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Genomic Insights into Antibiotic-Resistant Bacteria Associated with Plants: A Meta-Analysis of Publicly Available Whole Genome Sequences

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Abstract: This study aimed to investigate plant-associated antibiotic-resistant bacteria (ARB) using publicly available bacterial whole genome sequences (WGS) from the Bacterial and Viral Bioinformatics Resource Center (BV-BRC). A total of 1,058 WGS datasets were analyzed to identify bacterial genera, antibiotic resistance genes (ARGs), and plasmid mobility types. The dominant genera were *Xanthomonas, Mesorhizobium, Streptomyces, Pseudomonas*, and *Erwinia*, accounting for more than 65% of the isolates. *Streptomyces* and *Pseudomonas* exhibited the highest ARG abundances, averaging 0.6 and 0.3 ARGs per genome, respectively. ARG-carrying isolates were most frequent in peanut, sweet basil, bread wheat, sweet orange, and maize hosts. Ninety-three isolates (8.8%) harbored ARG-containing plasmids, among which 18% were conjugative, 25% mobilizable, and the remainder non-mobilizable. Conjugative and mobilizable plasmids were mainly found in *Pseudomonas* and *Xanthomonas* from tomato and kiwifruit hosts, while non-mobilizable plasmids predominated in *Agrobacterium, Streptomyces*, and *Bacillus*. The findings suggest that plant-associated bacteria, particularly *Pseudomonas*, *Xanthomonas*, and *Streptomyces*, constitute important ARG reservoirs and may facilitate resistance dissemination through conjugative and mobilizable plasmids in agricultural ecosystems.

Keywords: Antibiotic resistance, Horizontal gene transfer, Mobile genetic elements, Plant microbiome, Plasmid

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Introduction

Antimicrobial resistance (AMR) has become one of the most urgent global challenges [6], threatening the sustainability of both medical and agricultural systems. While the dissemination of antibiotic-resistant bacteria (ARB) is well documented in clinical and livestock environments, the role of plant-associated microbiomes as reservoirs and transmission routes for resistance genes remains underexplored. Plants host diverse microbial communities, including symbionts, commensals, and pathogens, that can exchange genetic material with soil and rhizosphere bacteria. These interfaces provide opportunities for horizontal gene transfer (HGT) and the accumulation of antibiotic resistance genes (ARGs) in agroecosystems.

Antibiotics widely used in animal husbandry often enter the agricultural environment through manure application and runoff, where they can exert selective pressure on soil and plant-associated microbiota [17]. For example, veterinary antibiotics have been frequently detected in arable soils, sediments, and surface waters near agricultural regions in Korea [8]. Similarly, sulfonamide residues are now routinely monitored across livestock and agricultural products, reflecting growing concern about environmental antibiotic contamination and its link to resistance emergence [10]. These studies highlight the potential for continuous antibiotic exposure in crop-associated environments, where resistance genes may persist or be transferred to plant-associated bacteria.

In addition, antibiotics have historically been used to control plant bacterial pathogens such as *Xanthomonas campestris* and *Erwinia amylovora*. Although such treatments are effective in reducing disease severity, they also create localized selective pressure favoring resistant strains [9]. The potential overlap between agricultural antibiotic use, microbial adaptation, and ARG dissemination across plant, soil, and water microbiomes underscores the need for genome-resolved analyses of resistance mechanisms in plant-associated bacteria.

Despite accumulating evidence of antibiotic residues and resistance in agricultural settings [17], there is limited genome-level understanding of how ARGs are distributed and mobilized within plant-associated microbial populations. Publicly available whole genome sequencing (WGS) resources, such as the Bacterial and Viral Bioinformatics Resource Center (BV-BRC) [12], provide an unprecedented opportunity to systematically investigate the genomic organization of ARGs, mobile genetic elements (MGEs), and plasmid mobility potential across diverse plant-associated taxa.

In this study, we conducted a comprehensive genomic analysis of 1,058 plant-associated bacterial genomes from BV-BRC to investigate the prevalence and diversity of ARGs, their association with MGEs, and their localization on plasmids with varying mobility potentials. By identifying representative conjugative plasmids carrying ARGs and MGEs, this study provides a genome-scale overview of antibiotic resistance dissemination within plant microbiomes and highlights the ecological significance of plants as emerging nodes in the global resistome network.

Results and Discussion

Taxonomic Composition of Plant-Associated Bacteria

A total of 1,058 bacterial genomes from the BV-BRC database were considered to be plant-associated isolates in this study. Results shown in Table 1 summarize the number of isolates obtained from plants at the genus level. Taxonomic analysis revealed that *Xanthomonas*, *Mesorhizobium*, *Streptomyces*, *Pseudomonas*, and *Erwinia* were the dominant genera, collectively representing more than 65% of all isolates. *Xanthomonas* and *Mesorhizobium* were particularly abundant in plant tissues such as tomato, chickpea, and soybean, consistent with their well-documented associations with plant pathogenicity [11] and nitrogen-fixing symbiosis [2], respectively. The diversity of plant-associated genera reflects the coexistence of symbiotic, commensal, and pathogenic bacteria within the plant microbiome.

Distribution and Abundance of Antibiotic Resistance Genes (ARGs)

AMRFinderPlus identified ARGs in approximately 29% of all isolates, corresponding to 312 genomes. The average ARG abundance per genome was 0.41, ranging from 0 to 12. *Streptomyces* and *Pseudomonas* exhibited the highest ARG counts, averaging 0.62 and 0.30 ARGs per genome, respectively (Table 2). These genera are common in soil and rhizosphere environments where natural antibiotics are produced, suggesting that intrinsic resistance may be an ecological adaptation to competitive conditions.

Among plant hosts, isolates from tomato, rice, sweet cherry, bread wheat, and apple showed moderate ARG prevalence, whereas those grouped under 'Others'—including a few isolates obtained from peanut—displayed notably high ARG abundance despite their low sample size. The peanut-associated isolates carried multiple ARGs, averaging about four genes per genome, suggesting

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Table 1. Distribution of dominant bacterial genera among plant hosts.

Genera	Chickpea	Potato	Tomato	Rice	Apple	Perennial ryegrass	Sweet cherry	Bread wheat	Kidney bean	Thale cress	Others
Xanthomonas	0	0	77	109	0	0	0	10	0	2	26
Mesorhizobium	204	0	0	0	0	0	0	0	0	0	0
Streptomyces	1	92	0	0	0	0	0	0	0	0	11
Pseudomonas	0	0	2	0	0	0	34	3	9	6	33
Erwinia	0	0	0	0	62	0	0	0	0	0	1
Labrys	0	6	3	0	0	0	0	0	1	0	28
Pectobacterium	0	29	1	0	0	0	0	0	0	0	3
Bacillus	0	2	5	1	0	0	0	4	3	2	14
Rathayibacter	0	0	0	0	1	23	0	0	1	0	0
Agrobacterium	4	0	4	0	0	0	0	0	0	2	12
Others	12	19	31	12	0	20	1	11	12	11	355

Distribution of 1,058 plant-associated bacterial isolates by genus and host plant type, based on metadata retrieved from the Bacterial and Viral Bioinformatics Resource Center (BV-BRC). The five most abundant genera (*Xanthomonas*, *Mesorhizobium*, *Streptomyces*, *Pseudomonas*, and *Erwinia*) accounted for more than 65% of all isolates.

Table 2. Average number of antibiotic resistance genes (ARGs) per genome across dominant bacterial genera and plant hosts.

Genera	No. of isolates	Average ARGs per genome	Major ARG classes detected	Representative host plants
Streptomyces	104	0.62	β-lactam, tetracycline	Potato, others
Pseudomonas	87	0.30	Aminoglycoside, β-lactam	Sweet cherry, tomato
Xanthomonas	224	0.27	β-lactam, multidrug efflux	Tomato, rice, wheat
Mesorhizobium	204	0.23	Macrolide, tetracycline	Chickpea
Bacillus	29	0.19	β-lactam, vancomycin	Bread wheat, maize
Agrobacterium	22	0.17	β-lactam, aminoglycoside	Chickpea, tomato
Erwinia	63	0.09	β-lactam	Apple
Labrys	38	0.07	Efflux pump-related	Perennial ryegrass
Pectobacterium	30	0.06	β-lactam	Potato
Others	257	0.21	Mixed types	Multiple hosts
Total / mean	1,058	0.41	—	—

Average abundance and major classes of antibiotic resistance genes (ARGs) detected in 1,058 plant-associated bacterial genomes. ARGs were predicted using AMRFinderPlus, and averages were calculated per assembled genome. *Streptomyces* and *Pseudomonas* exhibited the highest ARG frequencies, whereas *Mesorhizobium* and *Erwinia* contained comparatively few resistance determinants.

strong adaptation to antibiotic-exposed environments, possibly influenced by soil fertilization or prior antibiotic use in agricultural settings [16].

The most frequent ARG classes included β-lactam, tetracycline, and aminoglycoside resistance genes. The broad distribution of these ARGs across both symbiotic and free-living plant-associated genera highlights the diverse selective pressures acting on the plant microbiome. These findings indicate that antibiotic resistance is not confined to pathogenic taxa but is also maintained among environmental and mutualistic bacteria that inhabit plant-associated ecosystems.

Association of ARGs with Mobile Genetic Elements (MGEs)

Among the 1,058 plant-associated bacterial genomes analyzed, a total of 93 isolates (8.8%) harbored plasmids containing at least one ARG. MOB-suite typing further categorized these plasmids into 17 conjugative (18%), 23 mobilizable (25%), and the remainder as non-mobilizable plasmids (Table 3). Conjugative and mobilizable plasmids were primarily detected in

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Table 3. Representative antibiotic resistance gene (ARG)-carrying plasmids identified in plant-associated bacteria.

Genus	No. of isolates with ARG plasmids	Conjugative (%)	Mobilizable (%)	Non-mobilizable (%)	Major host plants	Representative plasmid type (rep/mob)
Pseudomonas	8	50	37.5	12.5	Tomato, Kiwifruit	MOBP, MPF_I
Xanthomonas	7	29	57	14	Tomato	IncP, MOBP
Agrobacterium	6	0	0	100	Chickpea, Tomato	MPF_T (chromid-like)
Streptomyces	5	0	0	100	Potato	—
Bacillus	4	0	0	100	Bread wheat	Rep_cluster_1869
Delftia	2	0	100	0	Peanut	MOBP
Others	61	13	21	66	Various	Mixed types
Total (n = 93)	—	18%	25%	57%	—	—

Plasmids were categorized by MOB_SUITE into conjugative, mobilizable, and non-mobilizable types. Conjugative and mobilizable plasmids, which represent the highest risk for horizontal gene transfer (HGT), predominated in *Pseudomonas* and *Xanthomonas* species. Non-mobilizable plasmids accounted for 100% of ARG plasmids in *Agrobacterium*, *Streptomyces*, and *Bacillus*.

Pseudomonas and *Xanthomonas* species isolated from eudicot hosts such as tomato, kiwifruit, and citrus, while non-mobilizable ARG plasmids were frequently identified in *Agrobacterium*, *Bacillus*, and *Streptomyces* isolates from monocot hosts including chickpea, potato, and bread wheat.

In this study, we observed 3 conjugative and 2 mobilizable plasmids carrying ARGs. These bacteria, including *Citrobacter*, *Pseudomonas*, *Xanthomonas*, and *Delftia*, have plasmids carrying beta-lactam and Aminoglycoside resistance genes. Figure 1 illustrates representative conjugative plasmids carrying ARGs and mobile genetic elements (MGEs). These plasmids typically contained ARGs adjacent to insertion sequences (IS) or transposon-related genes, suggesting potential for horizontal gene transfer. In particular, the *Citrobacter telavivensis* plasmid from a kiwifruit host carried a cluster of β-lactamase (*blaTEM*) associated with transposon Tn2, indicating an active transfer capability. Similarly, *Pseudomonas coronafaciens* plasmids carried *aph(6)-Id* and *aph(3"")-Ib* genes in proximity to transposon Tn6082, consistent with known ARG mobilization mechanisms.

These findings highlight the underappreciated role of plant-associated bacteria as potential intermediaries in the environmental antibiotic resistance network. The structural organization of conjugative plasmids (Figure 1) — with ARGs often co-located with MGEs and transfer modules — supports the hypothesis that plant surfaces and tissues may act as transitional niches linking agricultural and environmental resistomes. Continued surveillance of ARG-bearing plasmids in crop-associated microbiomes will

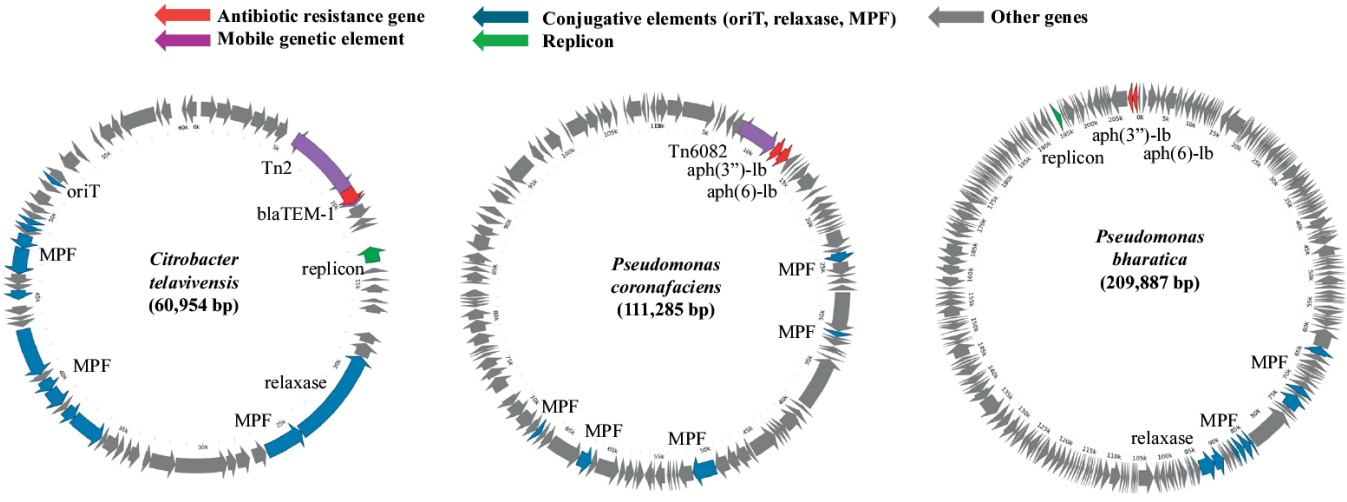

Figure 1. Representative Conjugative Plasmids Carrying Antibiotic Resistance Genes in Plant-Associated Bacteria.

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be crucial to understand and mitigate their contribution to horizontal gene transfer in agroecosystem.

Comparative analysis of ARG and MGE coordinates revealed 44 ARG–MGE co-localization events detected within 5 kb on the same contig across multiple plant-associated bacterial isolates. Of the 44 ARG–MGE associations identified, most were located on mobilizable or conjugative plasmids, underscoring their high potential for dissemination among plant-associated bacteria. The co-occurrence of ARGs with MGEs and conjugation-related genes suggests that the plant microbiome may serve as an active reservoir and vector for antibiotic resistance dissemination. Notably, these conjugative plasmids were recovered not only from phytopathogenic species such as *Xanthomonas* and *Erwinia*, but also from commensal genera (*Mesorhizobium* and *Pseudomonas*), indicating that resistance traits may circulate even among non-pathogenic members of the plant microbiota. These co-localization events were most frequently observed in *Pseudomonas, Xanthomonas, Agrobacterium,* and *Staphylococcus*, spanning both chromosomal and plasmid contexts. Insertion sequences and unit transposons were the dominant MGEs, including IS6100, ISBm2, ISSau6, and Tn5405, which are commonly involved in gene mobilization and horizontal transfer (Table 4).

In *Xanthomonas campestris* isolates from tomato, aminoglycoside resistance genes (*aph(6)-Id*, *aph(3″)-Ib*) were positioned within 0.6–2.8 kb of IS6100, suggesting recent or ongoing transpositional activity. *Agrobacterium fabrum* from chickpea carried β-lactamase genes (*bla* family) adjacent to ISBm2, typically located on plasmid-like contigs. Similarly, *Pseudomonas coronafaciens* and *P. bharatica* isolates from kiwifruit and tomato possessed conjugative plasmids harboring aminoglycoside ARGs within 1 kb of Tn6082, a well-known broad-host-range transposon [15]. Among Gram-positive taxa, *Staphylococcus saprophyticus* from bread wheat and *Bacillus fungorum* from maize contained β-lactam and multidrug resistance genes near ISSau6 or lineage-specific IS elements, respectively.

Importantly, most ARG–MGE linkages were found on contigs identified as conjugative or mobilizable plasmids, rather than chromosomal fragments. This genetic arrangement strongly suggests that a substantial fraction of ARGs in plant-associated bacteria occur within highly transferrable plasmid backbones. The physical proximity of resistance genes to insertion sequences and transposons within these plasmids provides a mechanistic basis for horizontal gene transfer among environmental, plant-associated, and potentially human-associated bacteria [4].

These results demonstrate that plant-associated microbiomes contain multiple mobile resistance elements embedded in plasmids and chromosomes capable of transfer across diverse bacterial taxa, underscoring their role as potential hubs for antibiotic resistance dissemination.

Ecological and Agricultural Implications

The prevalence of ARGs in *Pseudomonas*, *Xanthomonas*, and *Streptomyces* underscores the dual role of plant-associated bacteria as both beneficial microbiota and potential reservoirs of antimicrobial resistance. The detection of conjugative and mobilizable ARG-carrying plasmids in crops such as tomato and wheat highlights the possibility of resistance gene transfer between

Table 4. Representative ARG–MGE co-localization events in plant-associated isolates (≤5 kb on the same contig).

Genus (species)	Plant source	Contig context	MGE type (example)	Nearby ARG(s)	Resistance class
Xanthomonas campestris	Tomato	Chromosome	IS (IS6100)	*aph(6)-Id*, *aph(3″)-Ib*	Aminoglycoside
Agrobacterium fabrum	Chickpea	Chromosome / plasmid-like	IS (ISBm2)	β-lactamase (e.g., *bla* family)	β-lactam
Pseudomonas spp.	Tomato	Plasmid-like	Transposon (Tn6082)	*aph* family	Aminoglycoside
Staphylococcus spp.	Bread wheat	Chromosome	IS (ISSau6), Tn (Tn5405)	β-lactamase, *aad*	β-lactam; Aminoglycoside
Bacillus spp.	Maize	Chromosome	IS (lineage-typical)	Efflux/β-lactamase	Multidrug; β-lactam
Agrobacterium spp.	Tomato	Plasmid-like	IS (ISBm2)	*aph* family	Aminoglycoside

Selected examples of antibiotic resistance genes (ARGs) detected within 5 kb of mobile genetic elements (MGEs) on the same contig. MGE types were annotated with MobileElementFinder; ARGs were called by AMRFinder2. Full listings for all 57 isolates are provided in Supplementary Table S2.

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environmental, commensal, and phytopathogenic bacteria within agricultural systems. Because many of these bacteria colonize edible plant tissues and surfaces, they may serve as intermediate vectors facilitating ARG movement between soil environments, plants, and ultimately the human microbiome.

These findings reinforce previous evidence that agricultural soils and plant-associated bacteria represent critical nodes in the global resistome network. Sustained surveillance of plasmid-mediated ARGs and mobile elements in plant microbiomes is therefore vital for evaluating the ecological consequences of antimicrobial use in crop production and for developing science-based strategies to mitigate resistance dissemination in agroecosystems.

The identification of ARGs on conjugative and mobilizable plasmids in genera like *Pseudomonas* and *Xanthomonas* underscores the immediate need for targeted mitigation strategies. Our analysis suggests a critical distinction: while soil-native bacteria (*Streptomyces*) often carry innate ARGs on non-mobilizable elements, the highly mobile ARGs likely originate from livestock waste. Given that veterinary antibiotics and ARGs enter agricultural environments primarily through manure application, we propose a key intervention: implementing routine monitoring and pre-application remediation of manure by measuring both residual antibiotic levels and the abundance of mobilizable ARG markers before land spreading. This targeted approach is crucial for reducing selective pressure and diminishing the role of the plant microbiome as a node for antibiotic resistance gene transfer in agroecosystems.

Materials and Methods

Data Collection

Publicly available bacterial whole genome sequencing (WGS) data associated with plant sources were retrieved from the Bacterial and Viral Bioinformatics Resource Center (BV-BRC, https://www.bv-brc.org/) [12]. Metadata were screened to include only isolates annotated as originating from plant tissues (e.g., leaf, root, fruit, seed, or rhizosphere). A total of 1,058 isolates representing diverse bacterial genera and plant hosts were selected for downstream analyses.

Genome Assembly and Detection of Antibiotic Resistance Genes (ARGs) and Mobile Genetic Elements (MGEs)

Raw paired-end FASTQ files were quality-filtered using fastp (v0.23.2) [5] with default parameters to remove adapter sequences and low-quality bases. Cleaned reads were assembled de novo using SPAdes (v3.15.5) [1]. Antibiotic resistance genes were identified using AMRFinderPlus (v3.11.18) [7] implemented with default parameters and the latest NCBI AMR database (as of 2025-08). The number of ARGs per isolate was summarized for genus- and plant-level comparisons. Insertion sequences, transposons, and miniature inverted-repeat transposable elements (MITEs) were detected using MobileElementFinder (v1.0.3) (https://bitbucket.org/mhkj/mge_finder/src/master/). The resulting coordinates were compared with ARG positions from AMRFinderPlus outputs to identify ARG–MGE co-localization events (within 5 kb on the same contig).

Identification and Typing of Plasmids

Plasmid-like contigs were identified using geNomad (v1.6.2) [3] in nucleotide mode. Contigs predicted as plasmid-origin were further characterized using MOB_SUITE (v3.1.9) [13], which classifies plasmids based on mobility potential (conjugative, mobilizable, or non-mobilizable), replication initiator types (*rep*), and relaxase types (*mob*). Plasmids carrying ARGs were identified by cross-referencing plasmid contigs with AMRFinderPlus results.

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Plasmid Map Creation

Three representative conjugative plasmids identified by MOB-typer as carrying ARGs were selected for visualization. For each plasmid, coding sequences were annotated with Prokka [14], and ARGs were detected using AMRFinderPlus. MGEs were identified with MobileElementFinder, and conjugation- or replication-related genes were retrieved from the MOB-suite biomarkers.blast.txt output using a conservative BLAST filter (percent identity and coverage ≥ 80%). Circular plasmid maps were then drawn in Python using the pycirclize library, which displays genes as strand-oriented arrows with color coding for feature type.

Taxonomic and Statistical Analysis

Taxonomic classification was done using BLAST with the 16S rRNA gene database. Summary statistics and comparative analyses among genera and plant hosts were performed using R (v4.3.2) with packages *dplyr* and *tidyr*.

Data Availability: All data are available in the main text or in the Supplementary Information.

Author Contributions: TU and DL designed the study, SK collected sequence data information, TU performed the bioinformatic analysis, JH and JO conducted statistical analysis, TU wrote the first draft, and JH, JO, and DL finalized the manuscript.

Notes: The authors declare no conflict of interest.

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Additional Information:

Supplementary information The online version contains supplementary material available at https://doi.org/10.5338/KJEA.2025.44.35

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