

Genomic analysis and plant growth-promoting potential of a *Serratia marcescens* isolated from food

Análise genômica e potencial de promoção de crescimento vegetal de uma *Serratia marcescens* isolada de alimento

Análisis genómico y potencial de promoción del crecimiento vegetal de una *Serratia marcescens* aislada de alimento

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Abstract

A genomic analysis of the potential application of a *Serratia marcescens* strain in the plant-growth promotion. We performed whole-genome sequencing of *Serratia marcescens* isolated from a Minas Frescal Cheese. The genomic repertoire revealed a bacterium of agricultural and biotechnological interest. In the plant-growth promotion traits, we highlight genes encoding proteins possibly responsible for the biosynthesis of phytohormone indole acetic acid, organic compounds that act in iron uptake, and the Phosphate solubilization system. Genes encoding for enzymes like the versatile L-asparaginase stimulates the development of seeds and grains and can benefit the food industry due to a mitigation effect on acrylamide and notably, has medical applications as a chemotherapeutic agent or is applicable by its antimicrobial and anti-inflammatory properties. Moreover, functional diversity of genes encoding for resistance to different metals and metabolism of xenobiotics genes can be found in this strain, reinforcing its biotechnological potential. The versatile enzymes that can be produced by *S. marcescens* benefit the food, pharmaceutical, textile, agronomic, and cosmetic industries. The relevant genetic systems of *S. marcescens* described here may be used to promote plant growth and health and improve the environment. To the best of our knowledge, this is the first genome sequence report on *S. marcescens* isolated from cheese, with potential application as promoting plant growth and providing a baseline for future genomic studies on the development of this species.

Keywords: *Serratia marcescens*; Plant growth-promotion; Biotechnology.

Resumo

Análise genômica do potencial de aplicação de uma cepa de *Serratia marcescens* na promoção de crescimento vegetal. Foi realizado o sequenciamento do genoma completo de *Serratia marcescens* isolada de queijo Minas Frescal. O repertório genômico revelou uma bactéria de interesse agrícola e biotecnológico. Dentre as características de promoção do crescimento de plantas, destacamos genes que codificam proteínas possivelmente responsáveis pela biossíntese do fitohormônio ácido indol acético, compostos orgânicos que atuam na captação de ferro e o sistema de solubilização de Fosfato. Genes que codificam enzimas como a versátil L-asparaginase estimulam o desenvolvimento de sementes e grãos e podem beneficiar a indústria de alimentos devido ao efeito de mitigação da acrilamida e, notadamente, tem aplicações médicas como agente quimioterápico ou é aplicável por seus agentes antimicrobianos e propriedades anti-inflamatórias. Além disso, uma diversidade funcional de genes que codificam para resistência a

diferentes metais e metabolismo de xenobióticos pôde ser encontrada nesta linhagem, reforçando seu potencial biotecnológico. As enzimas versáteis que podem ser produzidas em *S. marcescens* beneficiam as indústrias alimentícia, farmacêutica, têxtil, agrônômica e cosmética. Os sistemas genéticos relevantes de *S. marcescens* descritos aqui podem ser usados para promover o crescimento e a saúde das plantas e melhorar o meio ambiente. Até onde sabemos, este é o primeiro relato de sequência de genoma de *S. marcescens* isolado de queijo, com potencial aplicação como promotor de crescimento de plantas e fornecendo uma linha de base para futuros estudos genômicos sobre o desenvolvimento desta espécie.

Palavras-chave: *Serratia marcescens*; Promoção de crescimento vegetal; Biotecnologia.

Resumen

Un análisis genómico de la posible aplicación de una cepa de *Serratia marcescens* en la promoción del crecimiento vegetal. Métodos: Se realizó la secuenciación del genoma completo de *Serratia marcescens* aislada de un queso Minas Frescal. El repertorio genómico reveló una bacteria de interés agrícola y biotecnológico. En los rasgos de promoción del crecimiento de las plantas, destacamos los genes que codifican proteínas posiblemente responsables de la biosíntesis del ácido acético indol fitohormono, compuestos orgánicos que actúan en la absorción de hierro y el sistema de solubilización de fosfato. Los genes que codifican para enzimas como la versátil L-asparaginasa estimulan el desarrollo de semillas y granos y pueden beneficiar a la industria alimentaria debido a un efecto de mitigación sobre la acrilamida y, en particular, tiene aplicaciones médicas como agente quimioterapéutico o es aplicable por sus propiedades antimicrobianas y antiinflamatorias. Además, una diversidad funcional de genes que codifican para la resistencia a diferentes metales y el metabolismo de los genes xenobióticos se puede encontrar en esta cepa, reforzando su potencial biotecnológico. Las enzimas versátiles que pueden ser producidas por *Serratia marcescens* benefician a las industrias alimentaria, farmacéutica, textil, agrónomica y cosmética. Los sistemas genéticos relevantes de *S. marcescens* descritos aquí pueden utilizarse para promover el crecimiento y la salud de las plantas y mejorar el medio ambiente. Hasta donde sabemos, este es el primer informe de secuencia del genoma de *S. marcescens* aislado del queso, con potencial aplicación como promotor del crecimiento vegetal y proporcionando una línea de base para futuros estudios genómicos sobre el desarrollo de esta especie.

Palabras clave: *Serratia marcescens*; Promoción del crecimiento vegetal; Biotecnología.

1. Introduction

Serratia marcescens, classified under the family *Yersiniaceae* of the order *Enterobacterales* (Adeolu et al., 2016), is capable of thriving in a broad range of environments.

The wide variety of gene repertoire enables *S. marcescens* to be a ubiquitous microorganism, successful in diverse environments and with multipurpose applications or effects. For example, marine *S. marcescens* demonstrated antioxidant and antibacterial activity against some Gram-positive and Gram-negative bacteria (Gangadharan et al., 2020). Moreover, oil spills in aquatic ecosystems can be bioremediated by a biodispersant produced by *S. marcescens* characterized by low toxicity, high biodegradability, and good ecological acceptability (dos Santos et al., 2021).

In the terrestrial environment, the species can act as a pathogen to animals (Friman et al., 2019; Ishii et al., 2012). However, it is agronomically relevant with its antifungal effect (Troskie et al., 2014). Furthermore, it can be considered a biocontrol agent with herbicidal activity (Kamran et al., 2017) and as a plant growth-promoting rhizobacteria (PGPR), improving the health and development of their host plant by acting on the solubilization of inorganic P present in the soil (Rodríguez & Fraga, 1999).

Alternative approaches can improve the soil and global water healthy, once continuously contaminated by the human being, to maintain the exorbitant life cycle. Due to the use of bacteria systems in biotechnology plus the promise of *S. marcescens* role in several mechanisms, it could be used in different scenarios, including azo dyes degradation to soil decontamination (Mahmood et al., 2017).

Functional diversity of genes encoding for enzymes have evidenced an important assignment for *S. marcescens* in the biotechnological industry, including segments such as food, cosmetics, chemical, and pharmaceutical (dos Santos et al., 2021; Falade & Ekundayo, 2021).

Both disease and therapy are present in the dual role of *S. marcescens* in the clinic, responsible for outbreaks (Cristina et al., 2019) was even identified as an opportunist in outbreaks during covid-19 treatment (Amarsy et al., 2020). However, it has shown an extensive presence of enzymes with antimicrobial and anti-inflammatory properties proving effective to even resistant microorganisms and with the possibility of use as a chemotherapeutic agent in different cancer cell lines (Abdel-Razik et al., 2019; Pavithra & Rajasekaran, 2020).

The broad niche and functional diversity of the *S. marcescens* are probably influenced by and, at the same time, influence on the highly dynamic genome (Cristina et al., 2019), turning relevant the periodical investigation of the genetic background of emerging *S. marcescens* strains from various sources. Moreover, the potential application of the strain to promote plant growth was explored from the genotypic perspective.

2. Material and Methods

2.1 Isolation and characterization of the *Serratia marcescens*

The *Serratia marcescens* strain was isolated from a Gram-negative pool of bacteria from a previous analysis of Minas Frescal Cheese according to the methodology of Silva et al., 2020. Subsequently, the strain was isolated in Mueller Hinton Agar. Genomic DNA of the bacterial strain was extracted with a NucleoSpin Tissue kit (Macherey-Nagel & Germany, 2018) in conformity with the manufacturer's protocol.

2.2 Whole genome sequence analysis

A genomic library was constructed using a Nextera XT Kit (Illumina Inc., San Diego, C) by Genone Company. Total genomic DNA was sequenced using a MiSeq platform from Illumina Inc. (Genone Company). The sequence was assembled and the draft genome using Prokka (Seemann, 2014) in the Galaxy site <https://www.usegalaxy.org> and RAST (Brettin et al., 2015) in the site <http://rast.nmpdr.org/rast.cgi>. The DFAST - Prokaryotic genome annotation pipeline from the site <https://dfast.ddbj.nig.ac.jp/dfc/> (Tanizawa et al., 2016; Tanizawa et al., 2018) and PATRIC in the site <https://www.patricbrc.org/> (Davis et al., 2020).

3. Results

3.1 Characterization of the *Serratia marcescens*

The bacterial strain was identified to be *Serratia marcescens* and was deposited at the Genbank under the number SUB9616311, BioProject and Biosample accession number are PRJNA729465 and SAMN19116778, respectively. The genome has Total Length (bp) 4,969,854 and GC Content 59.6%; 4,722 CD; 4 rRNA; 81 tRNA; 2 CRISPR.

3.2 Genomic repertoire

The diversified genomic repertoire of *S. marcescens* made it possible to group them into different sets of genes according to the benefits presented. Table 1 presents genes related to several systems involved in plant-growth promotion.

Table 1 - Genes involved in the plant growth promotion traits.

Location	Gene	Product	Pathway
71101..72780	<i>ipdC1</i>	Indole-3-pyruvate decarboxylase	Synthesis of the phytohormone indole acetic acid (IAA)
1745616..1747277	<i>ipdC2</i>	Indole-3-pyruvate decarboxylase	
1348409..1349596	<i>tyrB1</i>	Aromatic-amino-acid aminotransferase	
2400258..2401487	<i>tyrB2</i>	Aromatic-amino-acid aminotransferase	
841137..842327	<i>aspC</i>	aspartate aminotransferase	
1317606..1319021	-	Aromatic-L-amino-acid decarboxylase	
3385706..3386512	<i>trpA</i>	tryptophan synthase alpha chain	
3386512..3387702	<i>trpB</i>	tryptophan synthase beta chain	
3387744..3389105	<i>trpC</i>	bifunctional indole-3-glycerol phosphate synthase/phosphoribosylanthranilate isomerase	
3389109..3390107	<i>trpD</i>	anthranilate phosphoribosyltransferase	
3390124..3390705	<i>trpG</i>	anthranilate synthase component 2	
3390705..3392267	<i>trpE</i>	anthranilate synthase component 1	
3392647..3393528	<i>trpH</i>	hypothetical protein	
1346991..1348388	<i>gabP</i>	GABA permease	GABA transport
2555735..2557189	<i>gabD</i>	Succinate-semialdehyde dehydrogenase [NADP(+)] GabD	GABA degradation
1496042..1497370	<i>puuA1</i>	Gamma-glutamylputrescine synthetase PuuA	GABA biosynthesis
2065828..2067198	<i>puuA2</i>	Gamma-glutamylputrescine synthetase PuuA	
3048881..3050299	<i>puuA3</i>	Gamma-glutamylputrescine synthetase PuuA	
2035575..2036876	<i>puuB1</i>	Gamma-glutamylputrescine oxidoreductase	
3044542..3045822	<i>puuB2</i>	Gamma-glutamylputrescine oxidoreductase	
3045834..3047330	<i>puuC</i>	NADP/NAD-dependent aldehyde dehydrogenase PuuC	
3047900..3048661	<i>puuD</i>	Gamma-glutamyl-gamma-aminobutyrate hydrolase PuuD	
2554457..2555722	<i>puuE</i>	4-aminobutyrate aminotransferase PuuE	
1497856..1498413	<i>puuR1</i>	HTH-type transcriptional regulator PuuR	
3047346..3047903	<i>puuR2</i>	HTH-type transcriptional regulator PuuR	
4129206..4130669	<i>prr1</i>	Gamma-aminobutyraldehyde dehydrogenase	Polyamine transport
4134757..4136181	<i>prr2</i>	Gamma-aminobutyraldehyde dehydrogenase	
707261..708193	<i>gbuA</i>	Guanidinobutyrase	
751743..752852	<i>potF</i>	Putrescine-binding periplasmic protein	
2139577..2140893	<i>potE</i>	Putrescine transporter PotE	
2998784..2999827	<i>potD</i>	Spermidine/putrescine transport system substrate-binding protein PotD	
3003984..3004766	<i>potC</i>	Spermidine/putrescine transport system permease protein PotC	
3004763..3005623	<i>potB</i>	Spermidine/putrescine transport system permease protein PotB	
3005607..3006722	<i>potA</i>	Spermidine/putrescine transport system ATP-binding protein PotA	
3050608..3051978	<i>puuP</i>	Putrescine importer	
2229642..2230538	<i>miaA</i>	tRNA dimethylallyltransferase	Cytokinin biosynthesis
281151..282575	<i>miaB</i>	tRNA-2-methylthio-N(6)-dimethylallyl adenosine synthase	
2812914..2814890	<i>speA</i>	Biosynthetic arginine decarboxylase	Putrescine biosynthesis
2815085..2816005	<i>speB</i>	Agmatinase	
2732182..2734347	<i>speC</i>	Ornithine decarboxylase	
2772843..2773637	<i>speD</i>	S-adenosylmethionine decarboxylase proenzyme	
2773665..2774528	<i>speE1</i>	Polyamine aminopropyltransferase	
3724779..3725567	<i>speE2</i>	Polyamine aminopropyltransferase	
2137352..2139514	<i>speF</i>	Inducible ornithine decarboxylase	
2810851..2812005	<i>metK</i>	S-adenosylmethionine synthase	
4488192..4490330	<i>cadA</i>	Inducible lysine decarboxylase	Cadaverine, putrescine biosynthesis
4486753..4488096	<i>cadB</i>	putative cadaverine/lysine antiporter	
4484830..4486383	<i>cadC</i>	Transcriptional activator CadC	

2772843..2773637	<i>speD</i>	S-adenosylmethionine decarboxylase proenzyme	Spermidine/Spermine biosynthesis
2773665..2774528	<i>speE1</i>	Polyamine aminopropyltransferase	
3724779..3725567	<i>speE2</i>	Polyamine aminopropyltransferase	
906353..906919	<i>speG1</i>	Spermidine N(1)-acetyltransferase	
1734415..1734954	<i>speG2</i>	Spermidine N(1)-acetyltransferase	
4243961..4244512	<i>speG3</i>	Spermidine N(1)-acetyltransferase	Chitin degradation
3336851..3338128	<i>chiA1</i>	Chitinase	
3889421..3891112	<i>chiA</i>	Chitinase	
4797788..4799287	<i>chiB</i>	Chitinase	
286807..288246	<i>Chid</i>	Chitinase	
4841474..4842253	<i>budA</i>	Alpha-acetolactate decarboxylase	Acetoin Synthesis
4842286..4843971	<i>budB</i>	Acetolactate synthase, catabolic	
1902321..1904015	<i>ilvB1</i>	Acetolactate synthase isozyme 1 large subunit	
2829574..2831214	<i>ilvB2</i>	Acetolactate synthase isozyme 1 large subunit	
4878208..4879854	<i>ilvG</i>	Acetolactate synthase isozyme 2 large subunit	
1882791..1884509	<i>ilvI</i>	Acetolactate synthase isozyme 3 large subunit	
1904019..1904312	<i>ilvN</i>	Acetolactate synthase isozyme 1 small subunit	
4877954..4878211	<i>ilvM</i>	Acetolactate synthase isozyme 2 small subunit	
1882297..1882788	<i>ilvH</i>	Acetolactate synthase isozyme 3 small subunit	Siderophore Production
1395126..1396316	<i>entC1</i>	Isochorismate synthase	
2301840..2303045	<i>entC2</i>	Isochorismate synthase	
2300204..2301832	<i>entE</i>	Enterobactin synthase subunit E	
2304690..2308634	<i>entF</i>	Enterobactin synthase subunit F	
2299340..2300200	<i>entB</i>	Enterobactin synthase subunit B	
2303257..2304513	<i>entS1</i>	Enterobactin exporter	
3630309..3631592	<i>entS2</i>	Enterobactin exporter	
2050892..2051299	<i>exbD1</i>	Biolpolymer transporter protein	
2623298..2623714	<i>exbD2</i>	Biolpolymer transporter protein	
2622308..2623288	<i>exbB</i>	Biolpolymer transporter protein	Plant polymer degradation enzymes
4916366..4916845	<i>Bfr</i>	Bacterioferritin	
2540910..2542397	<i>uxaA</i>	Altronate dehydrolase	
2539477..2540889	<i>uxaC</i>	Uronate isomerise	
3907226..3908329	<i>bcsZ</i>	Endoglucanase (cellulase)	Inorganic P solubilisation
1361417..1363789	<i>Gcd</i>	Quinoprotein glucose dehydrogenase	
2197430..2197960	<i>Ppa</i>	Inorganic pyrophosphatase	
4233863..4235413	<i>Ppx</i>	Exopolyphosphatase	Organic P mineralization and glyphosate degradation
1113239..1114927	<i>appA1</i>	Oligopeptide-binding protein AppA	
1534333..1536141	<i>appA2</i>	Oligopeptide-binding protein AppA	
2127176..2127904	<i>phnF</i>	phosphonate metabolism transcriptional regulator PhnF	
2127905..2128348	<i>phnG</i>	phosphonate C-P lyase system protein PhnG	
2128352..2128933	<i>phnH</i>	Alpha-D-ribose 1-methylphosphonate 5-triphosphate synthase subunit PhnH	
2128933..2130018	<i>phnI</i>	Alpha-D-ribose 1-methylphosphonate 5-triphosphate synthase subunit PhnI	
2130011..2130871	<i>phnJ</i>	Alpha-D-ribose 1-methylphosphonate 5-phosphate C-P lyase	
2130871..2131659	<i>phnK</i>	Putative phosphonates utilization ATP-binding protein PhnK	
2131676..2132380	<i>phnL</i>	Alpha-D-ribose 1-methylphosphonate 5-triphosphate synthase subunit PhnL	
2132380..2133516	<i>phnM</i>	Alpha-D-ribose 1-methylphosphonate 5-triphosphate diphosphatase	
2133516..2134085	<i>phnN</i>	Ribose 1,5-bisphosphate phosphokinase PhnN	
254558..254986	<i>phnO</i>	Aminoalkylphosphonate N-acetyltransferase	
2134697..2135479	<i>phnP</i>	Phosphoribosyl 1,2-cyclic phosphate phosphodiesterase	
3102067..3103170	<i>phnW</i>	2-aminoethylphosphonate--pyruvate transaminase	

3103180..3103986	<i>phnX</i>	Phosphonoacetaldehyde hydrolase	
595332..596759	<i>phoA1</i>	Alkaline phosphatase	
2579746..2581278	<i>phoA2</i>	Alkaline phosphatase	
62219..62941	<i>phoC1</i>	Acid Phosphatase	
2519813..2520520	<i>phoC2</i>	Acid Phosphatase	
3069061..3069759	<i>phy</i>	Phloretin hydrolase	
3995977..3996864	<i>ugpA</i>	sn-glycerol-3-phosphate transport system permease protein UgpA	
3994579..3995898	<i>ugpB</i>	sn-glycerol-3-phosphate-binding periplasmic protein UgpB	
409995..411041	<i>ugpC1</i>	sn-glycerol-3-phosphate import ATP-binding protein UgpC	
3515382..3516494	<i>ugpC2</i>	sn-glycerol-3-phosphate import ATP-binding protein UgpC	
3997712..3998782	<i>ugpC3</i>	sn-glycerol-3-phosphate import ATP-binding protein UgpC	
3996861..3997706	<i>ugpE</i>	sn-glycerol-3-phosphate transport system permease protein UgpE	
3998782..3999519	<i>ugpQ</i>	glycerophosphoryl diester phosphodiesterase	Transporters
486980..487813	<i>phnC</i>	Phosphate-import ATP-binding protein PhnC	
487855..488787	<i>phnD</i>	Phosphate-import protein PhnD	
488866..489729	<i>phnE1</i>	Phosphate-import permease protein PhnE	
489726..490625	<i>phnE2</i>	Phosphate-import permease protein PhnE	
3783048..3783938	<i>pstA1</i>	Phosphate transport system permease protein PstA	
4240052..4241701	<i>pstA2</i>	Phosphate transport system permease protein PstA	
3783987..3784763	<i>pstB</i>	Phosphate import ATP-binding protein PstB	
3782090..3783046	<i>pstC</i>	Phosphate transport system permease protein PstC	
4237923..4240055	<i>pstC1</i>	Phosphate transport system permease protein PstC1	
117742..118704	<i>pstS1</i>	Phosphate-binding protein PstS	
3780958..3781998	<i>pstS2</i>	Phosphate-binding protein PstS	
115697..116386	<i>phoB</i>	Phosphate regulon transcriptional regulatory protein PhoB	Regulatory Genes
2349154..2349864	<i>phoR1</i>	Phosphate regulon sensor protein PhoR	
3101192..3101911	<i>phoR2</i>	Phosphate regulon sensor protein PhoR	
3692913..3693824	<i>pqqB</i>	Coenzyme PQQ synthesis protein PqqB	Coenzyme PQQ synthesis
3693834..3694589	<i>pqqC</i>	Pyrrroloquinoline-quinone synthase	
3694589..3694867	<i>pqqD</i>	Coenzyme PQQ synthesis protein PqqD	
3694860..3695996	<i>pqqE</i>	Coenzyme PQQ synthesis protein PqqE	
3694860..3695996	<i>pqqF</i>	Coenzyme PQQ synthesis protein PqqF	
1233855..1235876	<i>cheA</i>	Chemotaxis protein CheA	
1233322..1233822	<i>Chew</i>	Chemotaxis protein CheW	
1227314..1227703	<i>cheY</i>	Chemotaxis protein CheY	
1228855..1229685	<i>cheR</i>	Chemotaxis protein methyltransferase	
1227806..1228855	<i>cheB</i>	Chemotaxis response regulator protein-glutamate methylesterase	
1226659..1227303	<i>cheZ</i>	Protein phosphatase CheZ	
1231458..1233128	<i>Tse</i>	Methyl-accepting chemotaxis serine transducer	Chemotaxis
1231458..1233128	<i>tas1</i>	Methyl-accepting chemotaxis aspartate transducer	
1229765..1231381	<i>Tap</i>	Methyl-accepting chemotaxis protein IV	
1231458..1233128	<i>tsr1</i>	Methyl-accepting chemotaxis protein I	
2195616..2197169	<i>tsr2</i>	Methyl-accepting chemotaxis protein I	
2252585..2254210	<i>tsr3</i>	Methyl-accepting chemotaxis protein I	
3733251..3734873	<i>tsr4</i>	Methyl-accepting chemotaxis protein I	
3840672..3842600	<i>Tar</i>	Methyl-accepting chemotaxis protein II	
1039135..1040082	<i>znuA</i>	High-affinity zinc uptake system protein ZnuA	Zinc solubilisation
1040913..1041698	<i>znuB</i>	High-affinity zinc uptake system membrane protein ZnuB	

183244..183957	<i>znuC1</i>	High-affinity zinc uptake system ATP-binding protein ZnuC	
1040158..1040916	<i>znuC2</i>	High-affinity zinc uptake system ATP-binding protein ZnuC	
110912..3111802	<i>znuC3</i>	High-affinity zinc uptake system ATP-binding protein ZnuC	
3532752..3534362	<i>pitA1</i>	Low-affinity inorganic phosphate transporter 1	
4649865..4651367	<i>pitA2</i>	Low-affinity inorganic phosphate transporter 1	
4488192..4490330	<i>cadA</i>	Inducible lysine decarboxylase	
4486753..4488096	<i>cadB</i>	putative cadaverine/lysine antiporter	
4484830..4486383	<i>cadC</i>	Transcriptional activator CadC	
3972332..3974650	<i>zntA</i>	Zinc/cadmium/lead-transporting P-type ATPase	
3469580..3470563	<i>zntB1</i>	Zinc transport protein ZntB	
3534549..3535577	<i>zntB2</i>	Zinc transport protein ZntB	
4931416..4931847	<i>zntR</i>	HTH-type transcriptional regulator ZntR	
220203..222914	<i>copA</i>	Cu ⁺ exporting ATPase	Copper
2940939..2941868	-	rhizopine-binding protein	
2944548..2945468	-	rhizopine-binding protein	
3659835..3660758	-	rhizopine-binding protein	Rhizopine degradation and transport
499977..501107	<i>iolG2</i>	Myo-inositol 2-dehydrogenase	
4613990..4615003	<i>iolG2</i>	Inositol 2-dehydrogenase/D-chiro-inositol 3-dehydrogenase	
1188384..1189376	<i>dcyD</i>	D-cysteine desulphydrase	D-cysteine desulphydrase

Source: Data from the research using the bioinformatics tools already described in the methodology.

The genes encoded in the set described in table 1 are related to several physiological processes in plants and contribute directly or indirectly to their growth and development, including mechanisms as the solubilization of minerals and siderophores that act in iron uptake.

The sequence analysis indicated that in the present *Serratia marcescens* genome was observed interesting genes for industries (Table 2).

Table 2. Genes involved in the antimicrobial activities or important enzymes for industry.

Location	Gene	Product	Pathway
1490734..1491864	<i>lgrD1</i>	Linear gramicidin synthase subunit D	
2106391..2109378	<i>lgrD2</i>	Linear gramicidin synthase subunit D	
2287830..2289554	<i>lgrD3</i>	Linear gramicidin synthase subunit D	Gramicidin synthesis
3621738..3630248	<i>lgrD4</i>	Linear gramicidin synthase subunit D	
2321416..2324511	<i>tycB</i>	Tyrocidine synthase 2	Tyrocidine synthesis
3339016..3340038	<i>ansA</i>	L-asparaginase 1	
810898..811944	<i>ansB</i>	L-asparaginase 2	Asparaginase synthesis
3305129..3306745	<i>aprA1</i>	Serralyisin C	
3975333..3976796	<i>aprA2</i>	Serralyisin	Serralyisin
2419429..2423367	<i>swrW</i>	Serrawetin W1 synthetase	Serrawettin
1935071..1936036	<i>pvcA</i>	paerucumarin biosynthesis protein PvcA	Paerucumarin
1934111..1934974	<i>pvcB</i>	pyoverdine chromophore biosynthetic protein PvcB	Pioverdin
3492125..3493030	<i>rdmC</i>	Aclacinomycin methylesterase	Aclacinomycin
1793656..1794648	<i>vgb</i>	Virginiamycin B lyase	Virginiamycin
4541527..4542810	<i>codA</i>	Cytosine deaminase	Cytosine
1932827..1934086	<i>rebG</i>	4'-demethylrebeccamycin synthase	Rebeccamycin
2384684..2385199	<i>ubiC</i>	Chorismate pyruvate-lyase	4-hydroxybenzoate Production
1087373..1088089	-	Laccase domain protein	Laccase
1758635..1759366	-	Laccase domain protein	Laccase

1365960..1366358	<i>pulS</i>	Pullulanase secretion protein	Pullulanase
3193302..3195146	-	Lipase	Lipase
3825243..3827231	<i>apeE</i>	Lipase	
1304805..1305767	<i>yfeX1</i>	putative deferrochelataase/peroxidase YfeX	Predicted dye-decolorizing peroxidase (DyP), YfeX-like subgroup
4817785..4818684	<i>yfeX2</i>	putative deferrochelataase/peroxidase YfeX	
160868..162139	<i>clpX</i>	ATP-dependent Clp protease ATP-binding subunit ClpX	
160103..160726	<i>clpP1</i>	ATP-dependent Clp protease proteolytic subunit	
2965578..2966171	<i>clpP2</i>	ATP-dependent Clp protease proteolytic subunit	Protease
785408..785728	<i>clpS</i>	ATP-dependent Clp protease adapter protein ClpS	
2177784..2179724	<i>ftsH</i>	ATP-dependent zinc metalloprotease FtsH	
162286..164688	<i>lon</i>	Lon protease	
503103..503648	-	antibiotic biosynthesis monooxygenase	
599468..599815	-	antibiotic biosynthesis monooxygenase	Antibiotic biosynthesis
905395..905697	-	antibiotic biosynthesis monooxygenase	
2877296..2877583	-	antibiotic biosynthesis monooxygenase	
2719913..2721460	<i>sacC</i>	Levanase	Levanase
3493198..3494697	-	Carboxypeptidase M32	Carboxipeptidase
128463..129065	<i>ahpC/P</i> <i>rx1</i>	Alkyl hydroperoxide reductase C	
505946..506422	<i>OsmC/</i> <i>Ohr</i>	OsmC/Ohr family protein	Redox-relevant proteins Peroxioredoxin
4681856..4682587	<i>Prx5</i>	Hybrid peroxiredoxin hyPrx5	
4260562..4261026	<i>Bcp</i>	Peroxioredoxin Bcp	
1630232..1631041	<i>oxyR1</i>	Hydrogen peroxide-inducible genes activator	
2417256..2418143	<i>oxyR2</i>	Hydrogen peroxide-inducible genes activator	
4680787..4681704	<i>oxyR3</i>	Hydrogen peroxide-inducible genes activator	
793069..794040	<i>trxB</i>	Thioredoxin reductase	
3922748..3923074	<i>trxA</i>	thioredoxin-1	
4036817..4037236	<i>trxC</i>	thioredoxin-2	
3685812..3687032	-	FMN oxidoreductase / NADH oxidase	
1426084..1428279	<i>katG</i>	Catalase-peroxidase	
1602395..1603831	<i>katA</i>	Catalase	
3132548..3133099	<i>btuE</i>	Thioredoxin/glutathione peroxidase BtuE	
555140..555643	<i>Dps</i>	DNA protection during starvation protein	
3182642..3183220	<i>sodB</i>	Superoxide dismutase [Fe]	Redox-relevant proteins
3195388..3195909	<i>sodC</i>	Superoxide dismutase [Cu-Zn]	
3842725..3843345	<i>sodA</i>	Superoxide dismutase [Mn]	
748967..749230	<i>grxA</i>	Glutaredoxin 1	
1065094..1065741	<i>grxB</i>	Glutaredoxin 2	
3184654..3185001	<i>grxD</i>	Glutaredoxin 4	
4062518..4062748	<i>nrdH</i>	Glutaredoxin-like protein NrdH	
4668552..4669904	<i>Gor</i>	Glutathione reductase	
1305840..1306949	<i>ybdK</i>	Putative glutamate--cysteine ligase 2	
1774900..1776462	<i>gshA</i>	Glutamate--cysteine ligase	
891799..892272	<i>soxR</i>	Redox-sensitive transcriptional activator SoxR	
2314122..2317031	-	Non Ribosomal Peptide Synthetase	NRPS
2141301..2143492	-	CRISPR with 37 repeat units	Crispr
2151971..2152778	-	CRISPR with 14 repeat units	
2060837..2062021	<i>thlA</i>	Beta-ketothiolase	Butanol Biosynthesis
1699934..1701244	<i>fadI</i>	3-ketoacyl-CoA thiolase FadI	
4021254..4022417	<i>fadA</i>	3-ketoacyl-CoA thiolase	
2059895..2060818	<i>Hbd</i>	3-hydroxybutyryl-CoA dehydrogenase	Fosmidomicyn
4858741..4859607	<i>paaF</i>	2,3-dehydroadipyl-CoA hydratase	
2291302..2293044	-	putative acyl-CoA dehydrogenase fadE25	

2293034..2294734	-	Cyclohexane-1-carbonyl-CoA dehydrogenase	
3359406..3362078	<i>adhE</i>	Aldehyde-alcohol dehydrogenase	
3716600..3718120	<i>ald1</i>	Long-chain-aldehyde dehydrogenase	
2617805..2618833	<i>adh1</i>	Alcohol dehydrogenase	
3670580..3671665	<i>adh2</i>	Alcohol dehydrogenase	
3718188..3719204	<i>adhA</i>	Alcohol dehydrogenase 1	
213877..215097	<i>fsr</i>	Fosmidomycin resistance protein	
251867..253057	<i>bcr1</i>	Bicyclomycin resistance protein	Bicyclomycin
1540827..1542023	<i>bcr2</i>	Bicyclomycin resistance protein	

Source: Data from the research using the bioinformatics tools already described in the methodology.

The wide variety of gene repertoire allows *S. marcescens* to arouse the interest of different branches of the industry, especially food, chemical, and pharmaceuticals. In the latter, the emphasis would be on agents with antimicrobial capacity that are increasingly important in this sector.

Some sets of genes can indirectly support plant growth promotion. Table 3 displays genes that enable the degradation of xenobiotics substances in the environment.

Table 3. Selected metabolism xenobiotics genes.

Position	Gene	Product	Pathway
244791..245300	<i>bphC</i>	Biphenyl-2,3-diol 1,2-dioxygenase	Biphenyl degradation
3359406..3362078	<i>bphJ2</i>	Aldehyde-alcohol dehydrogenase	
1431084..1432136	-	nitronate monooxygenase	Degradation of nitronates
270893..271597	<i>azoR1</i>	FMN-dependent NADH-azoreductase	Degradation of azo dyes
1197216..1197815	<i>azoR2</i>	FMN-dependent NADH-azoreductase	
3483743..3484348	<i>azoR3</i>	FMN-dependent NADH-azoreductase	
1385273..1385860	-	Nitroreductase	Degradation of nitro compounds
2028972..2030684	<i>atsA</i>	Arylsulfatase	Degradation of aryl sulfates
2789519..2791282	-	Arylsulfatase	
3296973..3297431	<i>iorA</i>	isoquinoline 1-oxidoreductase alpha subunit (EC 1.3.99.16)	N-heterocyclic aromatic compound degradation
3294751..3296973	<i>iorB</i>	isoquinoline 1-oxidoreductase beta subunit (EC 1.3.99.16)	
2434314..2434766	<i>aroQ</i>	3-dehydroquinate dehydratase	Quinate degradation
4552790..4553890	<i>aroB</i>	3-dehydroquinate synthase	
598436..599455	-	Cytochrome P450	Metabolism of xenobiotics by cytochrome P450
2295600..2296796	-	Cytochrome P450	
1819025..1820365	<i>pcaK</i>	4-hydroxybenzoate transporter PcaK	Hydroxybenzoate degradation
4302728..4304077	<i>mhbT</i>	3-hydroxybenzoate transporter MhbT	
1333277..1335343	<i>paaZ</i>	Bifunctional protein PaaZ	Phenylacetate degradation
1335661..1336599	<i>paaA</i>	1,2-phenylacetyl-CoA epoxidase, subunit A	
1336621..1336908	<i>paaB</i>	1,2-phenylacetyl-CoA epoxidase, subunit B	
1336917..1337675	<i>paaC</i>	1,2-phenylacetyl-CoA epoxidase, subunit C	
1337685..1338182	<i>paaD</i>	Putative 1,2-phenylacetyl-CoA epoxidase, subunit D	
1338196..1339254	<i>paaE</i>	1,2-phenylacetyl-CoA epoxidase, subunit E	
1339263..1340036	<i>paaF1</i>	2,3-dehydroadipyl-CoA hydratase	
1340040..1340831	<i>paaG</i>	1,2-epoxyphenylacetyl-CoA isomerise	
1340834..1342363	<i>paaH</i>	3-hydroxyadipyl-CoA dehydrogenase	
1342360..1342800	<i>paaI</i>	Acyl-coenzyme A thioesterase PaaI	
1342797..1344002	<i>paaJ</i>	3-oxoadipyl-CoA/3-oxo-5,6-dehydrosuberil-CoA thiolase	
1344018..1345325	<i>paaK</i>	Phenylacetate-coenzyme A ligase	
1345404..1346342	<i>paaX</i>	Transcriptional repressor PaaX	
4858741..4859607	<i>paaF2</i>	2,3-dehydroadipyl-CoA hydratase	

3548984..3550480	caeA	Carboxylesterase	Organophosphates, Carbamates and Pyrethroids Degradation
3703319..3704146	ybfK		
1108361..1109335	nhl1		
3730397..3731275	nhl2		
499125..499748	gstB1	Glutathione S-transferase	Degradation of various xenobiotics compounds
525352..526008	gstB2		
713294..713914	gstB3		
1351981..1352598	gstB4		
903120..903623	yqjA1	Inner membrane protein YqjA	Degradation of various xenobiotics compounds
2535596..2536276	yqjA2	Inner membrane protein YqjA	
2534611..2534982	yqjC	Protein YqjC	
2534141..2534446	yqjD1	putative protein YqjD	
4065045..4065353	yqjD2	putative protein YqjD	
2531706..2532692	yqjG	Glutathionyl-hydroquinone reductase YqjG	
2533737..2534138	yqjE	Inner membrane protein YqjE	
2532763..2533158	yqjF	Inner membrane protein YqjF	
309356..310000	yqjI	Transcriptional regulator YqjI	
599468..599815	yqjZ	putative protein YqjZ	

Source: Data from the research using the bioinformatics tools already described in the methodology.

Healthy environmental conditions are essential for plant survival and growth. For example, the set of genes in Table 3 supports the degradation of substances discarded by industries, such as synthetic textile dyes and heavy metals, helping to support the soil quality.

Growth-promoting bacteria that have the ability to survive in places with the presence of antibiotics and heavy metals have greater added value. Table 4 presents some relevant genes in this context.

Table 4. Genes responsible for the resistance to different metals and antibiotics.

Position	Gene	Product	Pathway
3559798..3561174	<i>czcD</i>	Cobalt-zinc-cadmium resistance protein	Cobalt-zinc-cadmium resistance
3259449..3259841	-	transcriptional regulator	
4722901..4724295	<i>cpxA1</i>	Sensor histidine kinase CpxA	Multidrug Resistance Cascade
4824636..4825931	<i>cpxA2</i>	Sensor histidine kinase CpxA	
4721578..4722057	<i>cpxP</i>	Periplasmic protein CpxP	
4722206..4722904	<i>cpxR1</i>	Transcriptional regulatory protein CpxR	
4823922..4824602	<i>cpxR2</i>	Transcriptional regulatory protein CpxR	Magnesium transporter Magnesium and cobalt efflux protein
4231962..4233395	<i>mgtE</i>	Magnesium transporter MgtE	
277974..278876	<i>corC</i>	Magnesium and cobalt efflux protein CorC	Zinc/cadmium/mercury/lead -transporting
3972332..3974650	<i>zntA</i>	zinc/cadmium/mercury/lead-transporting ATPase	
356111..357073	<i>zntB</i>	zinc transporter ZitB	Zinc transporter
1039135..1040082	<i>znuA</i>	zinc ABC transporter substrate-binding protein	
1040158..1040916	<i>znuC</i>	zinc import ATP-binding protein ZnuC	
1040913..1041698	<i>znuC</i>	zinc ABC transporter permease	
220203..222914	<i>copA</i>	Copper-exporting P-type ATPase	Copper Resistance
1054097..1054855	<i>cutC</i>	copper homeostasis protein CutC	
1679204..1679566	<i>scsA</i>	copper resistance protein	
2927427..2928308	<i>Crd</i>	copper resistance protein D	
4495263..4495946	<i>cutF</i>	copper homeostasis/adhesion lipoprotein NlpE	
1679204..1679566	<i>scsA</i>	copper resistance protein	
1677118..1679154	<i>scsB</i>	protein-disulfide reductase	
1676405..1677121	<i>scsC</i>	thioredoxin domain-containing protein	
1675912..1676412	<i>scsD</i>	protein disulfide oxidoreductase	Aminoglycoside
2560078..2560518	<i>aac6'-Ic</i>	Aminoglycoside acetyltransferase	
3238359..3239495	<i>srt-2</i>	Beta-lactamase	Cefotaxime, cephalosporin
3578532..3579713	<i>tet(41)</i>	Tetracycline efflux pump	Tetracycline
4526805..4527437	<i>crp</i>	Regulator of MdtEF multidrug efflux pump expression.	Fluoroquinolone, macrolide, penam

893514..896538	mexI	Inner membrane transporter of the efflux complex MexGHI-OpmD	Fluoroquinolone, tetracycline
2907627..2910747	oqxB	Efflux pump	Fluoroquinolone, glycylcycline, nitrofurantoin, tetracycline
3357594..3357995	h-ns	Repressor of the membrane fusion protein genes	Cephalosporin, cephamycin, fluoroquinolone, macrolide, penam, tetracycline

Source: Data from the research using the bioinformatics tools already described in the methodology.

Bacterial resistance to metals and antimicrobials present in *S. marcescens* can bring advantages and allow the plant to survive in environments with multiple stresses, making the bacteria attractive, even for use in bioremediation of the environment.

Complementary characteristics in PGPR bacteria, such as the ability to defend against plant parasites, which can play an important role, are described in table 5.

Table 5. Genes responsible for the nematocidal and larvicidal kill genes.

Position	Gene	Product	Pathway
4140944..4142197	<i>glyA</i>	Serine hydroxymethyl transferase	Acetaldehyde
3359406..3362078	<i>adhE</i>	Aldehyde-alcohol dehydrogenase	
3670580..3671665	<i>adh</i>	Alcohol dehydrogenase	
3045834..3047330	<i>puuC</i>	NADP/NAD-dependent aldehyde dehydrogenase PuuC	
919496..919756	<i>hcnA</i>	Hydrogen cyanide synthase subunit HcnA	Cyanide
919749..921017	<i>hcnB</i>	Hydrogen cyanide synthase subunit HcnB	
918375..919499	<i>hcnC</i>	Hydrogen cyanide synthase subunit HcnC	
1655365..1656882	<i>purF</i>	Amidophosphoribosyltransferase	Member of the purine/pyrimidine phosphoribosyltransferase family
3336851..3338128	<i>chiA1</i>	Chitinase	Chitin degradation
3889421..3891112	<i>chiA</i>	Chitinase	
4797788..4799287	<i>chiB</i>	Chitinase	
286807..288246	<i>chid</i>	Chitinase	
2419429..2423367	<i>swrW</i>	Serrawetin W1 synthetase	Serrawettin

Source: Data from the research using the bioinformatics tools already described in the methodology.

The presence of compounds of microbial origin with insecticidal and larvicide potential is interesting for plant growth promoter candidates because it also allows its use in biocontrol activity.

4. Discussion

4.1 Genes involved in the plant growth promotion traits

In the present *Serratia marcescens* genome was observed genes related to several systems involved in plant-growth promotion (table 1). Among the systems found, the Tryptophan biosynthesis pathway, a system related to several physiological processes in plants, including the biosynthesis of phytohormone indole acetic acid (IAA) (Khan et al., 2017), another system also observed in the present sample. Unfortunately, IAA biosynthesis does not have its mechanism fully elucidated. However, it is known that phytohormones such as auxins and cytokinins are involved in critical physiological processes of plants such as cell wall elongation and cell division stimulus, respectively (Xie et al., 2020). The IAA can act as an inducer compound of Induced Systemic Resistance (ISR). The ISR is an important plant defense mechanism against a broad range of pathogens,

parasitic weeds, and even insect herbivores. PGPR producing IAA may enhance the resistance against pathogens. The ISR has already been shown to be effective in rhizobacterium *S. marcescens* acting as a PGPR (Ryu et al., 2013).

The present genome also contains genes that express the non-protein amino acid gamma-aminobutyric acid (GABA), a well-known neurotransmitter in the mammalian body first isolated in 1949, but with less than 20 years of study in plant organisms. Until no less than six years ago, the influence of GABA in the plant-growth was described (Ramesh et al., 2017) identify a plant 'GABA receptor' that inhibits anion passage through the aluminum-activated malate transporter family of proteins (ALMT) and propose that GABA regulation of ALMT activity could function as a signal that modulates plant growth, development, and stress response.

This study also demonstrates other growth promoters in plants that act indirectly, such as the biosynthesis and transport capacity of several polyamines, more precisely putrescine, cadaverine, and spermine, which stimulate the endogenous production of growth promoters such as IAAs and reducing growth inhibitors (A. A. Amin et al., 2011). Chitin degradation is also an indirect growth mechanism present in this *Serratia* strain, proving to be an important factor in several microbiological agents in controlling pathogenic fungi in several plant species (Das et al., 2010). The capacity of acetoin synthesis complements promoting indirect growth as a precursor agent of volatile bacterial compounds (Sharifi & Ryu, 2018).

It also has a mechanism for the production of siderophores, organic compounds that act in iron uptake. Since iron is abundant in its insoluble form in the soil, siderophores act on the excretion of substances, forming soluble compounds with iron and then being absorbed (Parmar & Chakraborty, 2016). The siderophores that the present strain produces are Bacterioferritin, enterobactin, and isochorismate.

Another system for promoting plant growth found in this genome involving the solubilization of minerals is the Phosphate solubilization system, both organic and inorganic. Phosphate is commonly found in the soil in its insoluble form (Rodríguez & Fraga, 1999), so the performance of these mechanisms becomes essential for the absorption of the mineral. It is worth noting that the present strain also contains the *gcd* and *pqq* gene complex, which respectively code for glucose dehydrogenase and pyrroloquinoline quinone, also called the quinoprotein glucose dehydrogenase complex. A complex that acts in the release of gluconic acid in the soil, helping in the solubilization of inorganic phosphate. Highlighting that the *pqq* gene acts as a cofactor for the performance of glucose dehydrogenase (Abreo & Altier, 2019). Although phosphate is rarely present in its organic form in the soil, with average measurements around 1 ppm or even less in some cases, its role is also crucial in promoting plant growth. To be absorbed, soil bacteria act by hydrolyzing organic phosphate to inorganic phosphate and then proceed to absorption with the originally inorganic phosphate (Rodríguez & Fraga, 1999).

Still, on mineral solubilization, the present *S. marcescens* genome has zinc solubilization genes, which in turn have a direct relationship with gross growth. Bearing in mind that zinc deficiency can cause plant growth retardation, chlorosis, reduced leaf size, greater susceptibility to heat and fungal infections, it can affect grain and pollen yield, water uptake, and, in some plant species, the yellowing of the leaves (Kamran et al., 2017). Moreover, the solubilization of zinc also ends up helping in the production of siderophores.

Other genes presented by this strain promote chemotaxis activity. This activity is important because it is known that PGPR tends to have positive chemotaxis towards higher concentrations of sugars, thus being able to bring more substrates to plants and directly influence growth (Pedraza et al., 2010).

4.2 Genes involved in antimicrobial activities or important enzymes for industry

The functional diversity of the *S. marcescens* genome presents genes of interest for the pharmaceutical and medical sector, likewise the food, cosmetics, and fuel industries (Table 2).

Among some products, we can highlight the versatile enzyme L-asparaginase that includes the medical application of its antimicrobial and anti-inflammatory properties besides its use as a chemotherapeutic agent in different cancer cell lines (Abdel- Razik et al., 2019). The strategy of using novel therapeutic agents isolated from *S. marcescens* has been previously demonstrated in a marine strain with antioxidant and antibacterial activity against some Gram-positive and Gram-negative bacteria. (Gangadharan et al., 2020).

The food sector benefits from L-asparaginase mitigation effect due to toxic acrylamide, making it an essential component in food processing industries. This sector can demand the enzyme either considering its application in plant growth promotion. The L-Asparagine is the most abundant metabolite for the storage and transport of nitrogen in plants and impacts vegetable production. The L-asparaginase breaks down asparagine into aspartic acid and ammonia, providing nutrition directly and indirectly as a precursor of other amino acids that stimulate plant growth. Furthermore, the L-asparaginase is essential for developing seeds and grains (Damare & Kajawadekar, 2020).

The antimicrobial property is also of particular interest in Gramicidin D, a natural antimicrobial peptide produced by the soil microorganism *Bacillus brevis* ATCC 8185 during its sporulation phase. This ionophoric antibiotic forms membrane channels resulting in pores' formation, leading to cell disruption and loss of solutes and ions. The Gramicidin D has been effective against antibiotic resistant microorganisms, inhibiting the genetic material synthesis and respiration and reducing ATP, leading to cell death (Pavithra & Rajasekaran, 2020).

The high hemolytic activity of Gramicidin D turns it more suitable where there is low hemolytic activity, as in antimalarial activity against *Plasmodium falciparum* (Gumila et al., 1997) and plants with some benefits already been demonstrated in oat roots (Hodges et al., 1971).

The food sector can also benefit from the presence of the peptide tyrocidine that has an unexplored antifungal effect against some agronomically relevant fungal phytopathogens (Troskie et al., 2014). The tyrocidines can be associated with gramicidin, either encoded by our *S. marcescens* strain in an antimicrobial compound called tyrothricin that shows activity against bacteria, fungi, and some viruses. This antibiotic demonstrated a low risk of resistance development in vitro, turning it a valuable therapeutic option to consider against the antibiotic resistance process (Stauss-Grabo et al., 2014).

Additionally, even new strategies proposed to treat antibiotic resistance, like bacterial predation, effective against some Gram-negative bacteria (Rames, 2020), find a barrier in our strain as a result of the metalloprotease serralysin that can reduce the ability of some predators to attach to the *S. marcescens*, conferring protection (Garcia et al., 2018). Serralysin, a virulence factor used medicinally as a proteolytic enzyme, is therapeutically useful in the management of pain and inflammation as a broad spectrum anti-inflammatory drug (Tiwari, 2017), digests non-living tissue, blood clots, cysts, and arterial plaque (Rouhani et al., 2020) and has an anticancer potential (Araghi et al., 2019).

Our *S. marcescens* sample revealed the peroxiredoxins OsmC/Ohr, Prx5, and Prx6 proteins. Peroxiredoxins are ubiquitous peroxidases that play an important role in antioxidant defense and regulating cell signaling pathways (Perkins et al., 2015). Ohr is involved in the host-pathogen interface, while OsmC participates more in the oxidative defense (Alegria et al., 2017). Moreover, Prx5 and Prx6 are being related to cancer prevention, although more studies are necessary to understand the interaction pattern with cancer cells (Forshaw et al., 2019).

For the best of our knowledge, all the four proteins associated with peroxiredoxins discussed above (OsmC/Ohr, Prx5, and Prx6) were not reported in *Serratia marcescens* before, revealing its potential and possible use in the host-pathogen interface and cancer management.

The use of substances produced by the *Serratia* genus and present in our lineage has benefits, including agronomy. Plant protecting properties of the biosurfactant serrawettin, for example, turns the *S. marcescens* an interesting candidate for controlling and preventing Oomycete pathogens infestation of plants (Strobel et al., 2002). Mechanisms of plant growth

promotion include the synthesis of siderophores which can solubilize and sequester iron from the soil. The presence of the siderophore pyoverdine may provide iron to plants. This supply helps the bacteria to protect plants against the inhibitory effects of high concentrations of nickel, lead, and zinc (Burd et al., 2000).

The *S. marcescens* genome also carries genes encoding enzymes like Laccase, a component of prokaryotic lignin-degrading systems. This ligninolytic genetic repertoire is reinforced by the gene YefX encoding dye-decolorizing peroxidase (DyP). This heme peroxidase is more efficient in degrading lignin than classical peroxidase considering the ability of DyP to degrade aromatic compounds that constitute approximately 90% of the lignin (Melo-Nascimento et al., 2020). Thus, the industry can benefit from lignin uses. Additions of alkali lignin to pet and human food can be an important fiber source, especially considering that high nutritional fiber relates to low occurrences of colon câncer (Naseem et al., 2016).

The DyP ability to degrade lignin can benefit its utilization as a carbon source. Considering that lignin is one of the most abundant organic macromolecules in the biosphere, it can constitute a renewable carbon feedstock, potentially reducing the use of petroleum-derived chemicals (Brown & Chang, 2014).

The dye-decolourizing activity that gives name to the peroxidase may also benefit the industry operating in bioremediation, degrading synthetic dyes, and remediating phenolic environmental pollutants. Particularly important considering that synthetic dyes are employed in diverse industries such as food, textile, plastics, food, and pharmaceutical (Falade and Ekundayo, 2021). Bioremediation strategies using *S. marcescens* have been developed as a promising alternative for marine ecosystems impacted by petroderivatives (dos Santos et al., 2021).

The versatility is also present in Lipases, ubiquitous enzymes that hydrolyze ester bonds of triglycerides at oil-water. Its enantioselectivity in biocatalytic hydrolysis is being used in the pharmaceutical industry to produce key intermediates of the diltiazem hydrochloride used in circulatory disorders pharmacos and the anti-inflammatory ketoprofen (Long et al., 2007; Shibatani et al., 2000). Another application of the enzyme is its use to produce monoacylglycerols and diacylglycerols, which have the advantage of being biodegradable and non-toxic and are widely used as emulsifiers in food, pharmaceutical, and cosmetic industries (Zied et al., 2018). In addition, the lipases are known for their ability in the industry of oil and lipid processing, detergent production, and biotransformation (García-Silvera et al., 2018; Zied et al., 2018). Some studies have shown some applicability for *S. marcescens* lipase, such as petroleum biodegradation regenerating contaminated areas, generation of emulsifiers from cheap vegetable oils, and biodiesel production (García-Silvera et al., 2018; Peixoto et al., 2017; Zied et al., 2018).

Some microorganisms have been using the Butanol biosynthesis system for biofuel production. Butanol is a sustainable technology for alternate and renewable energy, being less corrosive and with higher energy content per unit mass than traditional fuels. The butanol potential includes its use as a solvent and a platform chemical in the cosmetic and pharmaceutical industry (Lv et al., 2021).

4.3 Selected metabolism of xenobiotics genes

4.3.1 Degradation of azo dyes and hydroxybenzoate degradation

There is a need for healthy environmental conditions, such as water purity and soil integrity and strength, to promote plant growth. The global aquatic resources undergo endless threats due to the discharge of several substances such as synthetic textile dyes and heavy metals, mainly from industries (Mahmood et al., 2017).

The azo dyes are a group of synthetic chemicals present in wastewaters dumped by textile industries. The water contaminated by this group of dyes affects the nearby waters used for agriculture and other purposes. Moreover, it is hard to remove from agricultural soils because of their complex structure (Mahmood et al., 2017).

Following these lines, the contaminated water irrigates plants that incorporate these chemical substances bringing harmful effects both for the plant and for the consumer (Mahmood et al., 2017).

Our group found in the *S. marcescens* genome the system of degradation azo dyes (Table 3). It is of common knowledge that this system is responsible for decolorized azo dyes through NADH-ubiquinone: oxidoreductase enzyme activity. This group of dyes is associated with impaired plant metabolism, health, and growth (Mahmood et al., 2017).

The *S. marcescens* use may provide the soil and plant azo dyes decontamination, which can be associated with plant growth and metabolism improvement. Besides, healthy soil is essential to promote a whole agriculture quality (Ahmed et al., 2016).

Plants naturally contain relevant levels of phenolic compounds that are essential to many metabolism events, such as growth, reproduction, and protection against pathogens (Wang et al., 2015). In these lines, the *S. marcescens* genome showed a hydroxybenzoate degradation gene set, which must be considered.

4.3.2 Degradation of nitro compounds, degradation of arylsulfatase and N-heterocyclic aromatic compound degradation

Other harmful substances are released in the environment, such as 2,4,6-Trinitrotoluene (TNT), released from demilitarization facilities. This compound is highly toxic and hazardous to all organisms, plants, and humans included. The nitroreductase protein family is involved in reducing nitrogen-containing compounds, such as TNT (You et al., 2015). Some bacteria strains are already used in plants as a detoxifying tool for this kind of environment. Here we report the presence of the nitroreductase protein family in the *S. marcescens* genome, which can also be used for the plant environment decontamination and improvement.

It is common knowledge that arylsulfatase is important to SO_4^{2-} plant uptake throughout the mineralization of organic sulfur (S) to SO_4^{2-} and it is from bacteria strains (Knauff, Schulz, & Scherer, 2003). Sulfur plays a fundamental role in plant metabolic processes and protein production, which prompts the plant growth or development and filling of grains, for example (Hawkesford, 2007). The S absence is harmful to the plant, and the arylsulfatase is essential to provide this nutrient for the plant (Knauff et al., 2003).

Besides, heterocyclic compounds are a group of chemicals also found in the environment. Some of these compounds can accumulate in the soil, leading to toxicity to plants and humans (Seo, Keum, & Li, 2009). The *S. marcescens* genome sequencing showed the arylsulfatase system and N-heterocyclic aromatic compound degradation system presence, which indicates one more important role of this bacterium in promoting plant growth and health.

4.3.3 Quinate degradation

Quinate is an important compound produced and used by plants. It is a precursor for chlorogenic acids (CGAs) biosynthesis. The CGAs act in leaves and fruits as a protective agent against pathogens and fungus and play an antioxidant role, protecting the plant against UV radiation damage (Gritsunov et al., 2018).

The quinate degradation system is essential to provide the active compound from the quinate pathway and could be used to help in plant protection promotion, which could allow their growth and metabolism improvement.

4.3.4 Metabolism of xenobiotics by cytochrome P450 and hydroxybenzoate degradation and degradation of various xenobiotics compounds

The cytochrome P450 (CYP) is an enzymatic protein superfamily found in several organisms, such as mammals, fungi, plants, and bacteria. It is composed of enzymes essential in many plant metabolic pathways, plant growth, development, and defense (Xu et al., 2015). The CYP family is also important in the detoxication of herbicides in plants (Stiborová et al., 2000).

Although the cytochrome P450 is already found in plants, exogenous origin use could be an essential tool for improving plant metabolism. Our group described, throughout the genome *S. marcescens* sequencing, the presence of this xenobiotics metabolism system. When applied in plant improvement, this strain could be used to deliver this system to the plant, and it can be applied in several contexts. For example, the use of contaminated soil for agriculture or plant cultures that demand high herbicide doses require a robust detox mechanism, which could not be sufficient (Gong et al., 2005). In these scenarios, the use of exogenous systems of xenobiotics metabolism could allow this kind of culture and even improve plant growth and health.

Besides, many systems of degradation of xenobiotics compounds were found in *S. marcescens* sequencing. These pathways are essential in restraining oxidative damage, xenobiotics detox, and many stress responses that are important in plant metabolism and growth (Gong et al., 2005). These systems are composed of several proteins, such as glutathione S-transferases (GSTs). Gong and colleagues (2005) showed that in vivo, the GSTs expression was related to changes in plant growth and shoot regeneration in vitro. These data demonstrate de GSTs influence in plant growth and metabolism, which could be applied in biotechnological approaches through *S. marcescens* usage.

4.3.5 Phenylacetate degradation

The Phenylacetic acid (PAA), also known as phenylacetate, belongs to a group called auxins, a class of hormones essential in plant metabolism (Cook, 2019).

PAA was described as a growth-promoting hormone, and later studies, comparing PAA with the auxin IAA, demonstrated PAA's higher activity in stimulating lateral root. The few studies with this auxin suggest PAA's predominant role in root growth and plant regular growth maintenance (Cook, 2019). Possibly PAA is important in other plant mechanisms, but more studies must deep investigate its whole function.

The *S.marcescens* sequencing showed a phenylacetate degradation system which must be considered in its biotechnology use, once this strain characteristic could promote the antagonist effect proposed.

4.4 Genes responsible for the resistance to different metals and antibiotics

The success of bioremediation is related to the bacteria's ability to survive in a contaminated environment, among others, by antimicrobials and heavy metals (Table 4). It is the case of our strain. For example, the Cpx Regulatory System Up-regulates the Multidrug Resistance Cascade. The Cpx Stress Response has a global effect in a diversity of signal transduction pathways, including the bacterial resistance to antimicrobials (Guest & Raivio, 2016).

The excessive presence of heavy metals in the environment leads to several problems in soil, such as impaired fertility, decreased microbial activity, and yield losses. This problem affects plant growth and metabolism and carries toxicity to human health (Kacálková et al., 2009). The *S.marcescens* sequencing showed some relevant genes in heavy metals transporting and zinc/cadmium/mercury/lead-transporting ATPase. These systems are important to transport these heavy metals and could be used in a biotechnology approach to a detox tool for plants that grow in the contaminated soil.

Besides these systems, the copper resistance system was also found in *S. marcescens* sequencing. The excessive copper accumulation in plants leads to several deleterious effects, such as reduced seed germination, impaired plant growth, low yield,

and formation of ROS (reactive oxygen species) (H. Amin et al., 2021). Therefore, the presence of an exogenous system could control copper plant concentration and promote plant growth and health.

Metal resistance has been described in a co-selection mechanism with antibiotic resistance, particularly relevant under environmental conditions of metal stress. The selective pressure to survive under stress conditions might contribute to plant growth-promoting bacteria evolve mechanisms to tolerate the uptake of heavy metal and/or the antibiotic presence in soil, for example (Yang et al., 2021).

PGPR bacteria presenting antibiotic and metal resistance genes in parallel have been identified in environments with multiple stress in which the survivor bacterium is probably benefited by acquiring resistance to both causes of stress (Wani & Irene, 2013).

This co-selection may occur as a co-resistance when genes encoding resistance to heavy metals and antimicrobial agents are physically linked to each other (Bazzi et al., 2020). This association has already been described in *S. marcescens* with tetracycline resistance and also to chloramphenicol and kanamycin in this case, which is genetically linked to As, Cu, Hg, and Ag resistance genes (Gilmour et al., 2004).

Other ways occur with the Cross-resistance when the same resistance mechanism confers resistance to both heavy metals and antimicrobial agents. Frequently related to multi-drug efflux pumps and the least common mechanism of co-selection, the Co-regulatory resistance occurs when resistant genes to antimicrobial agents and heavy metals are controlled by a mutual regulatory protein (Bazzi et al., 2020). These mechanisms of co-selection support the direct correlation between antibiotic resistance genes with the concentration of antibiotics and metals found in the manure of Chinese swine farms (Yang et al., 2021).

4.5 Genes responsible for the nematicidal and larvicidal kill genes

Compounds of microbial origin have been showing a positive protection effect combating plant-parasites (table 5). For example, in the root-knot nematode that impacts the global agricultural production, acetaldehyde demonstrated nematicidal activity by direct contact killing besides the fumigation inhibiting egg hatching (Huang et al., 2020).

The nematicidal effect of other substances as serrawettin and chitinase potentially produced by our strain has already been found in *Serratia* sp. genetically related to *S. marcescens*. The presence of these compounds, according to the author, is important to turn this strain into an attractive candidate as a sustainable alternative for biocontrol in crops of agricultural interest (Méndez-Santiago et al., 2021).

The broad niche and functional diversity of the *S. marcescens* are probably influenced by the highly dynamic genome (Cristina et al., 2019), turning relevant a periodical investigation of the genetic background from various sources, concerning its possible pathogenicity. This research collaborates in this context with the genetic repertoire of a *Serratia marcescens* isolated from food. In addition, the potential application of this strain as a plant growth promoter was evaluated from a genotypic perspective.

5. Conclusion

The *S. marcescens* systems described here are relevant in the plant biotechnology approach representing an alternative in promoting plant growth and health. All these systems could improve different mechanisms, both in the plants and their environment. In addition, understanding the genetic background governing this strain may bring new insights into the ecology of *Serratia marcescens*.

To the best of our knowledge, this is the first genome sequence report on *S. marcescens* isolated from cheese, with potential application as promoting plant growth and providing a baseline for future genomic studies. Future investigations of others *Serratia marcescens* isolated from food will allow comparative analysis that may help to establish a model of the genetic background of the association between *S. marcescens* with plants and the food production process.

References

- Abdel- Razik, N. E., EL-Baghdady, K. Z., EL-Shatoury, E. H., & G Mohamed, N. (2019). Isolation, optimization, and antitumor activity of l-asparaginase extracted from *Pectobacterium carotovorum* and *Serratia marcescens* on human breast adenocarcinoma and human hepatocellular carcinoma cancer cell lines. *Asian Journal of Pharmaceutical and Clinical Research*, 332–337. <https://doi.org/10.22159/ajpcr.2019.v12i2.29646>
- Abreo, E., & Altier, N. (2019). Pangenome of *Serratia marcescens* strains from nosocomial and environmental origins reveals different populations and the links between them. *Scientific Reports*, 9(1), 46. <https://doi.org/10.1038/s41598-018-37118-0>
- Adeolu, M., Alnajjar, S., Naushad, S., & S. Gupta, R. (2016). Genome-based phylogeny and taxonomy of the 'Enterobacteriales': proposal for Enterobacterales ord. nov. divided into the families Enterobacteriaceae, Erwiniaceae fam. nov., Pectobacteriaceae fam. nov., Yersiniaceae fam. nov., Hafniaceae fam. nov., Morgane. *International Journal of Systematic and Evolutionary Microbiology*, 66(12), 5575–5599. <https://doi.org/10.1099/ijsem.0.001485>
- Ahmed, F., Arshad, M., Ditta, A., Hussain, A., Naveed, M., Hasnain, M., & Nazir, Q. (2016). Combining Textile Effluent Wastewater with Organic Fertilizer for Improved Growth and Productivity of Wheat and Soil Health. *Journal of Environmental and Agricultural Sciences*, 8, 14–20.
- Alegria, T. G. P., Meireles, D. A., Cussiol, J. R. R., Hugo, M., Trujillo, M., de Oliveira, M. A., & Netto, L. E. S. (2017). Ohr plays a central role in bacterial responses against fatty acid hydroperoxides and peroxyxynitrite. *Proceedings of the National Academy of Sciences*, 114(2), E132–E141. <https://doi.org/10.1073/pnas.1619659114>
- Amarsy, R., Pean de Ponfilly, G. ., Benmansour, H. ., Jacquier, H., Cambau, E. & Mégarbane, B. (2020). *Serratia marcescens* outbreak in the intensive care unit during the COVID-19 pandemic: A paradoxical risk? *Médecine et Maladies Infectieuses*, 50(8), 750–751. <https://doi.org/10.1016/j.medmal.2020.05.004>
- Amin, A. A., Gharib, F. A. E., El-Awadi, M., & Rashad, E.-S. M. (2011). Physiological response of onion plants to foliar application of putrescine and glutamine. *Scientia Horticulturae*, 129(3), 353–360. <https://doi.org/10.1016/j.scienta.2011.03.052>
- Amin, H., Arain, B. A., Jahangir, T. M., Abbasi, A. R., Mangi, J., Abbasi, M. S., & Amin, F. (2021). Copper (Cu) tolerance and accumulation potential in four native plant species: a comparative study for effective phytoextraction technique. *Geology, Ecology, and Landscapes*, 5(1), 53–64. <https://doi.org/10.1080/24749508.2019.1700671>
- Araghi, A., Hashemi, S., Sepahi, A. A., Faramarzi, M. A., & Amin, M. (2019). Purification and study of anti-cancer effects of *Serratia marcescens* serralysin. *Iranian Journal of Microbiology*, 11(4), 320–327. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/31719964>
- Bazzi, W., Abou Fayad, A. G., Nasser, A., Haraoui, L.-P., Dewachi, O., Abou-Sitta, G., & Matar, G. M. (2020). Heavy Metal Toxicity in Armed Conflicts Potentiates AMR in *A. baumannii* by Selecting for Antibiotic and Heavy Metal Co-resistance Mechanisms. *Frontiers in Microbiology*, 11, 68. <https://doi.org/10.3389/fmicb.2020.00068>
- Brettin, T., Davis, J. J., Disz, T., Edwards, R. A., Gerdes, S., Olsen, G. J., & Xia, F. (2015). RASTtk: A modular and extensible implementation of the RAST algorithm for building custom annotation pipelines and annotating batches of genomes. *Scientific Reports*, 5(1), 8365. <https://doi.org/10.1038/srep08365>
- Brown, M. E., & Chang, M. C. Y. (2014). Exploring bacterial lignin degradation. *Current Opinion in Chemical Biology*, 19(1), 1–7. <https://doi.org/10.1016/j.cbpa.2013.11.015>
- Burd, G. I., Dixon, D. G., & Glick, B. R. (2000). Plant growth-promoting bacteria that decrease heavy metal toxicity in plants. *Canadian Journal of Microbiology*, 46(3), 237–245. <https://doi.org/10.1139/w99-143>
- Cook, S. D. (2019). An Historical Review of Phenylacetic Acid. *Plant and Cell Physiology*, 60(2), 243–254. <https://doi.org/10.1093/pcp/pcz004>
- Cristina, M., Sartini, M., & Spagnolo, A. (2019). *Serratia marcescens* Infections in Neonatal Intensive Care Units (NICUs). *International Journal of Environmental Research and Public Health*, 16(4), 610. <https://doi.org/10.3390/ijerph16040610>
- Damare, V. S., & Kajawadekar, K. G. (2020). *A preliminary study on L-asparaginase from mangrove detritus-derived fungi and its application in plant growth promotion – MycoAsia*. Retrieved from <http://mycoasia.org/a-preliminary-study-on-l-asparaginase-from-mangrove-detritus-derived-fungi-and-its-application-in-plant-growth-promotion/>
- Das, S. N., Dutta, S., Kondreddy, A., Chilukoti, N., Pullabhotla, S. V. S. R. N., Vadlamudi, S., & Podile, A. R. (2010). Plant Growth-Promoting Chitinolytic *Paenibacillus elgii* Responds Positively to Tobacco Root Exudates. *Journal of Plant Growth Regulation*, 29(4), 409–418. <https://doi.org/10.1007/s00344-010-9152-1>
- Davis, J. J., Wattam, A. R., Aziz, R. K., Brettin, T., Butler, R., Butler, R. M., & Stevens, R. (2020). The PATRIC Bioinformatics Resource Center: expanding data and analysis capabilities. *Nucleic Acids Research*, 48(D1), D606–D612. <https://doi.org/10.1093/nar/gkz943>
- dos Santos, R. A., Rodríguez, D. M., Ferreira, I. N. da S., de Almeida, S. M., Takaki, G. M. de C., & de Lima, M. A. B. (2021). Novel production of biodispersant by *Serratia marcescens* UCP 1549 in solid-state fermentation and application for oil spill bioremediation. *Environmental Technology*, 1–12. <https://doi.org/10.1080/09593330.2021.1910733>

- Falade, A. O., & Ekundayo, T. C. (2021). Emerging biotechnological potentials of DyP-type peroxidases in remediation of lignin wastes and phenolic pollutants: a global assessment (2007–2019). *Letters in Applied Microbiology*, 72(1), 13–23. <https://doi.org/10.1111/lam.13392>
- Forshaw, T. E., Holmila, R., Nelson, K. J., Lewis, J. E., Kemp, M. L., Tsang, A. W., & Furdui, C. M. (2019). Peroxiredoxins in Cancer and Response to Radiation Therapies. *Antioxidants*, 8(1), 11. <https://doi.org/10.3390/antiox8010011>
- Friman, M. J., Eklund, M. H., Pitkälä, A. H., Rajala-Schultz, P. J., & Rantala, M. H. J. (2019). Description of two *Serratia marcescens* associated mastitis outbreaks in Finnish dairy farms and a review of literature. *Acta Veterinaria Scandinavica*, 61(1), 54. <https://doi.org/10.1186/s13028-019-0488-7>
- Gangadharan, A., Jolly, J., & John, N. (2020). Bioprospecting of novel therapeutic agents from marine bacterium; *Serratia marcescens*. *Materials Today: Proceedings*, 25, 298–301. <https://doi.org/10.1016/j.matpr.2020.01.465>
- García-Silvera, E. E., Martínez-Morales, F., Bertrand, B., Morales-Guzmán, D., Rosas-Galván, N. S., León-Rodríguez, R., & Trejo-Hernández, M. R. (2018). Production and application of a thermostable lipase from *Serratia marcescens* in detergent formulation and biodiesel production. *Biotechnology and Applied Biochemistry*, 65(2), 156–172. <https://doi.org/10.1002/bab.1565>
- García, C. J., Pericleous, A., Elsayed, M., Tran, M., Gupta, S., Callaghan, J. D., & Kadouri, D. E. (2018). Serralysin family metalloproteases protects *Serratia marcescens* from predation by the predatory bacteria *Micavibrio aeruginosavorus*. *Scientific Reports*, 8(1), 14025. <https://doi.org/10.1038/s41598-018-32330-4>
- Gilmour, M. W., Thomson, N. R., Sanders, M., Parkhill, J., & Taylor, D. E. (2004). The complete nucleotide sequence of the resistance plasmid R478: defining the backbone components of incompatibility group H conjugative plasmids through comparative genomics. *Plasmid*, 52(3), 182–202. <https://doi.org/10.1016/j.plasmid.2004.06.006>
- Gong, H., Jiao, Y., Hu, W., & Pua, E.-C. (2005). Expression of glutathione-S-transferase and its role in plant growth and development in vivo and shoot morphogenesis in vitro. *Plant Molecular Biology*, 57(1), 53–66. <https://doi.org/10.1007/s11103-004-4516-1>
- Gritsunov, A., Peek, J., Diaz Caballero, J., Guttman, D., & Christendat, D. (2018). Structural and biochemical approaches uncover multiple evolutionary trajectories of plant quinate dehydrogenases. *The Plant Journal*, 95(5), 812–822. <https://doi.org/10.1111/tpj.13989>
- Guest, R. L., & Raivio, T. L. (2016). Role of the Gram-Negative Envelope Stress Response in the Presence of Antimicrobial Agents. *Trends in Microbiology*, 24(5), 377–390. <https://doi.org/10.1016/j.tim.2016.03.001>
- Gumila, C., Ancelin, M. L., Delort, A. M., Jeminet, G., & Vial, H. J. (1997). Characterization of the potent in vitro and in vivo antimalarial activities of ionophore compounds. *Antimicrobial Agents and Chemotherapy*, 41(3), 523–529. <https://doi.org/10.1128/AAC.41.3.523>
- Hawkesford, M. J. (2007). *Sulfur and plant ecology: a central role of sulfate transporters in responses to sulfur availability*. https://doi.org/10.1007/978-1-4020-5887-5_1
- Hodges, T. K., Darding, R. L., & Weidner, T. (1971). Gramicidin-D-stimulated influx of monovalent cations into plant roots. *Planta*, 97(3), 245–256. <https://doi.org/10.1007/BF00389205>
- Huang, D., Yu, C., Shao, Z., Cai, M., Li, G., Zheng, L., & Zhang, J. (2020). Identification and Characterization of Nematicidal Volatile Organic Compounds from Deep-Sea *Virgibacillus dokdonensis* MCCC 1A00493. *Molecules*, 25(3), 744. <https://doi.org/10.3390/molecules25030744>
- Ishii, K., Adachi, T., Imamura, K., Takano, S., Usui, K., Suzuki, K., & Sekimizu, K. (2012). *Serratia marcescens* Induces Apoptotic Cell Death in Host Immune Cells via a Lipopolysaccharide- and Flagella-dependent Mechanism*. *Journal of Biological Chemistry*, 287(43), 36582–36592. <https://doi.org/10.1074/jbc.M112.399667>
- Kacáková, L., Tlustoš, P., & Száková, J. (2009). Phytoextraction of cadmium, copper, zinc and mercury by selected plants. *Plant, Soil and Environment*, 55(No. 7), 295–304. <https://doi.org/10.17221/100/2009-PSE>
- Kamran, S., Shahid, I., Baig, D. N., Rizwan, M., Malik, K. A., & Mehnaz, S. (2017). Contribution of Zinc Solubilizing Bacteria in Growth Promotion and Zinc Content of Wheat. *Frontiers in Microbiology*, 8(DEC), 2593. <https://doi.org/10.3389/fmicb.2017.02593>
- Khan, A. R., Park, G.-S., Asaf, S., Hong, S.-J., Jung, B. K., & Shin, J.-H. (2017). Complete genome analysis of *Serratia marcescens* RSC-14: A plant growth-promoting bacterium that alleviates cadmium stress in host plants. *PLOS ONE*, 12(2), e0171534. <https://doi.org/10.1371/journal.pone.0171534>
- Knauff, U., Schulz, M., & Scherer, H. W. (2003). Arylsulfatase activity in the rhizosphere and roots of different crop species. *European Journal of Agronomy*, 19(2), 215–223. [https://doi.org/10.1016/S1161-0301\(02\)00035-7](https://doi.org/10.1016/S1161-0301(02)00035-7)
- Long, Z.-D., Xu, J.-H., Zhao, L.-L., Pan, J., Yang, S., & Hua, L. (2007). Overexpression of *Serratia marcescens* lipase in *Escherichia coli* for efficient bioregulation of racemic ketoprofen. *Journal of Molecular Catalysis B: Enzymatic*, 47(3–4), 105–110. <https://doi.org/10.1016/j.molcatb.2007.04.004>
- Lv, Y., Jiang, Y., Peng, W., Fang, Y., Dong, W., Zhou, J., & Jiang, M. (2021). Genetic manipulation of non-solvent-producing microbial species for effective butanol production. *Biofuels, Bioproducts and Biorefining*, 15(1), 119–130. <https://doi.org/10.1002/bbb.2152>
- Mahmood, F., Shahid, M., Hussain, S., Shahzad, T., Tahir, M., Ijaz, M., & Babar, S. A. K. (2017). Potential plant growth-promoting strain *Bacillus* sp. SR-2-1/1 decolorized azo dyes through NADH-ubiquinone:oxidoreductase activity. *Bioresource Technology*, 235, 176–184. <https://doi.org/10.1016/j.biortech.2017.03.098>
- Melo-Nascimento, A. O. dos S., Sant'Anna, B. M. M., Gonçalves, C. C., Santos, G., Noronha, E., Parachin, N., & Bruce, T. (2020). Complete genome reveals genetic repertoire and potential metabolic strategies involved in lignin degradation by environmental ligninolytic *Klebsiella variicola* PICD1. *PLOS ONE*, 15(12), e0243739. <https://doi.org/10.1371/journal.pone.0243739>
- Méndez-Santiago, E. W., Gómez-Rodríguez, O., Sánchez-Cruz, R., Folch-Mallol, J. L., Hernández-Velázquez, V. M., Villar-Luna, E., & Wong-Villarreal, A. (2021). *Serratia* sp., an endophyte of *Mimosa pudica* nodules with nematicidal, antifungal activity and growth-promoting characteristics. *Archives of*

Microbiology, 203(2), 549–559. <https://doi.org/10.1007/s00203-020-02051-2>

Naseem, A., Tabasum, S., Zia, K. M., Zuber, M., Ali, M., & Noreen, A. (2016). Lignin-derivatives based polymers, blends and composites: A review. *International Journal of Biological Macromolecules*, 93, 296–313. <https://doi.org/10.1016/j.ijbiomac.2016.08.030>

Parmar, H. Y., & Chakraborty, H. (2016). Effect of siderophore on plant growth promotion. *International Journal of Applied and Pure Science and Agriculture*, 2(3). Retrieved from <https://ijapsa.com/papers/volume-2/issue-3/effect-of-siderophore-on-plan-growth-promotion/>

Pavithra, G., & Rajasekaran, R. (2020). Gramicidin Peptide to Combat Antibiotic Resistance: A Review. *International Journal of Peptide Research and Therapeutics*, 26(1), 191–199. <https://doi.org/10.1007/s10989-019-09828-0>

Pedraza, R. O., Motok, J., Salazar, S. M., Ragout, A. L., Mentel, M. I., Tortora, M. L., & Díaz-Ricci, J. C. (2010). Growth-promotion of strawberry plants inoculated with *Azospirillum brasilense*. *World Journal of Microbiology and Biotechnology*, 26(2), 265–272. <https://doi.org/10.1007/s11274-009-0169-1>

Peixoto, F. B. S., Peixoto, J. C. D. C., Assunção, E. N. de, Peixoto, E. M., Pereira, J. O., & Astolfi-Filho, S. (2017). Petroleum biodegrading and co-resistance to antibiotics by *Serratia marcescens* strain isolated in Coari, Amazonas. *Acta Scientiarum. Biological Sciences*, 39(4), 489. <https://doi.org/10.4025/actasciobiolsci.v39i4.36223>

Perkins, A., Nelson, K. J., Parsonage, D., Poole, L. B., & Karplus, P. A. (2015). Peroxiredoxins: guardians against oxidative stress and modulators of peroxide signaling. *Trends in Biochemical Sciences*, 40(8), 435–445. <https://doi.org/10.1016/j.tibs.2015.05.001>

Rames, A. (2020). Predatory Bacteria: A Possible Key for the Lock of Antibiotic Resistance. In *Transactions on Science and Technology* (Vol. 7). Retrieved from <http://tost.unise.org/>

Ramesh, S. A., Tyerman, S. D., Gilliam, M., & Xu, B. (2017). γ -Aminobutyric acid (GABA) signalling in plants. *Cellular and Molecular Life Sciences*, 74(9), 1577–1603. <https://doi.org/10.1007/s00018-016-2415-7>

Rodríguez, H., & Fraga, R. (1999). Phosphate solubilizing bacteria and their role in plant growth promotion. *Biotechnology Advances*, 17(4–5), 319–339. [https://doi.org/10.1016/S0734-9750\(99\)00014-2](https://doi.org/10.1016/S0734-9750(99)00014-2)

Rouhani, M., Valizadeh, V., Molasalehi, S., & No-Rouzian, D. (2020). Production and Expression Optimization of Heterologous Serra-tiopeptidase. *Iranian Journal of Public Health*, 931–939. Retrieved from <http://ijph.tums.ac.ir/index.php/ijph/article/view/20663>

Ryu, C.-M., Choi, H. K., Lee, C.-H., Murphy, J. F., Lee, J.-K., & Kloepper, J. W. (2013). Modulation of Quorum Sensing in Acyl-homoserine Lactone-Producing or -Degrading Tobacco Plants Leads to Alteration of Induced Systemic Resistance Elicited by the Rhizobacterium *Serratia marcescens* 90-166. *The Plant Pathology Journal*, 29(2), 182–192. <https://doi.org/10.5423/PPJ.SI.11.2012.0173>

Seemann, T. (2014). Prokka: rapid prokaryotic genome annotation. *Bioinformatics*, 30(14), 2068–2069. <https://doi.org/10.1093/bioinformatics/btu153>

Seo, J.-S., Keum, Y.-S., & Li, Q. (2009). Bacterial Degradation of Aromatic Compounds. *International Journal of Environmental Research and Public Health*, 6(1), 278–309. <https://doi.org/10.3390/ijerph6010278>

Sharifi, R., & Ryu, C.-M. (2018). Revisiting bacterial volatile-mediated plant growth promotion: lessons from the past and objectives for the future. *Annals of Botany*, 122(3), 349–358. <https://doi.org/10.1093/aob/mcy108>

Shibatani, T., Omori, K., Akatsuka, H., Kawai, E., & Matsumae, H. (2000). Enzymatic resolution of diltiazem intermediate by *Serratia marcescens* lipase: molecular mechanism of lipase secretion and its industrial application. *Journal of Molecular Catalysis B: Enzymatic*, 10(1–3), 141–149. [https://doi.org/10.1016/S1381-1177\(00\)00122-3](https://doi.org/10.1016/S1381-1177(00)00122-3)

Silva, C. R., Okuno, N. T., Macedo, V. H. L. de M., Freire, I. D. R., Miller, R. M., & Marin, V. A. (2020). Resistome in gram-negative bacteria from soft cheese in Brazil. *Revista de Ciências Médicas e Biológicas*, 19(3), 430. <https://doi.org/10.9771/cmbio.v19i3.35460>

Stauss-Grabo, M., Atiye, S., Le, T., & Kretschmar, M. (2014). Decade-long use of the antimicrobial peptide combination tyrothricin does not pose a major risk of acquired resistance with gram-positive bacteria and candida spp. *Pharmazie*, 69(11), 838–841. <https://doi.org/10.1691/ph.2014.4686>

Stiborová, M., Schmeiser, H., & Frei, E. (2000). Oxidation of xenobiotics by plant microsomes, a reconstituted cytochrome P450 system and peroxidase: a comparative study. *Phytochemistry*, 54(4), 353–362. [https://doi.org/10.1016/S0031-9422\(00\)00123-0](https://doi.org/10.1016/S0031-9422(00)00123-0)

Strobel, G. A., Morrison, S. L., & Cassella, M. (2002). *Protecting plants from oomycete pathogens by treatment with compositions containing serratamolide and oocydin a from Serratia marcescens*. <https://doi.org/C07D493/08>

Tanizawa, Y., Fujisawa, T., Kaminuma, E., Nakamura, Y., & Arita, M. (2016). DFAST and DAGA: web-based integrated genome annotation tools and resources. *Bioscience of Microbiota, Food and Health*, 35(4), 173–184. <https://doi.org/10.12938/bmfh.16-003>

Tanizawa, Y., Fujisawa, T., & Nakamura, Y. (2018). DFAST: a flexible prokaryotic genome annotation pipeline for faster genome publication. *Bioinformatics*, 34(6), 1037–1039. <https://doi.org/10.1093/bioinformatics/btx713>

Tiwari, M. (2017). The role of serratiopeptidase in the resolution of inflammation. *Asian Journal of Pharmaceutical Sciences*, 12(3), 209–215. <https://doi.org/10.1016/j.ajps.2017.01.003>

Troskie, A. M., de Beer, A., Vosloo, J. A., Jacobs, K., & Rautenbach, M. (2014). Inhibition of agronomically relevant fungal phytopathogens by tyrocidines, cyclic antimicrobial peptides isolated from *Bacillus aneurinolyticus*. *Microbiology*, 160(9), 2089–2101. <https://doi.org/10.1099/mic.0.078840-0>

Wang, J.-Y., Zhou, L., Chen, B., Sun, S., Zhang, W., Li, M., ... He, Y.-W. (2015). A functional 4-hydroxybenzoate degradation pathway in the phytopathogen *Xanthomonas campestris* is required for full pathogenicity. *Scientific Reports*, 5(1), 18456. <https://doi.org/10.1038/srep18456>

Wani, P. A., & Irene, O. I. (2013). Screening of Microbes for Their Metal, Antibiotic Resistance and Plant Growth Promoting Activity. *Current Research in Bacteriology*, 7(1), 22–31. <https://doi.org/10.3923/crb.2014.22.31>

Xie, Q., Essemine, J., Pang, X., Chen, H., & Cai, W. (2020). Exogenous application of abscisic acid to shoots promotes primary root cell division and elongation. *Plant Science*, 292, 110385. <https://doi.org/10.1016/j.plantsci.2019.110385>

Xu, J., Wang, X., & Guo, W. (2015). The cytochrome P450 superfamily: Key players in plant development and defense. *Journal of Integrative Agriculture*, 14(9), 1673–1686. [https://doi.org/10.1016/S2095-3119\(14\)60980-1](https://doi.org/10.1016/S2095-3119(14)60980-1)

Yang, F., Zhang, F., Li, H., Wu, H., Zhao, H., Cheng, X., & Zhu, J. (2021). Contribution of environmental factors on the distribution of antibiotic resistance genes in agricultural soil. *European Journal of Soil Biology*, 102, 103269. <https://doi.org/10.1016/j.ejsobi.2020.103269>

You, S.-H., Zhu, B., Han, H.-J., Wang, B., Peng, R.-H., & Yao, Q.-H. (2015). Phytoremediation of 2,4,6-trinitrotoluene by Arabidopsis plants expressing a NAD(P)H-flavin nitroreductase from *Enterobacter cloacae*. *Plant Biotechnology Reports*, 9(6), 417–430. <https://doi.org/10.1007/s11816-015-0379-y>

Zied, Z., Edahech, A., Rigano, F., Micalizzi, G., Mondello, L., Kharrat, N., & Cacciola, F. (2018). Monoacylglycerol and diacylglycerol production by hydrolysis of refined vegetable oil by-products using an immobilized lipase from *Serratia* sp. W3. *Journal of Separation Science*, 41(23), 4323–4330. <https://doi.org/10.1002/jssc.201800432>