetic process (GO:0019290); positive regulation of peroxidase activity (GO:2000470); regulation of superoxide dismutase activity (GO:1901668)
Ferrichrome-iron receptor	<i>fhuA</i> ; ORF <i>AHA_1953</i>	<i>Aeromonas hydrophila</i> subsp. <i>hydrophila</i> ATCC 7966; <i>Synechocystis</i> sp. PCC 6803/Kazusa; <i>E. coli</i> K12	Siderophore-uptake transmembrane transporter activity (GO:0015344)	Iron-ion homeostasis (GO:0055072)
Iron-dependent repressor IdeR/DtxR	<i>ideR</i> ; ORF <i>MTCY05A6.32</i>	<i>Mycobacterium tuberculosis</i> ATCC 25618; <i>M. bovis</i> ATCC BAA-935	Metal (Cd, Co, Mn, Ni, Zn) binding	Response to oxidative stress (GO:0006979); siderophore biosynthesis from catechol (GO:0019540)
Iron-regulated protein A precursor	<i>irpA</i>	<i>Synechococcus elongatus</i> PCC 7942	Metal-ion binding	Iron acquisition, uptake or storage

Abundance of iron-acquisition genes/ORFs across seasons (WS, SS, BS)

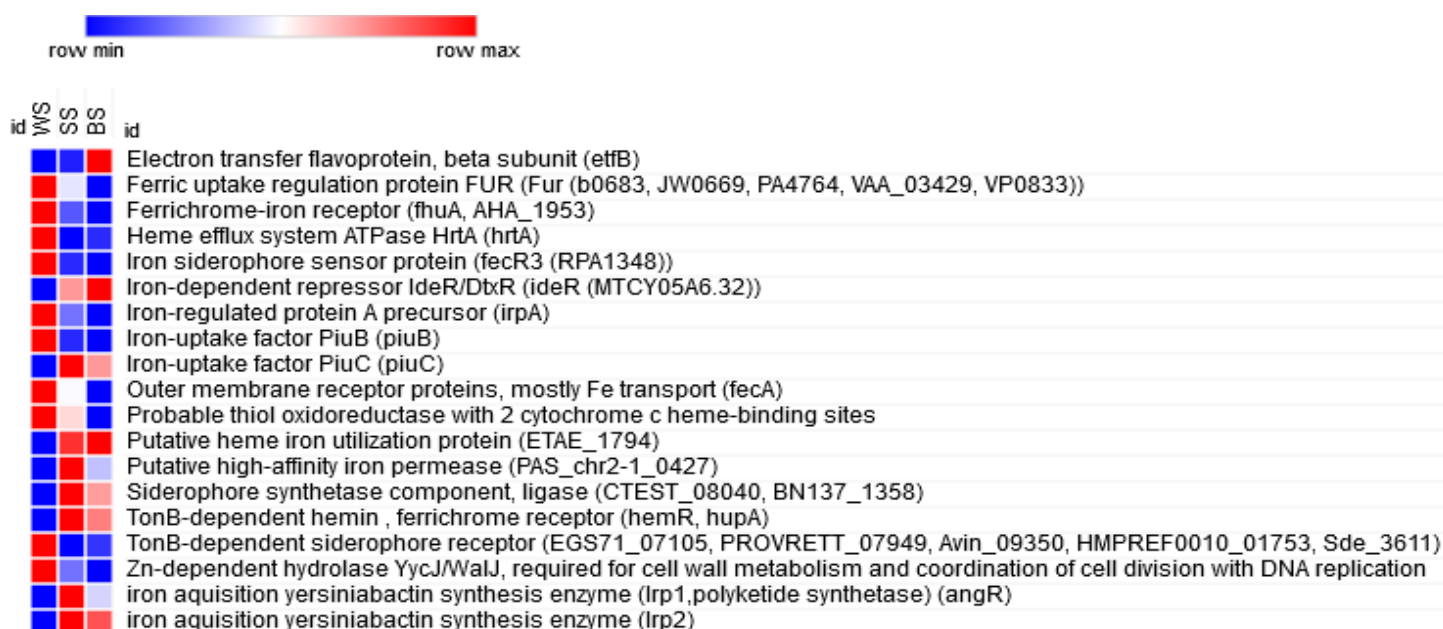


Figure 1: Relative richness (heatmap) of iron-acquisition metabolism putative products, enzymes, genes and ORF names in WS, SS and BS.

Heatmap visualization (Figure 1) showed that iron-acquisition-related genes, ORFs and protein products were detectable in all three soil samples, but were more heavily represented in WS than in either SS or BS. *piuC*, *ETA_E_1794*, *PAS_chr2-1_0427*, *CTEST_08040/BN137_1358*, *hemR/hupA*, *angR* and *Irp2* were relatively richer in SS and BS than WS (marginally richer in SS than BS), whereas *fur* (*b0683*, *JW0669*, *PA4764*, *VAA_03429*, *VP0833*), *fhuA/AHA_1953*, *hrtA*, *fecR3/RPA1348*, *irpA*, *piuB*, *fecA*, the TonB-dependent siderophore receptor cluster, and the Zn-dependent hydrolase *YycJ/WalJ* were richer in WS than in SS or BS.

Taxonomic/functional diversity of predicted source organisms

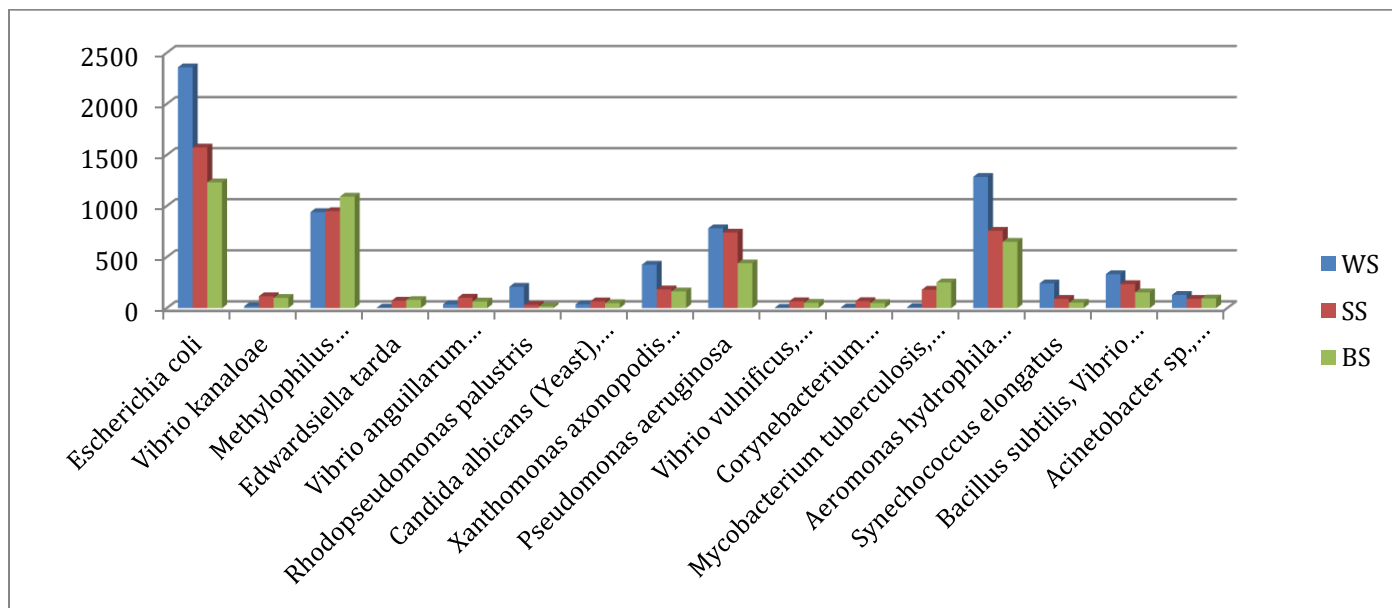


Figure 2: Functional diversity of predictive microbes involved in iron acquisition metabolism and their level of metabolic activities in WS, SS and BS

Figure 2 summarizes the level of metabolic activity contributed by each predicted source organism in WS, SS and BS. *E. coli*, *Aeromonas hydrophila* subsp. *hydrophila*, *Synechocystis* sp., *Pseudomonas aeruginosa*, *Xanthomonas axonopodis* pv. *citri*, *Bacillus subtilis*, *Vibrio anguillarum*, *V. parahaemolyticus*, *Staphylococcus aureus*, *Synechococcus elongatus* and *Rhodopseudomonas palustris* accounted for the largest share of predicted iron-acquisition activity overall, and this was consistently higher in WS than in SS or BS. *Mycobacterium tuberculosis* and *M. bovis* were, by contrast, more prominent in SS and BS than WS, and *Methylophilus methylotrophus* contributed a smaller but consistent share across samples. This pattern is broadly consistent with reports linking iron acquisition in soil/rhizosphere systems to *Staphylococcus*, *Pseudomonas*, *Enterobacter* and *Bacillus* (Kobylarz *et al.*, 2014; Gi *et al.*, 2015).

DISCUSSION

Because soil iron is largely present as poorly soluble Fe^{3+} oxides/hydroxides, microbial siderophore secretion is a principal route by which iron becomes available to associated plants (Fahad, 2012). The genes and ORFs recovered here map onto several complementary strategies for acquiring this iron rather than a single pathway: (i) siderophore-mediated acquisition (*fhuA/AHA_1953*, the yersiniabactin biosynthesis genes *Irp1/Irp2/angR*, and the TonB-dependent siderophore receptor cluster), in which a secreted chelator solubilizes extracellular Fe^{3+} for transport back into the cell; (ii) heme/hemin-based acquisition (*hemR*, *hupA*, *hrtA*, *ETA_E_1794*), which allows use of host- or organism-derived heme iron directly, bypassing the need for extracellular chelation; and (iii) regulatory control of both of the above via *fur* and *ideR/MTCY05A6.32*, transcriptional repressors that switch

iron-acquisition genes on only under iron-limited conditions and off once intracellular iron is replete, preventing iron overload and associated oxidative stress (Fillat, 2014; Wells *et al.*, 2013). The co-occurrence of all three strategies within the same rhizosphere community suggests functional redundancy: different taxa (and, within a taxon, different induced systems) can supply iron under different micro-conditions of pH, oxygen tension and iron speciation, which is plausibly advantageous in a fluctuating rhizosphere environment.

The higher iron-acquisition gene richness observed in WS (rain-fed season) than SS (dry season) or BS is consistent with the soil chemistry reported for these same samples (Table 1): WS had lower Ca^{2+} and higher relative organic-matter turnover than SS, both of which can lower Fe^{3+} solubility and select more strongly for siderophore- and heme-based iron scavengers (Saha *et al.*, 2016). We note, however, that no direct measurement of total or plant-available soil iron was made on these samples, so this remains an inference rather than a demonstrated cause; direct iron measurement in future sampling would allow this link to be tested directly.

It is also important to distinguish, as several reviewers of this class of study rightly emphasize, between functional potential (the presence of a gene in community DNA) and functional activity (that gene actually being transcribed and translated under field conditions). Shotgun metagenomics, as used here, characterizes the former only. A microbe carrying *fur* or *fhuA* is not necessarily expressing iron-acquisition machinery at the time of sampling — expression is itself iron-status dependent, which is precisely why these are regulated genes. Metatranscriptomic or metaproteomic follow-up on the same soils would be needed to confirm that the potential identified here translates into active iron mobilization in the cowpea rhizosphere, and we recommend this as a priority next step.

Several of the taxa most strongly associated with iron-acquisition genes in this study — *Pseudomonas*, *Bacillus* and *E. coli*-related sequences in particular — overlap with genera already reported as plant-growth-promoting rhizobacteria (PGPR) in legumes generally and cowpea specifically, including siderophore-producing PGPR isolated directly from chickpea rhizosphere (Ali *et al.*, 2015) and cowpea root-nodule-associated endosymbionts (Bejarano *et al.*, 2014). This overlap strengthens the case for treating *Pseudomonas*- and *Bacillus*-type isolates as priority candidates for bio-inoculant development from this system, while flagging that some of the reference organisms used here for annotation (e.g., pathogenic *E. coli*, *Vibrio* and *Mycobacterium* strains) are the closest curated database matches rather than a claim that pathogenic strains themselves are present and beneficial in this soil; culture-based confirmation of the actual rhizosphere isolates would be needed before any inoculant development proceeds.

Implications for Agricultural Extension

The candidate iron-acquisition genes and taxa identified here point to concrete, if preliminary, extension activities:

- **Priority bio-inoculant candidates:** *Pseudomonas*- and *Bacillus*-type rhizobacteria carrying siderophore and *fur*-regulated iron-acquisition systems are reasonable first candidates for isolation and greenhouse-scale inoculant trials, pending culture-based confirmation of the specific strains present in this soil.
- **Farmer training content:** extension officers could be equipped to (i) recognize visual iron-deficiency chlorosis symptoms in cowpea, (ii) understand when soil conditions (e.g., high pH/Ca, as in SS here) are more likely to limit iron availability, and (iii) integrate any future microbial inoculant with, rather than in place of, existing nutrient-management practice until efficacy is field-confirmed.
- **Participatory technology development:** on-farm demonstration plots comparing inoculated vs. non-inoculated cowpea, run jointly with farmers, would generate the field-level replication this laboratory study currently lacks, while simultaneously building farmer familiarity with the technology.

- **Delivery channels:** farmer field schools and demonstration plots remain the most direct channel for this kind of technology; mobile-based advisory services could subsequently be used to schedule inoculant application relative to planting and rainfall.
- **Adoption barriers:** cost, inoculant availability/shelf life, and unfamiliarity with microbial products (versus chemical fertilizer) are the barriers most likely to need addressing explicitly in any extension package built around these findings.

CONCLUSION

This gene-level metagenomic survey of one cowpea rhizosphere system in Ogbomoso, Nigeria identified a diverse set of genes and ORFs — spanning siderophore-mediated, heme-based, and regulatory (*fur/ideR*) iron-acquisition strategies — distributed across taxa including *Pseudomonas*, *Bacillus*, *E. coli*-related, *Aeromonas*, *Synechocystis/Synechococcus*, *Vibrio* and *Mycobacterium*-related sequences. Iron-acquisition gene richness and the functional diversity of contributing organisms were both higher in the rain-fed (WS) than the dry (SS) or bulk (BS) soil sample analyzed. Because these findings rest on a single composite sample per season without field replication or inferential statistics, they should be treated as hypothesis-generating rather than conclusive: we recommend they be followed up with a replicated field design, direct soil-iron measurement, and metatranscriptomic confirmation of gene expression before specific bio-inoculant or extension recommendations are finalized at scale. In the meantime, the taxa and genes identified here offer a concrete starting point for culture-based isolation work and for designing the on-farm demonstration trials needed to bring microbial-based iron mobilization to cowpea farmers.

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