



Pseudomonas koreensis AB36 from a gold mine: genomic insights into adaptation to extreme conditions and potential plant growth promotion

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Abstract

The genus *Pseudomonas* is one of the most varied and widespread bacterial genera, with species found in most environment. They are known to degrade organic and inorganic compounds, produce secondary metabolites, and enhance plant growth. The genome of *Pseudomonas koreensis* AB36, a heavy metal resistant organism isolated from a gold mine was sequenced to unveil the versatile metabolic potential of the organism. The genome is a single circular chromosome of 5,902,614 bp, with G + C content of 60.1%. There are 4154 similar orthologous gene clusters shared among strain AB36 and other sequenced *P. koreensis* strains with 7 clusters found alone in the genome of strain AB36. Genome mining of the organism predicted 8 biosynthetic gene clusters using antiSMASH including three non-ribosomal peptide synthetase (NRPS) clusters, arylpolyene and bacteriocin. The genome contains putative genes for heavy metal transport/resistance. These results show the heavy metal resistance ability and degradation of xenobiotic compounds of strain AB36 as well as its potential to adapt to various environments.

Keywords Heavy metals · Stress adaptation · Bioremediation · Secondary metabolite · Plant growth promotion · Pan-genomics

Abbreviations

ANI	Average nucleotide identity
BPGA	Bacterial pan-genome analysis
Cd	Cadmium
Cr	Chromium
COG	Clusters of orthologous groups
GO	Gene ontology
GIs	Genomic islands
HCN	Hydrogen cyanide
IAA	Indole-3-acetic acid
KEGG	Kyoto encyclopaedia of genes and genomes

Pb	Lead
antiSMASH	The antibiotics & Secondary metabolite analysis shell

Introduction

Environmental pollution has increased because of industrialization and urbanization and has become a worldwide issue that requires coordinated monitoring, control, and clean-up efforts (Nahurira et al. 2019). Heavy metal contamination of aquatic and terrestrial ecosystems poses a public health risk, because these metals have risen above the acceptable limit (Ayangbenro and Babalola 2017; Fashola et al. 2020a, b; Ndeddy Aka and Babalola 2017). Metals are a naturally occurring component of the earth's crust, but human actions have increased their concentration in the environment. This is harmful to all life forms and continue to pose substantial risks to public health and the environment (Nahurira et al. 2019).

Microorganisms with high potential have been used in clean-up operations to remediate metal contaminants and improve the condition of degraded ecosystems. Bacteria strains of the genus *Pseudomonas* are commonly used in remediation of polluted environment. They are one of the

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most diverse genera, commonly found in soil, and are well known for their broad and versatile metabolic characteristics (Camara et al. 2007; Babalola and Ayangbenro 2019; Balogun et al. 2015). They are involved in the decomposition of organic matter, bioremediation, plant growth-promotion and show pathogenic effects (Kwon et al. 2003; Olanrewaju et al. 2017). They are also sources of various enzymes and metabolites of industrial and biotechnological importance.

Pseudomonas koreensis is a Gram-negative, rod-like, non-spore forming motile bacterium with growing biotechnological importance was initially identified from Korean agricultural soil by Kwon et al. (2003). A growing number of studies have reported a variety of functions of *P. koreensis* related to plant growth-promotion (Guo et al. 2020; Ben Zineb et al. 2020), biocontrol of phytopathogens (Lin et al. 2016; Hultberg et al. 2010), removal of heavy metals (Ayangbenro et al. 2019; Babu et al. 2015), biosurfactant production (Hultberg et al. 2010; Toribio et al. 2011), phosphorus solubilisation (Srivastava et al. 2019; Ben Zineb et al. 2020), lipase production (Anbu 2014), antimicrobial production (Kaur et al. 2019) and biofloculant production (Ayangbenro et al. 2019). *P. koreensis* are of tremendous interest for the development of innovative products for industrial and biotechnological applications because of their versatile nature. Nevertheless, there is limited knowledge about the genetic make of the organism and its environmental applications. With advances in genome sequencing, the systematic analysis of the whole-genome and mining of biosynthetic pathways for novel compounds have been made possible.

We demonstrated that exposure of environmental microbiota to heavy metals facilitated the acquisition of an arsenal of metal resistant genes that confer resistance and/or tolerance to heavy metals, such as lead (Pb), Cadmium (Cd), and Chromium (Cr), as part of an ongoing investigation on microbe-metal interactions. To this end, the biochemical and genome sequence of strain AB36 is analysed to unveil the genetics behind the versatility of the organism and its environmental application.

Materials and methods

Isolation and characterization

As previously described by Ayangbenro et al. (2019), the strain was isolated from a gold mining soil in Vryburg (S 26.1681354 E 25.246582), South Africa, using serial dilutions on Luria–Bertani agar supplemented with heavy metals (50 mg L⁻¹ each of Pb(NO₃)₂, CdSO₄, and K₂CrO₄). The metal solutions were filter sterilized through 0.22 µm membrane filters (Millipore Corporation, Bedford, MA, USA). The pH of the soil sample was 5.8, while the concentrations of heavy metals were 0.262, 0.347, 0.536, 1.858, 0.699, and

0.96 mg kg⁻¹ for Cd, Cr, Cu, Pb, Ni, and Zn, respectively. The moisture content of the soil sample was 0.153% with 84.0% sand, 2.0% silt, and 14.0% clay. We isolated several bacteria and one was identified as *Pseudomonas koreensis* AB36.

Plant growth-promoting traits

The strain was screened for phosphate solubilization, ammonia, hydrogen cyanide (HCN), indole-3-acetic acid (IAA), and siderophore production as previously described by Chukwuneme et al. (2020) and Ayangbenro et al. (2023). For ammonium production, freshly prepared strain AB36 10 µL (0.2 OD) was inoculated into 10 mL of peptone water. Test tubes with inoculated bacteria were incubated at 25°C for 7 days, after which 1 mL of Nessler's reagent was added, and color change was observed. Positive ammonia production is indicated by a yellow or brown color change in the medium.

Strain AB36 was tested for its ability to solubilize phosphate by spotting 10 µL of the isolate onto Pikovskaya agar and incubating it at 28°C for 7 days. The ability of the isolate to solubilize phosphate was demonstrated by the presence of a distinct halo zone surrounding the culture spot. The halo zone around the isolate was measured in triplicate.

For hydrogen cyanide production, strain AB36 was streaked on a nutrient agar plate after being cultured in nutrient broth supplemented with 4.4 g L⁻¹. Sterile Whatman filter paper (no. 1) was placed on top of the plate after being soaked in a solution containing 2% sodium carbonate and 0.5% picric acid. The plate was sealed with parafilm and incubated for 4 days at 28°C. HCN production was demonstrated by a color change from yellow on Whatman filter paper to dark brown.

Strain AB36 (100 µL) was added to nutrient broth (5 mL) supplemented with 0.1% tryptophan, and the mixture was incubated at 28°C for 48 h. Following incubation, cells were harvested by centrifugation at 10,000 rpm for 10 min. Four milliliters of Salkowski reagent (50 mL, 35% perchloric acid, and 1 mL of 0.5 M FeCl₃ solution) were added 2 mL of the supernatant and 2 drops of 10 mM orthophosphoric acid. The mixture was incubated at room temperature for 25 min. The development of a pink color indicates IAA production.

Chrome azurol S (CAS from Merck, SA) was used as an indicator dye to measure the siderophore synthesis by strain AB36. In short, 10 mL of iron (III) solution (1 mM FeCl₃·6H₂O in 10 mM HCl) was combined with 60.5 mg of CAS that had been dissolved in 50 mL of distilled water. After dissolving 72.9 mg of hexadecyltrimethylammonium (HDTMA, Merck, SA) bromide in 40 mL of distilled water, the mixture was gradually added and continuously stirred with a magnetic stirrer. The mixture was then autoclaved for 15 min at 121°C. Poured into Petri plates, the final mixture (100 mL) was stirred in with 900 mL of sterilized LB broth that had been adjusted to pH 6.8. Freshly prepared bacterial cultures were spot inoculated on Petri plates after solidification and incubated for 7

days at 25°C. Siderophore production was considered positive when a yellowish halo surrounded the bacterial colonies. The supernatant from the centrifuged bacterial cells was collected in tubes after centrifugation at 3000 g for 10 min. The siderophore concentration was determined by mixing 100 µL of CAS assay solution with 100 µL of supernatant and equilibrating for 3–4 h, followed by the measurement of absorbance at 630 nm using a UV spectrophotometer (ThermoSpectronic, Merck chemicals, SA). The percentage siderophore produced was calculated by the equation:

$$\% \text{ Siderophore units} = \frac{Ar - As}{Ar} \times 100$$

where Ar = Absorbance of reference at 630 nm (CAS reagent), As = Absorbance of sample at 630 nm.

Genomic DNA extraction and sequencing

The genomic DNA of the organism was extracted according to the manufacturer's instructions using the Zymo Research soil microbe miniprep DNA extraction kit (Zymo Research, CA, USA). The purity of the DNA was determined using a 1% agarose gel stained with ethidium bromide. Strain AB36 genome was sequenced on MiSeq platform (Illumina) in paired-end module at Molecular Research DNA, Shallowater, TX, USA. The library was prepared with the Illumina Nextera DNA sample preparation kit, and the final library concentration was determined with the Life Technologies, Inc. Qubit double-stranded DNA high-sensitivity test kit. The average library size was determined using an Agilent 2100 Bioanalyzer (Agilent Technologies), followed by library pooling and dilution to 12.0 pM. With an average coverage of 50x, the paired-end sequence was produced using an Illumina 600-cycle v.3 reagent kit.

Genome assembly, annotation, and bioinformatics analysis

FastQC (v 1.0.4) (Andrews 2010) was used to assess the raw sequence quality, and raw reads were trimmed with Trimmomatic (v 0.36) (Bolger et al. 2014) to eliminate adapter and low-quality sequences. SPAdes (v 3.12.0) assembler (Nurk et al. 2013) was used for de novo assembly of the reads into contigs. Default parameters were used for all analyses. The assembled genome was annotated with the Rapid Annotations using Subsystems Technology (v.2.0) (Aziz et al. 2008) and the NCBI Prokaryotic Genome Annotation Pipeline (PGAPv.4.7) (Haft et al. 2017). Functional genome annotation was performed using KofamKOALA (Aramaki et al. 2020) and the genomic islands were predicted in IslandViewer (Bertelli et al. 2017). OrthoANiu (Yoon et al. 2017) was used to calculate the genomic average nucleotide

identity (ANI) and the circular view of the genome was generated with CGview (Grant and Stothard 2008). Protein comparisons with OrthoVenn 2.0 using default settings were used to identify orthologous clusters and Gene Ontology (GO) annotation among *P. koreensis* AB36, *P. koreensis* strain D26, *P. koreensis* strain CRS05 R5, *P. koreensis* strain LB-090714, *P. koreensis* strain P2, *P. koreensis* strain BS3658, and *P. koreensis* strain P19E3 (Xu et al. 2019).

Pan-genome and core-genome analyses

Bacterial pan-genome analysis (BPGA) is a computer pipeline for comparative genomic analysis and pan-genome building that is fast and efficient (Chaudhari et al. 2016). Pan- and core-genome of 7 *P. koreensis* strains (AB36, BS3658, CRS05_R5, D26, LB-090714, P2 and P19E3) were obtained by BPGA pipeline. The pan-genome curve fitting was calculated using power-law regression based on Heaps' law as follows:

$$y = \frac{1}{4} A_{\text{pan}} x^{\delta} B_{\text{pan}} \ln C_{\text{pan}}$$

where A_{pan} , B_{pan} , and C_{pan} are fit parameters, y is the pan-genome size, x is the genome number.

Since power-law regression accurately depicts the declining rate of gene discovery with an increase in the number of genomes analyzed, it is a good choice for modeling this connection. The power-law regression can be used to predict the potential total size of the pan-genome as more genomes are analyzed, it is therefore justified for pan-genome analysis because it accurately reflects the underlying biological phenomenon where the pan-genome expands with the inclusion of more strains, albeit at a decreasing rate.

KEGG and COG classifications

The BPGA platform is deciphered for future “omics” methods by analyzing data subsets under the KEGG (Kyoto Encyclopedia of Genes and Genomes)/COG (Clusters of Orthologous Groups) categories. BPGA uses USEARCH's ublast function to find the best hits in various reference databases and classify the genes using COG and KEGG categories (Chaudhari et al. 2016).

Prediction of genes involved in secondary metabolite production

The antibiotics & Secondary Metabolite Analysis Shell (antiSMASH) database (v 5.1.2) (Blin et al. 2019) was used to identify and analyse the putative biosynthetic gene clusters present in strain AB36.

Statistical analysis

The plant growth-promoting traits were produced in triplicate and analyzed by analysis of variance (ANOVA) using Duncan's multiple range tests (DMRT) at the $p=0.05$ level with SPSS (ver. 16.0, IBM SPSS Statistics, Chicago, IL, USA).

Results and discussion

Heavy metal resistance and biofloculating properties of strain AB36 were previously reported (Ayangbenro et al. 2019). Heavy metal-contaminated soil microbial communities have been found to have an abundance of genes conferring tolerance to heavy metals (Abou-Shanab et al. 2007; Xavier et al. 2019; Shu et al. 2020). Metallosensors cause the downregulation of metal uptake genes while activating metal efflux and storage genes (Ehrensberger and Bird 2011). They inhibit hazardous metal uptake by regulating membrane transporters, membrane channels, and efflux pumps. Furthermore, they induce the production of chelators and siderophore (Corretto et al. 2020). Metallo-sensing regulators and resistance genes are essential for the adaptation and tolerance to heavy metal-contaminated environments. Strain AB36 possesses heavy metal resistance genes involved in metal uptake.

Strain AB36 was screened for various plant growth-promoting traits, such as ammonia, HCN, IAA, siderophore production, and phosphate solubilization (Table 1). The isolate was positive for ammonia, HCN, IAA and siderophore production. Similarly, the isolate solubilized the phosphate. Proteobacteria possess many plant growth-promoting features (Bruto et al. 2014; Leontidou et al. 2020). Phosphate solubilization is a key process for promoting plant development. Through processes including the release of phosphatase, which releases phosphorus from its organic matter-bound state, and the synthesis of organic acids and chelating agents, which lower pH levels in the rhizosphere, bacteria can increase the amount of

phosphorus available to plants (Chukwuneme et al. 2020). There have been reports of several bacterial species, such as *P. koreensis*, solubilizing inorganic phosphates (Srivastava et al. 2019; Gu et al. 2020). Accordingly, our results are similar to those of previous studies on phosphate solubilization.

Genomic features of *Pseudomonas koreensis* strain AB36

The genome of *P. koreensis* strain AB36 includes a single circular chromosome of 5.9 Mbp with an average G + C content of 60.1% (Fig. 1). Functional analysis using Kofam-KOALA resulted in the annotation of 3475 genes (66.46%) from 5229 CDS (Table 2). The remaining CDS (33.54%) were not annotated to any function, likely representing poorly characterized or unknown genes. Table SI 1 presents the number of proteins in the genome of each *P. koreensis* strain used in this study and their G + C content. The number of unique genes present in the genome of each strain is presented in Table SI 2. Strain AB36 had the lowest number of unique genes compared with other *P. koreensis* strains, whereas strain D26 had the highest (Table SI 2). The RAST annotation resulted in the functional annotation of 2458 genes from 5242 CDSs (46.9%). Amino acids and derivatives metabolism (511), carbohydrate metabolism (260), cofactors, pigments, vitamins, prosthetic group (211), and protein metabolism (211) functions were determined using RAST database.

Phylogenetic relationship of strain ab36

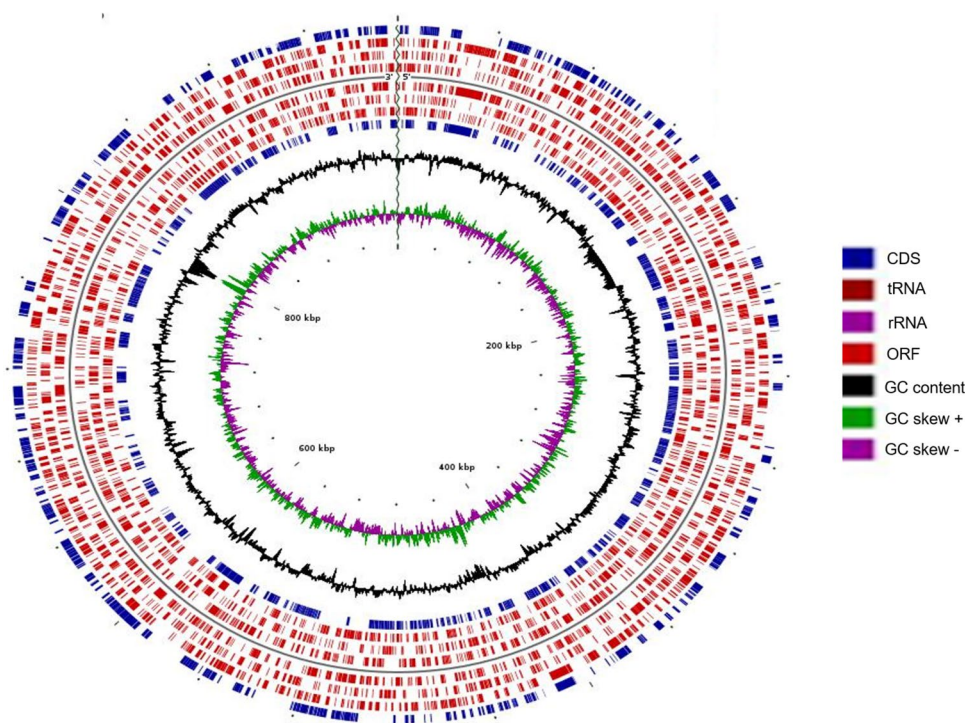
Strain AB36 was classified as *P. koreensis* based on the partial 16S rRNA gene sequence. Phylogenetic analysis based on the partial 16S rRNA sequences showed that strain AB36 clustered closely to *P. koreensis* strain 96C1 (Fig. 2). With *P. koreensis* D26 as the reference strain, average nucleotide identity (ANI) of the genome was performed to confirm the classification of strain AB36. ANI is a genome-to-genome similarity index applicable to prokaryotes that is

Table 1 Heavy metal tolerance and plant growth-promoting traits of strain AB36

Heavy metal tolerance	100 mg L ⁻¹	200 mg L ⁻¹	500 mg L ⁻¹
Cd	+	+	-
Cr	+	-	-
Pb	+	+	+
Plant growth-promoting traits			
Ammonia production	++		
Phosphate solubilization (cm)	0.633 ± 0.88		
Hydrogen cyanide production	+		
Indole-3- acetic acid production	+		
Siderophore production (%)	28.71 ± 2.03		

Legend: (+) positive for test; (–) negative for test

Fig. 1 The circular view of the chromosome of strain AB36 genome showing the coding sequence and the G+C content



independent of GC content. Our analysis showed that strain AB36 does not meet the cutoff for species differentiation against the reference sequence of *P. koreensis* D26 (93%). This is less than the 95% cut-off point for categorizing bacteria into the same species.

Comparison of orthologous gene clusters and genomic alignment

Genomic islands (GIs) often provide adaptive traits that enhance the fitness of bacteria within a niche (Citti et al. 2020; Zhu et al. 2019). In the *P. koreensis* AB36 genome sequence, some genomic islands were discovered, and their locations are shown in Fig. 3A. The genomic islands were smaller than the gene clusters and contained fewer genes.

Table 2 The genomic features of strain AB36

Gene features	Value
Contig	44
Genes (total)	5,300
CDS (total)	5,229
Genes (coding)	5,165
Genes (RNA)	71
rRNAs	2, 3, 2 (5S, 16S, 23S)
tRNAs	60
Pseudo Genes (total)	64

The functions of some genomic islands are related to heavy metal and antimicrobial resistance, whereas genes associated with virulence factors and pathogens were not detected. However, many genomic island functions are unknown. These findings suggest that genes from genomic islands likely originated horizontally from other bacteria in various habitats through various mechanisms.

We conducted comparative analyses with phylogenetically related species in the NCBI database using *P. koreensis* D26, *P. koreensis* CRS05 R5, and *P. koreensis* P19E3 to determine the functional context of strain AB36. The identification of orthologous gene clusters at the proteome level was the focus of the comparative investigations. Regarding orthologous protein clusters, 4154 proteins were shared among the four species (Fig. 3B). The analysis detected seven specific clusters in strain AB36 (Fig. 3C).

Pan-genome analysis

Seven genomes of *P. koreensis* were selected for the study to establish core- and strain-specific genes. Pan-genome analysis revealed 1862 unique coding genes among the selected genomes. With the addition of new strains, the number of core-genome genes decreased, whereas the number of pan-genome genes increased (Fig. 4A). The pan-genome of *P. koreensis* is open, which implies that adding more strains will result in the inclusion of new genes. Figure 4B shows the number of novel strain-specific genes. The genetic

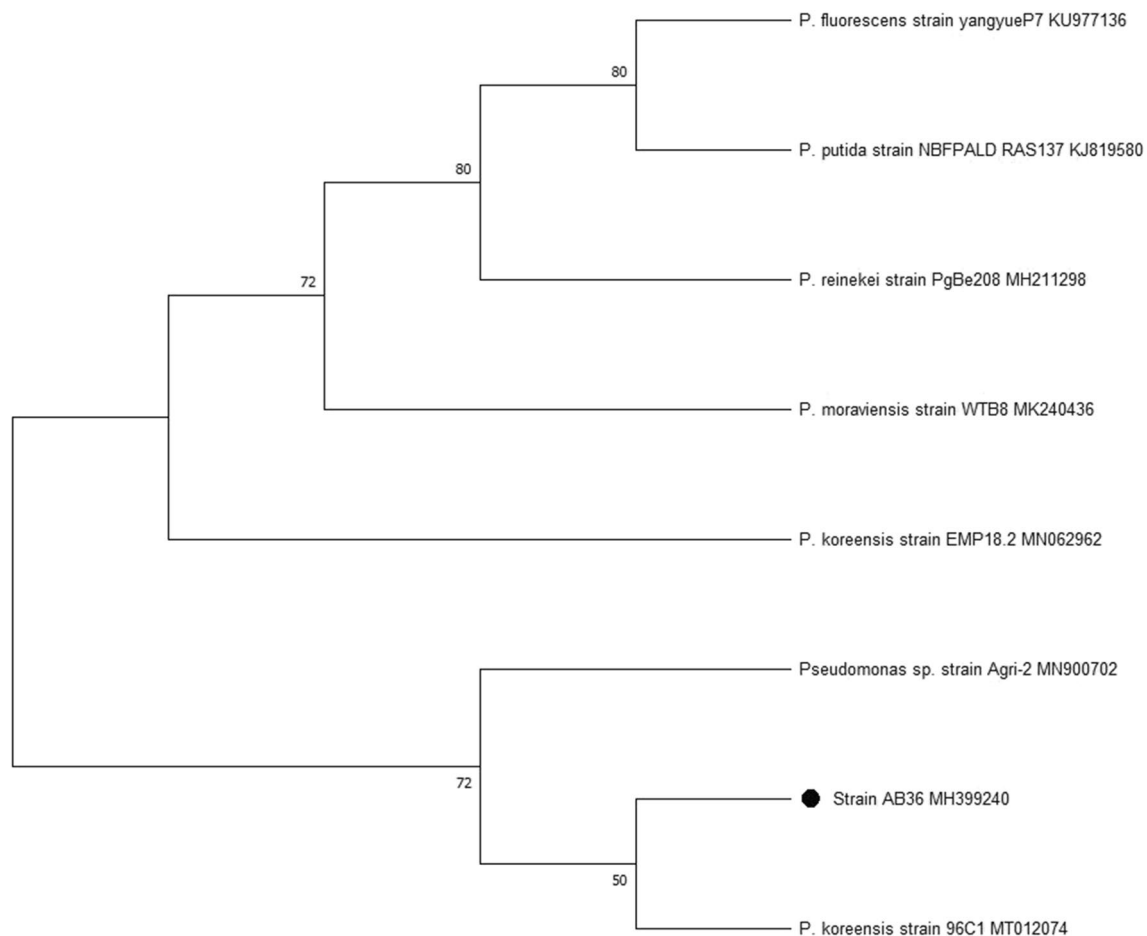


Fig. 2 The phylogenetic tree of strain AB36 and other *P. koreensis* 16S partial sequences using neighbor-joining algorithm with 1000 bootstrap values. MEGA X software (Kumar et al. 2018) was used for tree construction

variations between strains suggest that these strain-specific genes were acquired via lateral gene transfer from other species. Furthermore, only a few strains shared strain-specific genes, indicating that *P. koreensis* evolution is conserved.

Differentially enhanced functions of the *P. Koreensis* genes

The COG and KEGG databases were used to compare the distribution of the functional categories of the identified genes. The most common functions of the *P. koreensis* core genes were associated with metabolism in both databases (Figs. 5 and 6, Tables SI 3 and S4). However, the COG database (Fig. 5, Table SI 3) identified 33.44% functional categories for both unique and accessory genes, whereas the KEGG database identified 7% unique genes and 92.82% accessory genes (Fig. 6, Table SI 4). The COG database's overall fraction of genes assigned to metabolic activities was 69.3%, 38.7%, and 28.5% for core, accessory, and unique

genes, respectively, whereas the KEGG database showed a distribution of 66.7%, 66.6%, and 64.9% for core, accessory, and unique genes, respectively. Specifically, energy production and conversion (C), transcription (K), inorganic ion transport and metabolism (P), and signal transduction mechanisms (T) [COG database], energy metabolism, membrane transport, and signal transduction [KEGG database] were abundant in the core genes. This indicates that these genes were conserved in *P. koreensis*, and both databases support the idea that signal transduction genes were largely conserved. Replication, recombination, and repair (L), amino acid metabolism, cell wall/membrane/envelope biogenesis (M), carbohydrate metabolism, xenobiotic biodegradation, and metabolism genes were found to be more frequent in strain-specific genes than in core genes, indicating that they may have been horizontally transmitted from other species (Figs. 5 and 6, Tables S3 and S4). The total number of unique genes found in the seven genomes was 1862, with *P. koreensis* AB36 having the fewest (31) and

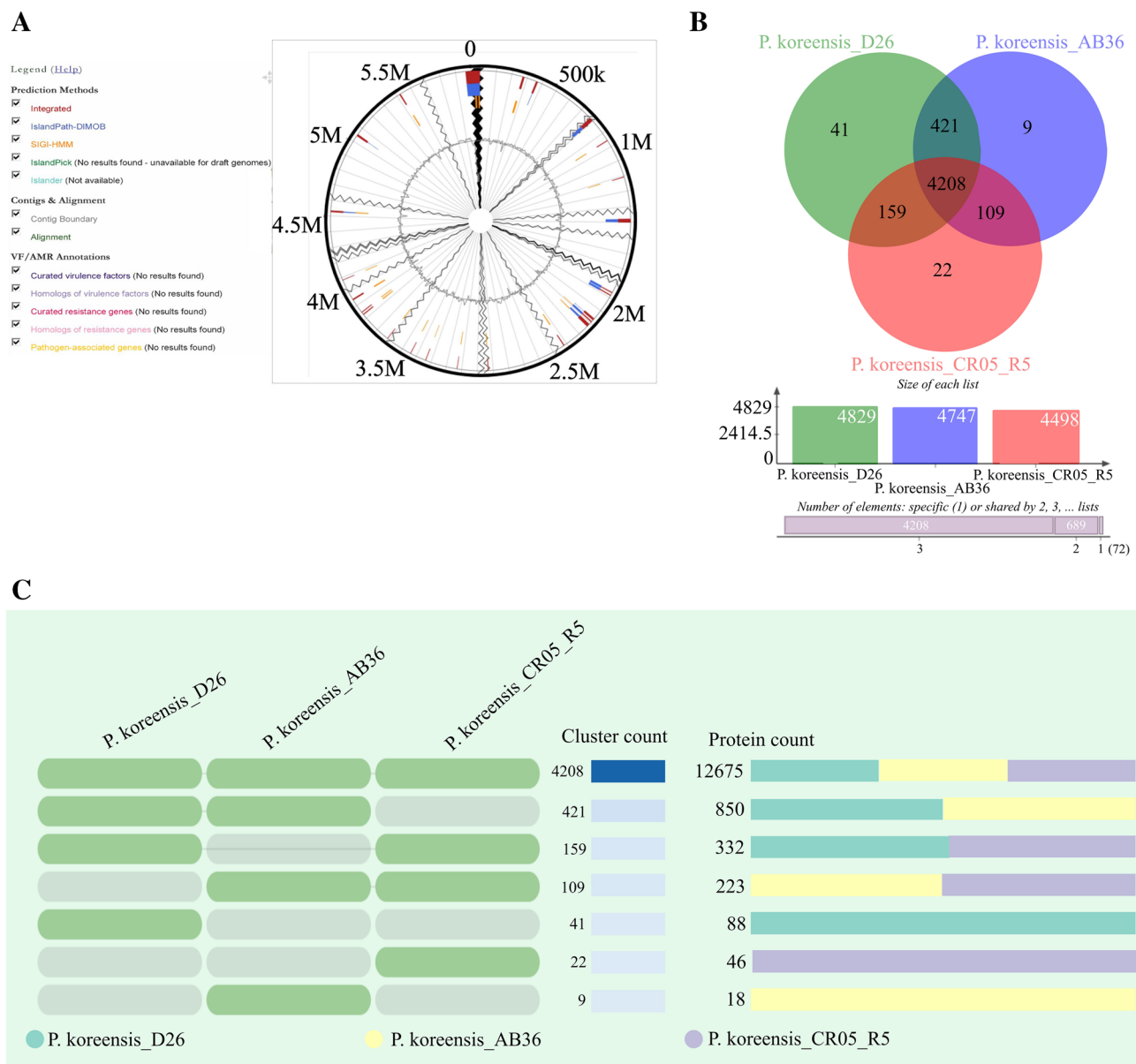


Fig. 3 Circular representation of the prediction of genomic islands in strain AB36 (A), OrthoVenn protein comparisons among the *P. koreensis* strains (B), and cluster and protein count among the *P. koreensis* strains (C)

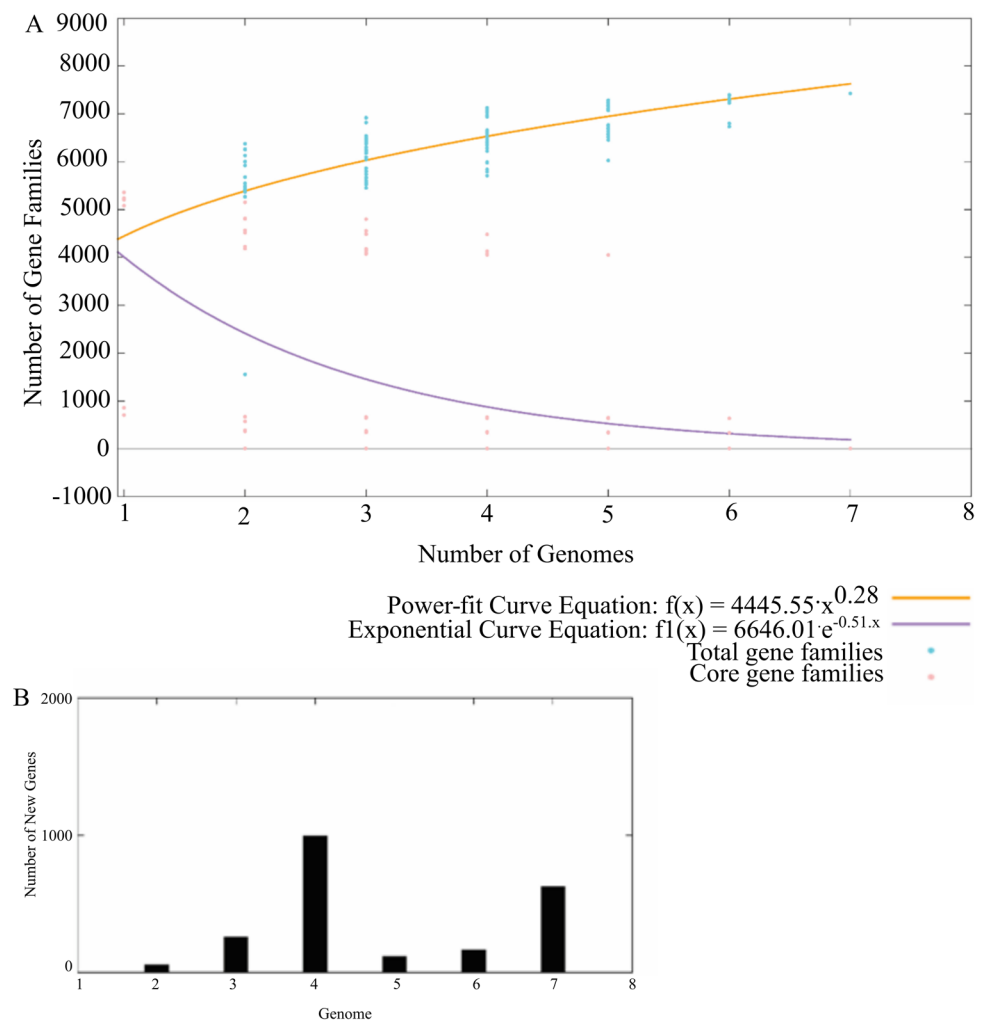
P. koreensis D26 having the most (693) (Table SI 2). The COG and KEGG databases of AB36 revealed its metabolic flexibility and plasticity. The important metabolic and regulatory processes that underpin the strain's survival and functionality in a variety of conditions are highlighted by the conservation of core genes associated with energy synthesis, membrane transport, and signal transduction. The increased frequency of distinct and accessory genes linked to functions such as cell wall biogenesis, carbohydrate metabolism, and xenobiotic biodegradation implies that AB36 has acquired specialized abilities, potentially via horizontal gene transfer, to adapt to particular environmental challenges or niches.

This genetic diversity implies that strain AB36 is not only well-equipped for basic metabolic functions but also has the potential to perform specialized roles in biodegradation and environmental adaptation, making it a valuable candidate for environmental remediation.

Adaptation and resistance to abiotic stress

Genome mining of *P. koreensis* AB36 revealed the presence of genes associated with adaptation to oxidative, nitrosative, osmotic, and temperature stress (Table SI 5–SI 7). Osmolyte production and transport (glutamine, glutamate,

Fig. 4 The pan-genome and core-genome analyses of *P. koreensis*



glycine-betaine), membrane integrity and protection mechanisms (cardiolipin), the osmoprotectant transport system, and sodium transporters were among the genes involved in osmotic stress tolerance found in the genome of strain AB36 (Table SI 5). These results indicate that the material can withstand increasing salinity in the environment.

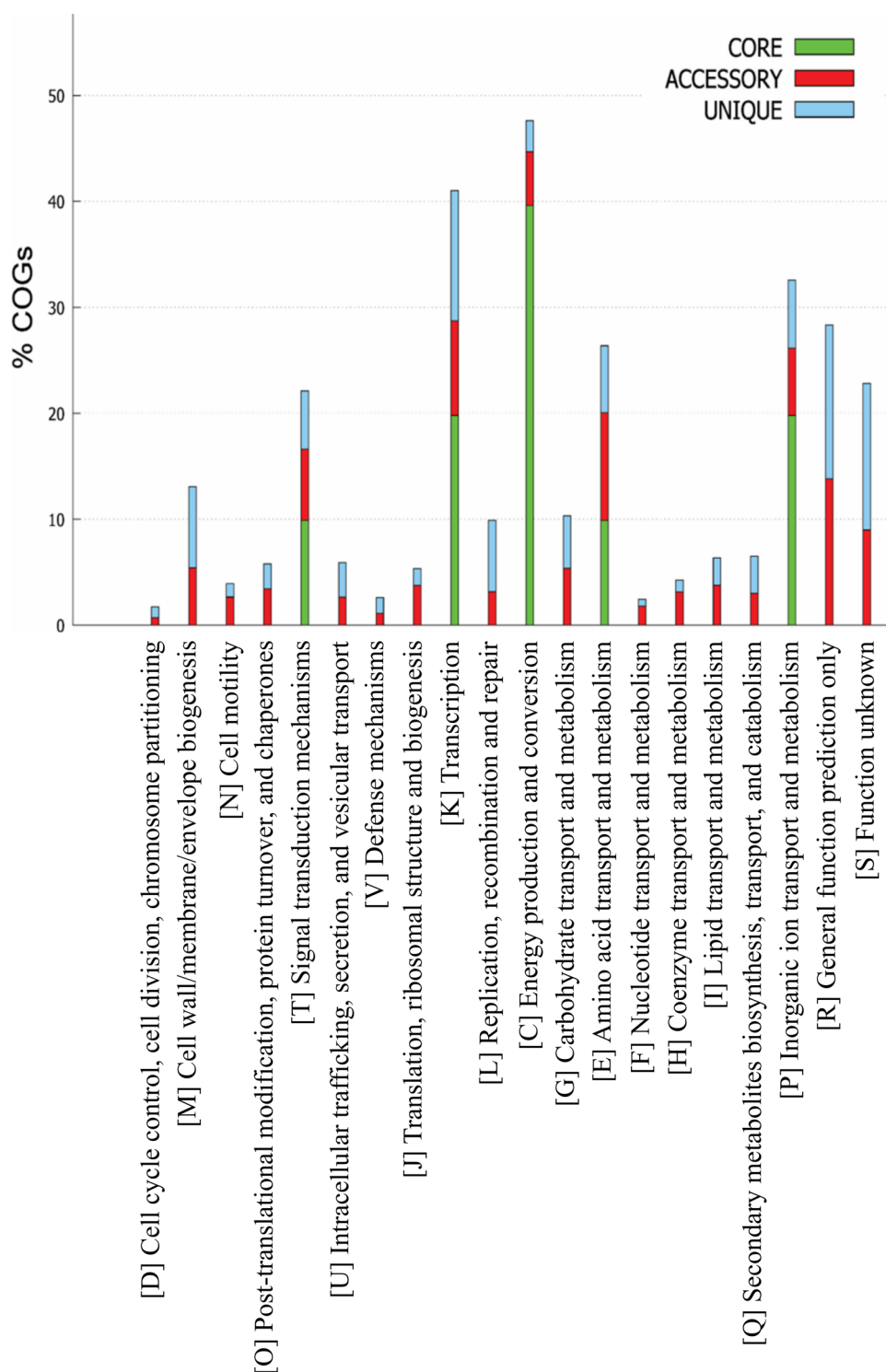
The accumulation and absorption of K^+ are among the earliest responses to osmotic stress. The Kdp-ATPase system (*kdpA, B, C*, and *F*) and *Kup* are among the genes found in strain AB36 that encode K^+ uptake transporters (Table SI 9). This indicates the organism can adapt to saline environments (Kempf and Bremer 1998). Bacteria accumulate osmoprotectants, such as polyols, sugars, and/or amino acids in response to salinity stress. This enables adaptation to environmental changes caused by the external environment by drought or salt stress (Ojuederie et al. 2019; Tiwari et al. 2016). Of the five pathways known for trehalose biosynthesis (Reina-Bueno et al. 2012; Eida et al. 2020), only the pathway involving the conversion of the terminal unit of a linear maltodextrin, such as starch or glycogen, to trehalose

maltooligosyl trehalose trehalohydrolase (*treZ*) can be attributed to strain AB36 (Table SI 11).

Glycine betaine is produced via a two-step enzymatic reaction involving choline dehydrogenase (*betA*) and betaine aldehyde dehydrogenase (*betB*). This reaction requires the external availability and uptake of choline, which is made possible by the choline BCCT transporter (*betT*) (Imhoff et al. 2021). The proline/betaine transporter (*proP*), in addition to choline, is involved in choline-betaine synthesis. Furthermore, *proX* and *proW* are suggested proline transporters (Frossard et al. 2012). In addition to the transcriptional regulator *bet*, genome mining of strain AB36 revealed the existence of these genes (*betI*) (Table SI 5).

Genes encoding the hydrolytic enzymes *katE* and *katG* were found in the genome, and they were implicated in oxidative and nitrosative stress responses (Table SI 6). Furthermore, genes encoding flavohemoprotein nitric oxide dioxygenase (*hmp*), which detoxifies nitric oxide free radicals were discovered (Eida et al. 2020). The presence of these genes suggests that strain AB36 exhibits high adaptability

Fig. 5 COG analysis showing the genes in *P. koreensis* strains



and resistance to reactive oxygen and nitrogen species produced under stressful conditions. A farnesyl diphosphate synthase gene (*ispA*) was also found in the genome, which is involved in carotenoid production. Key regulatory genes involved in the oxidative stress response include the superoxide radical response regulator (*soxRS*) and ferric uptake

regulator (*fur*) (Tables SI 2 and SI 10) (Seixas et al. 2021; Fasnacht and Polacek 2021).

P. koreensis AB36 contains cold shock proteins and chaperone proteins that are produced in response to temperature stress (Table SI 7). It has one *cspD* gene and affects transcription and translation efficiency when exposed to cold

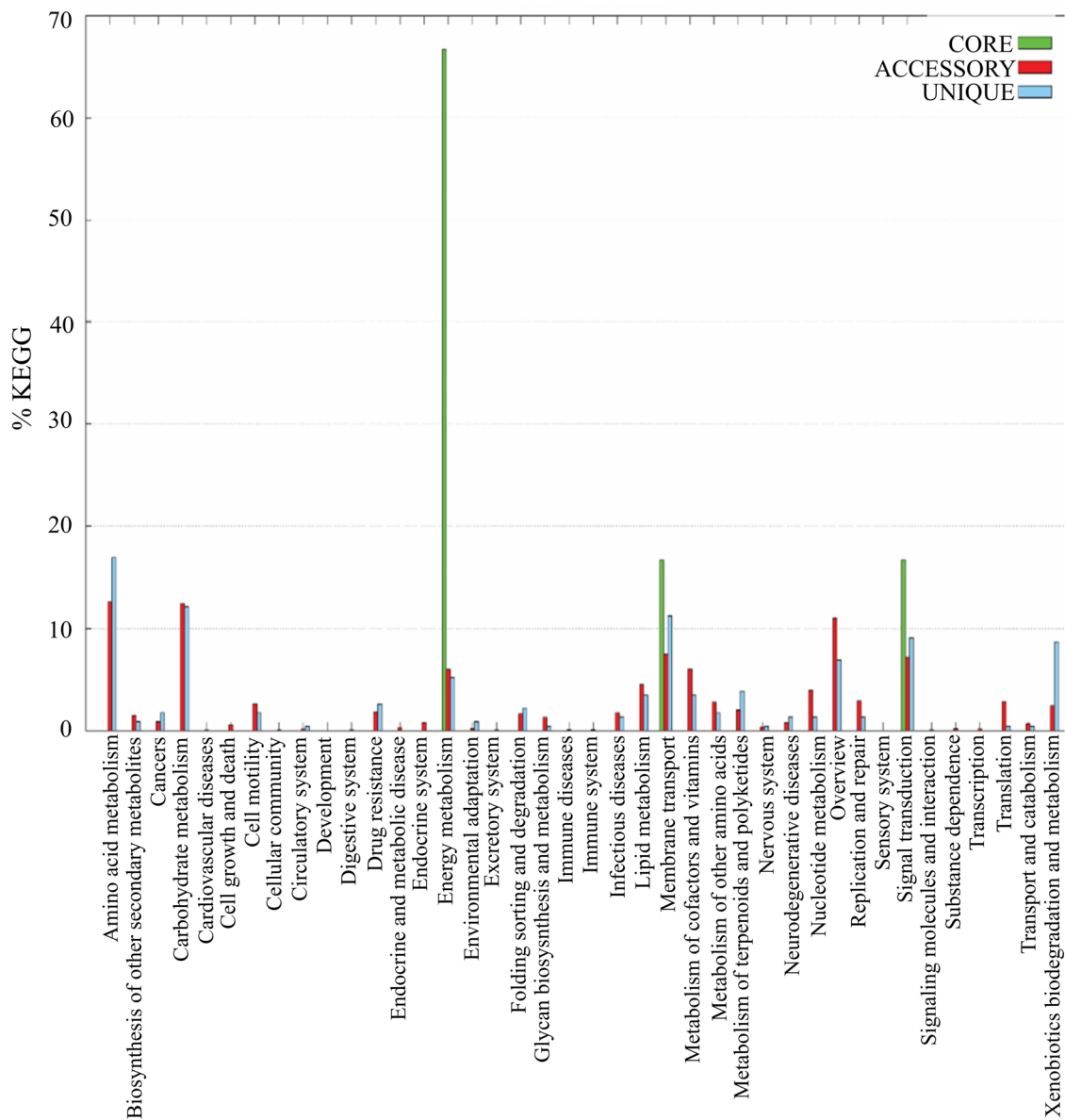


Fig. 6 KEGG analysis showing the genes in *P. koreensis* strains

stress. The genome also harbors several chaperones, such as *dnaJ*, *dnaK*, *groL*, and *hsp20*, which are involved in the heat stress response and assist in the proper folding of other proteins (Li et al. 2022; Liu et al. 2022). The presence of environmental stress resistance genes (such as temperature, heavy metal, osmotic, oxidative, and nitrosative) in the genome of *P. koreensis* AB36 demonstrates the ability to endure various abiotic pressures and to survive a wide range of harsh environmental conditions, making it a robust and adaptable organism.

The Sec (secretion) system, twin arginine translocation (tat), and type I, II, and VI secretion systems were identified and represent the principal secretion systems reported in

AB36 (Table SI 8). The Sec system is important for translocating unfolded proteins across the inner membrane in bacteria (Green and Mecsas 2016), including *P. koreensis*. It is also involved in various cell functions, including the synthesis of new cell wall and the uptake of nutrients, and this system helps in the export of proteins to the periplasm. This step is crucial for the survival of strain AB36 in various environments, especially in terms of acquiring nutrient. The tat system is especially critical for exporting complex proteins to extracellular spaces that require proper cytoplasmic folding within the cytoplasm, for example, stress and plant interaction proteins. In *P. koreensis*, the tat system may facilitate the transport of enzymes that are crucial for survival under stress conditions

(Palmer and Berks 2024), thereby enhancing the adaptability of the species. The system's ability to transport proteins that interact with plant roots suggests its role in symbiotic relationships, potentially aiding nutrient exchange (McNeillage et al. 2024). In this manner, these systems serve for the proper interaction of strain AB36 with the surrounding environment, supporting plant health, competing with other microbes, and responding to various environmental conditions.

Genes associated with heavy metal transport and organic compound degradation

There are many putative heavy metal resistance/transport genes strain AB36 genome of (Table 3). These genes include several transport genes, such as arsenate, cadmium, chromate, cobalt, nickel, and zinc, and genes encoding arsenical and copper resistance. Two putative genes were located on the genomic islands (Fig. 3A), as predicted by IslandViewer. They are tellurium-resistance protein and lead, cadmium, zinc, and mercury-transporting ATPases. In addition, it contains metal transport genes for chromate (*chrA*), magnesium and cobalt (*corA*),

magnesium (*mgtE*), nickel and cobalt (*rcnA*), and zinc (*znuB*, *znuC*, and *zntB*) (Table 3). These proteins and transporters are essential for the detoxification and efflux of toxic metal ions, allowing the strain to survive in polluted environments. For instance, it is known that the chromate transporter gene (*chrA*) actively exports chromate ions out of the cell, minimizing intracellular buildup and thus lessening the harmful effects of chromate (Chromiková et al. 2022). Heavy metals are important cofactors in several metabolic processes in bacteria (Giachino and Waldron 2020; Witkowska et al. 2021). Magnesium, for example, is critical for stabilizing ribosomes and nucleic acids, whereas cobalt is a key component of vitamin B12, which is required for DNA synthesis (Witkowska et al. 2021). The presence of these genes helps organisms to survive in the environment where they were isolated, tolerate high levels of heavy metals in the environment, and have a potential role in bioremediation (Ayangbenro et al. 2019). Strains like AB36 could be employed in the bioremediation of contaminated environments because they possess the genetic tools necessary to detoxify and immobilize heavy metals, thus contributing to environmental cleanup

Table 3 Genes involved in heavy metal transport and resistance

Locus tag	Gene	Protein name	Pathway
EVS84_RS25330 EVS84_RS01630	<i>arsC</i>	Arsenate reductase	Arsenate reduction and transport
EVS84_RS25325	<i>arsH</i>	Arsenical resistance protein ArsH	
EVS84_RS25805	-	Arsenic transporter	
EVS84_RS07285 EVS84_RS17565	<i>cadA</i>	Cadmium-translocating ATPase	Cadmium transport
EVS84_RS05820	<i>cadR</i>	Cd(II)/Pb(II)-responsive transcriptional regulator	
EVS84_RS15430	<i>chrA</i>	Chromate efflux transport	Chromate transport
EVS84_RS21645	<i>copC</i>	Copper resistance protein C	
EVS84_RS21650	<i>copD</i>	Copper resistance protein D	Copper resistance
EVS84_RS08210	<i>cueA</i>	Copper resistance metal-translocating ATPase	
EVS84_RS21640	-	Copper resistance protein B	
EVS84_RS25735	-	Copper chaperone PCu(A)C	
EVS84_RS08555	-	Copper resistance system multicopper oxidase	
EVS84_RS21635	-	Copper resistance system multicopper oxidase	
EVS84_RS17980	<i>corA</i>	Magnesium and cobalt transport protein CorA	Magnesium transport
EVS84_RS17330	<i>mgtA</i>	Magnesium-translocating ATPase	
EVS84_RS01835	<i>mgtE</i>	Magnesium transport	
EVS84_RS15435	<i>rcnA</i>	Nickel/cobalt efflux transport RcnA	
EVS84_RS07820	<i>znuB</i>	Zinc ABC transport permease protein	Zinc transport
EVS84_RS07815	<i>znuC</i>	Zinc ABC transport ATP-binding protein	
EVS84_RS00110 EVS84_RS07805	-	Zinc ABC transport solute-binding protein	
EVS84_RS00095	-	Zinc ABC transport substrate-binding protein	
EVS84_RS17800	<i>zntB</i>	Zinc transporter ZntB	
EVS84_RS23805	<i>terB</i>	Tellurite resistance protein	
EVS84_RS26605			Tellurite transport

efforts (Ayangbenro and Babalola 2017). This capability enhances the strain's applicability in sustainable agricultural practices, where it mitigates heavy metal contamination of soil, thereby ensuring safer crop production.

The ability of *Pseudomonas* species to detoxify various of xenobiotic chemicals is well documented (Babu et al. 2015; Camara et al. 2007; Baig et al. 2022; Muthukumar et al. 2023). The genome of strain AB36 contain several genes encoding xenobiotic compound degradation in the organism (Table 4). Azo dyes, insecticides, nitro compounds, barbiturates, epoxides, steroids, and other hazardous substances fall into this category (Table 4). Genes encoding enzymes for the breakdown of xenobiotic compounds were discovered in the genome (Table 4), including a nitroreductase (EVS84_RS15930), which is involved in the degradation and detoxification of aromatic arsenicals, herbicides, and other nitro compounds (Chen and Rosen 2020; Wang et al. 2021b); two dioxygenase (EVS84_RS14650 and EVS84_RS14645), which are involved in the degradation of benzoate (Wang et al. 2021a) and phthalate (Huang et al. 2022). Other genes involved in benzoate degradation and other aromatic compounds were present in the genome. They include the *pcaH*, *pcaC*, *pcaD*, and *pcaF* genes. The presence of genes in strain AB36 that encode enzyme for the degradation of xenobiotic compounds in strain AB36 highlights its potential for environmental bioremediation. These genes enable AB36 to break down and detoxify various harmful chemicals, making strain AB36 a promising candidate for cleaning up contaminated environments and mitigating pollution.

Plant growth-promoting traits and potential for nutrient acquisition, phytohormone production, and volatile compound production

The AB36 genome contains genes responsible for the absorption, transport, and metabolism of nitrogen, carbon-containing compounds, iron, phosphorus, and sulfur. In addition, genes involved in quorum sensing, chemotaxis, and motility are also present. These genes are presented in Table SI 9–SI 11 and suggests the ability of the organism to promote plant growth.

Nitrogen, phosphorus, potassium, and sulfur are essential for plant and bacterial development. Although the genome of strain AB36 does not possess genes for nitrogen fixation, it harbors genes for nitrate (*nirD*), urea (*ureABCDEF*, *atzF*, *urtABCDE*, and *uca*) which are implicated in major nitrogen metabolism pathways (Table SI 9). This facilitated the ability of strain AB36 to promote plant growth by increasing nitrogen use, which is important for both plants. The genome also contains genes for phosphate (*pstSCA*), potassium (*pstSCA*), potassium (*kdpABSF*), and sulfate (*cysDNTWZ*, and *ssuBCD*) (Table SI 9). Furthermore, genes encoding iron and siderophore transport/uptake, such as iron ABC transporter permease, *fur*, *efeOB*, MFS transporter, and GNAT family n-acetyltransferase (Table SI 10) are present. These genes enhance the acquisition of phosphate, potassium, sulfate, and iron, thereby enhancing soil nutrient stocks and status.

The AB36 genome contains genetic components involved in sulfate reduction and transport and sulfonate transport and degradation genes (Table SI 9). The presence of *ssuD* gene homologs encoding alkanesulfonate monooxygenase in the genome suggests that strain AB36 can degrade various soil sulfonates and use them as sulfur sources.

Table 4 Genes involved in the metabolism of xenobiotic compounds

Locus tag	Gene	Protein name	Pathway
EVS84_RS15930	-	Nitroreductase	Degradation of nitro compounds
EVS84_RS14650	<i>pcaG</i>	Protocatechuate 3,4-dioxygenase subunit alpha	Degradation of benzoate
EVS84_RS14645	<i>pcaH</i>	Protocatechuate 3,4-dioxygenase subunit beta	
EVS84_RS17700		benzoate/H(+) symporter BenE family transporter	
EVS84_RS14670	<i>pcaC</i>	4-carboxymuconolactone decarboxylase	Degradation of benzoate and aromatic compounds
EVS84_RS14665	<i>pcaD</i>	3-oxoadipate enol-lactonase	
EVS84_RS14640	<i>pcaF</i>	3-oxoadipyl-CoA thiolase	Microbial metabolism in diverse environment and benzoate degradation
EVS84_RS10660	-	Aryl-sulfatase	Degradation of alkyl-aryl sulfates
EVS84_RS04505	-	Nitronate monooxygenase	Degradation of nitronates
EVS84_RS19885			
EVS84_RS13545	-	FMN-dependent NADH-azoreductase	Degradation of azo dyes
EVS84_RS15735			
EVS84_RS09180	-	Toluene tolerance protein	
EVS84_RS12645	-	Aromatic ring-hydroxylating dioxygenase subunit alpha	Oxidation of aromatic compounds
EVS84_RS15505	-	5-carboxymethyl-2-hydroxymuconate Delta-isomerase	Degradation of homoprotocatechuate

The *P. koreensis* AB36 genome contains genes encoding sugar transporters and metabolism, such as glucose (*zwf*, *tal*, *tkt*, *pgi*, and *gap*), fructose (*pfkb* and *fba*), pyruvate (*pvk*), ribose (*rbsK* and *rbsD*), xylose (*xylA*, and *xylB*), maltose (*malO*), mannose (*manA*), trehalose (*treCPRZ*), galactoseamine (*nagA*), galactarate (*garD* and *garR*), glucarate (*gudD*), glucosides (*bglX*), and glycogen (*glgX*) (Table S11). This implies that this isolate can metabolize glucose, fructose, pyruvate, ribose, xylose, maltose, mannose, and trehalose (Medina-Salazar et al. 2022; Gu et al. 2020), and strain AB36 can utilize a wide spectrum of carbohydrates, which gives it a major advantage in terms of survival in diverse environments. In addition, genes capable of hydrolyzing and metabolizing were present in the genome.

The *luxR* gene is an important gene associated with bacterial communication and signaling (Olanrewaju et al. 2019; Connolly et al. 2022) was reported in the genome of strain AB36 (Table SI 12). This is in support of previous reports of the *luxR* genes in *P. koreensis* strains (Oni et al. 2020; Dai et al. 2022), and it indicates that strain AB36 uses a quorum-sensing mechanism to communicate with its environment. This communication enhances the bacterium's capacity to thrive in the rhizosphere, enhance plant nutrient uptake, and offer protection against plant diseases. Overall, these findings indicate that quorum sensing systems are important for the ecology and lifestyle of strain AB36.

AB36 encodes genes that regulate rapid sensing and adaptation to environmental changes. These genes included genes for chemotaxis (*cheABRWV*), motility (flagellar biosynthesis genes (*flgABCM*, *fliJDSEFGHILMOPR*, *flhBAF*)), pilus, and fimbria biosynthesis (*pilTUZPOMWVB*, *cpaB*, and a prepilin peptidase gene) (Table S13). These genes have been implicated in responses to environmental stress, nutrient deficiencies, and pathogen/predator invasion (Colin et al. 2021).

Strain AB36 harbors several genes implicated in nutrient acquisition that may be important in plant growth promotion. Plants release exudates through the roots in response to nutrient deficiency or stress response. Exudates released include organic acids, which increase soil acidity, resulting in the solubilization of phosphate, zinc, and siderophore production (which increases iron availability through chelation) (do Amaral et al. 2020). The ability of bacteria to produce siderophore and organic acids promotes plant growth promotion (Babalola et al. 2019). *P. koreensis* AB36 displays siderophore production and iron uptake and transport genes (MFS transporter, GNAT family N-acetyltransferase, *efeO*, *fur*) as well as genes involved in phosphate assimilation (alkaline phosphatase family proteins) (Table SI 9 and SI 10).

Phosphate is an essential macronutrient for plant growth. It is a fundamental component of nucleic acids, phospholipids, and ATP. However, it is not readily available to plants in the rhizosphere (Olanrewaju et al. 2017); hence, it is important for phosphate-solubilizing rhizobacterium to solubilize

it and make it freely available to plants. Genome analysis of AB36 revealed phosphate transporters such as the *pstSCA* genes (Table SI 9) (Eida et al. 2020).

Iron is required for DNA synthesis, respiration, and chlorophyll formation (for photosynthesis). Similar to phosphorus, iron is not freely available in soil because its insoluble forms are present at neutral pH (Waters et al. 2020). Iron is available to plants through the activities of siderophore. Genes involved in siderophore synthesis were identified by genome mining (Table SI 10). The production of siderophore by bacteria acts as a biocontrol mechanism against pathogens through the deprivation of pathogens from freely available iron (Olanrewaju et al. 2017). An efficient iron uptake system improves bacterial ability and survival in pathogen-enriched environment. Strain AB36 possesses genes encoding iron uptake proteins (*efeOB*), MFS transporters and ABC transporters (Table S10). In addition to solubilizing iron, AB36 can act as a biocontrol agent. Furthermore, plant growth promotion by rhizobacteria can be elicited through direct or indirect interactions between rhizobacteria and plant hosts (Olanrewaju and Babalola 2019). In addition, AB36 contains genes required for sulfate reduction and transport, such as *cysD*, *cysN*, *cysT*, *cysW*, and *csyZ* genes (Table SI 9). Sulfur-containing volatile compounds increase tolerance to salinity stress in plants (Srivastava et al. 2022; Chen et al. 2021).

The AB36 genome contains genetic elements implicated in glyoxylate pathways and the tricarboxylic acid cycle, including fumarate, succinate, and malate genes (Table SI 11). Furthermore, genes implicated in organic acid transport and catabolism, such as acetate, formate, and malonate, were identified (Table SI 13).

Genomic analysis of strain AB36 revealed multiple plant growth-promoting traits, making the strain a potential candidate for sustainable agriculture. Therefore, strain AB36 can help plants optimize their nutrient uptake and adapt to the surrounding environment. It can be further improved for agricultural use to enhance plant phytoremediation, increase yields, and assist sustainable farming practices because of its many metabolic roles, stress response pathways, and resilience.

Chemotaxis, motility and colonization

Plant colonization by bacteria involves root exudation from plants and recognition of exudates by bacteria, followed by responses of bacteria to root exudates/signals (Babalola et al. 2019; Olanrewaju et al. 2021). Chemotaxis genes and genes involved in flagellar biosynthesis and assembly were identified in the AB36 strain (Table SI 14). They contain genes that encode for flagellar body architecture, regulatory factors, and chemotaxis, such as *cheABRWV*, *flgABCM*, *fliJDSEFGHILMOPR*, *flhBAF*, *pilZPOMCWTVB*, *papC*, and *cpaB* (Table SI 8) (Eida et al. 2020). Some genes encoding type IV pilus were present. These include *pilO*, *pilT*, *pilW*, *pilV*, and

Table 5 Secondary metabolites of strain AB36 as predicted by antiSMASH

Cluster	Source	Location	Most similar known cluster	Similarity (%)	BGC-ID
NRPS (Non-ribosomal peptide synthetase)	Scaffold 1	7939—60,937	Pyoverdin	22	BGC0000413
NAGGN (N-acetylglutaminyglutamine amide)	Scaffold 1	207,868—222,749	-	-	-
Arylpolyene	Scaffold 3	312,982—356,586	APE Vf	40	BGC0000837
Bacteriocin	Scaffold 5	159,361—170,092	-	-	-
NRPS	Scaffold 6	147,169—210,718	Pyoverdin	19	BGC0000413
NRPS, Bacteriocin	Scaffold 7	24,645—86,854	Rimosamide	28	BGC0001760
Betalactone	Scaffold 8	106,022—129,274	Fengycin	13	BGC0001095
NRPS-like	Scaffold 16	1—23,134	Fragin	37	BGC0001599

pilB genes suggesting a robust mechanism for surface attachment and biofilm initiation (Sonani et al. 2023). Furthermore, methyl accepting and chemotaxis proteins (*cheA*, *B*, *W*, *R*, and *V*) involved in chemotaxis were also present (Table SI 8). These findings suggest that strain AB36 responds to environmental signals and moves either away from or toward the environment. The presence of genes associated with chemotaxis, motility, and type IV pilus production equips the bacteria to effectively locate, attach to, and colonize plant roots. A biofilm not only aids in plant colonization but also enhances the bacterium's resilience in the face of environmental challenges, making it a robust and effective plant growth-promoting bacterium (Knights et al. 2021; Xiong et al. 2020).

Biosynthesis of secondary metabolites

AntiSMASH was used to predict secondary metabolite biosynthetic gene clusters, yielding eight gene clusters (Table 5). The gene clusters include non-ribosomal peptide synthetase (NRPS), N-acetylglutaminyglutamine amide (NAGGN), arylpolyene, bacteriocin, and betalactone putative clusters. NAGGN is a low molecular weight modified dipeptide that functions in bacterial osmoregulation. In response to increased osmolarity in the environment, NAGGN is produced and accumulated (Sagot et al. 2010) and can help organisms to survive in saline environments. NRPS has been suggested to play a role in quorum sensing, which is essential for bacterial communication and biofilm formation, root development of plant hosts, and cyclodipeptide biosynthesis in *Pseudomonas* species (González et al. 2017; Huang et al. 2024). These gene clusters may help strain AB36 establish itself as a potent plant growth-promoting organism. The arylpolyene biosynthetic gene cluster, which is also involved in abiotic stress responses (Cimerancic et al. 2014) and drug resistance, shared 40%

similarity with one of the gene clusters. Strain AB36 may be resistant to oxidative stress and other environmental challenges owing to the production of arylpolyene gene cluster. These characteristics probably help the bacteria survive harsh environments and maintain plant health by reducing environmental stressors. The presence of these gene clusters involved in the biosynthesis of secondary metabolites in strain AB36 suggests that this strain is highly adaptive to various environmental stresses, can effectively compete with other microbes, and can produce bioactive compounds that promote plant growth and health and enhance crop resistance and yield, especially under harsh conditions.

Conclusions

Pseudomonas species are versatile microbes found in diverse environments, and they can produce and metabolize various chemical substances owing to their extensive metabolic capabilities. This versatility has sparked growing interest in exploiting beneficial traits for biotechnological and agricultural applications. *P. koreensis* AB36 can be used for phytoremediation and sustainable agriculture. Its genome reveals the presence of several genes involved in stress tolerance, plant growth promotion, and other biotechnological applications, including heavy metals, oxidative, nitrosative, temperature, and osmotic stress, iron, phosphate, potassium, carbohydrates, organic acids, volatile compounds, nitrogen, and siderophore abilities. This study deepens our understanding of the genetic features that govern interactions between beneficial bacteria, their hosts, and the environment, as well as their potential use in sustainable agriculture. Further genetic, metabolomics, and transcriptomics studies will confirm the involvement of the highlighted genes in the functional potential of *P. koreensis* AB36.

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Authors' contribution Conceptualization: Ayansina S. Ayangbenro, Olubukola O. Babalola; Methodology: Ayansina S. Ayangbenro, Oluwaseyi S. Olanrewaju, Adenike E. Amoo; Formal analysis and investigation: Ayansina S. Ayangbenro, Oluwaseyi S. Olanrewaju; Writing—original draft preparation: Ayansina S. Ayangbenro, Oluwaseyi S. Olanrewaju, Adenike E. Amoo; Writing—review and editing: Olubukola O. Babalola; Funding acquisition: Olubukola O. Babalola; Resources: Olubukola O. Babalola; Supervision: Olubukola O. Babalola.

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Data availability The genome sequence of *P. koreensis* AB36 has been deposited at DDBJ/ENA/GenBank database with accession number SEUB00000000 and SRR8529805 is the accession number for the Sequence Read Archive (SRA). The 16S partial sequence was also deposited in the NCBI GenBank database with accession number MH399240.

Declarations

Competing interests The author declare no competing interest.

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