Brazilian Journal of Biology®

ISSN 1519-6984 (Print)
ISSN 1678-4375 (Online)

Original Article

The potential use of *Pseudomonas* in terrestrial and space agriculture

O uso potencial de *Pseudomonas* na agricultura terrestre e espacial

I. H. Ruiz-Hernandez[a], L. A. Madrigal-Perez[b] and J. C. González-Hernández[a]*

[a] Tecnológico Nacional de México, Instituto Tecnológico de Morelia, Morelia, Michoacán, México

[b] Tecnológico Nacional de México, Instituto Tecnológico Superior de Ciudad Hidalgo, Ciudad Hidalgo, Michoacán, México

Abstract

In the last few years, there has been an increasing interest in solutions for sustainable agriculture to reduce negative impacts on the environment resulting from modern agricultural practices. The use of environmentally beneficial bacteria, like *Pseudomonas*, which can increase plant productivity by reducing growth time, is a promising opportunity for sustainable agriculture. *Pseudomonas* is a gram-negative bacterium genus, commonly present in soils, plants, and irrigation water. *Pseudomonas* has a wide range of metabolic routes that could benefit agriculture, such as nutrient uptake, pathogen suppression, heavy metal solubilization, drought tolerance, and high salt concentration tolerance. *Pseudomonas* may even be proposed as a potential tool for future agriculture on other planets, where the use of microorganisms would be essential for crop development in hostile and inhospitable environments. Hence, the present review discusses the potential use of *Pseudomonas* in sustainable agriculture on planet Earth and potentially on Mars, highlighting its role in plant growth enhancement and plant protection from pathogenic microorganisms.

Keywords: heavy metals, *Pseudomonas*, sustainable agriculture, space agriculture.

Resumo

Nos últimos anos, tem havido um interesse crescente em soluções para que a agricultura sustentável reduza os impactos negativos no ambiente, resultantes de práticas agrícolas modernas. A utilização de bactérias ambientalmente benéficas, como *Pseudomonas*, que podem aumentar a produtividade das plantas ao reduzir o tempo de crescimento, é uma oportunidade de investigação promissora para a agricultura sustentável. *Pseudomonas* são um gênero de bactérias Gram-negativas, comumente presentes em solos, plantas e água irrigada. Essas bactérias possuem uma gama de rotas metabólicas que podem beneficiar a agricultura, como absorção de nutrientes, supressão de patógenos, solubilização de metais pesados, tolerância à seca e a altas concentrações de sal. *Pseudomonas* podem até ser propostas como ferramenta potencial para a agricultura futura em outros planetas, onde o uso de microrganismos seria essencial para o desenvolvimento de culturas em ambientes hostis e inóspitos. Assim, a presente revisão discute o uso potencial de *Pseudomonas* na agricultura sustentável no planeta Terra e potencialmente em Marte, destacando o seu papel na melhoria do crescimento das plantas e na proteção delas contra microrganismos patogênicos.

Palavras-chave: metais pesados, *Pseudomonas*, agricultura sustentável, agricultura espacial.

1. Introduction

Every country on the planet depends on agriculture for its economy and well-being, however, contemporary farming methods, like monocropping, overreliance on chemicals, and deforestation, result in harmful ecological consequences such as soil erosion, reduced biodiversity, water contamination, and increased greenhouse gas emissions, underscoring the necessity for sustainable approaches to mitigate damage and guarantee lasting sustainability (Adedibu, 2023; Rahman et al., 2022).

In recent years, the development of new strategies to mitigate the effects caused by intensive agriculture and that can be used in polluted environments has become more relevant, which is why the practice of using various soil microorganisms that can provide nutrients to plants and soil, improve production yields and reduce the environmental impact caused by heavy metals or hydrocarbons has arisen (Arora et al., 2019; Prashar and Shah, 2016) some of these microorganisms are bacteria such as *Pseudomonas* with the ability to promote growth and survival in toxic environments (Misra et al., 2022).

Pseudomonas is a gram-negative bacterium genus with more than 120 distinct species commonly found

*e-mail: juan.gh@morelia.tecnm.mx
Received: January 25, 2023 – Accepted: May 3, 2024

in soil and water (Streeter and Katouli, 2016). Some *Pseudomonas* species are known for their capability to facilitate plant growth and protect plants against diseases (Backer et al., 2018). Additionally, *Pseudomonas* can help solubilize nutrients and heavy metals in soil, making them more accessible to plants and other nonpathogenic microorganisms (Fakhar et al., 2020).

For example, *P. putida*, *P. aeruginosa*, and *P. fluorescens* produce molecules that decrease plant growth time, such as organic acids, amino acids, antibiotics, and siderophores (Kim et al., 2013; Yeğin et al., 2020; De Werra et al., 2009). *Pseudomonas*-based bioinoculants for sustainable agriculture have been created based on these metabolic properties. Additionally, the presence of these *Pseudomonas* species in soils used in agriculture has awakened growing interest due to the provided benefits in various stages of plant development. Furthermore, *Pseudomonas* species contribute to the restoration of soils contaminated by herbicides, fertilizers, heavy metals, and hydrocarbons, thus decreasing growth time and increasing root size (Gutiérrez-Albanchez et al., 2021; Shahid et al., 2018; Velivelli et al., 2014). Therefore, the use of bacteria in agriculture possesses several benefits for crops since it optimally increases plant growth while protecting it from pathogens that can damage both seed and seedling growth.

2. Positive Effects of *Pseudomonas* Inoculation in the Soil

The positive effects of introducing beneficial microorganisms through bioinoculation with *Pseudomonas* are due to the adaptability to a hostile environment that may be polluted with heavy metals, herbicides, or fertilizers that can be solubilized or degraded. Most *Pseudomonas* have the ability to degrade hydrocarbons, nitrogenous compounds, and herbicides and decrease time required for plant growth (Kiki, 2022). For example, *P. protegens* (formerly known as *P. fluorescens*) may consume 80% of glyphosate, glufosinate, and phosphine in the presence or absence of iron atoms (Li et al., 2021). One of the key attributes of *Pseudomonas* is their ability to solubilize or degrade a wide range of contaminants, including hydrocarbons (Medić and Karadžić, 2022; Mullaeva et al., 2022), nitrogenous compounds (Yang et al., 2018), and herbicides (Yu et al., 2023). This versatile capacity not only contributes to the detoxification of the environment but also significantly reduces the time required for optimal plant growth.

2.1. The impact of heavy metals and hydrocarbons contamination on soil health

Currently, one-third of the world soils are contaminated with heavy metals (such as Cu^{+2}, Ni^{+2}, Cr^{+2}, Pb^{+2}, Zn^{+2}, and Cd^{+2}) from disparate sources, such as mining or hydrocarbon production. On the other hand, the concentration of naturally encountered metals is usually <1000 $mg^{*}kg^{-1}$, and most are nonbiodegradable. Nonetheless, the vast majority comes from anthropogenic activities (Alegría-Torres et al., 2020; Osman et al., 2019; Castro-González et al., 2019; Laghlimi et al., 2015). *Pseudomonas* bacteria have demonstrated the ability to withstand the toxic effects of heavy metals, showcasing their tolerance towards these harmful substances (see Table 1). Moreover, these bacteria possess the remarkable capability to release metabolites that can effectively bind and remove heavy metals from their surroundings through a process known as chelation.

On the other hand, species of *Pseudomonas* have been found in soils contaminated with hydrocarbons. For instance, *P. aeruginosa* is known for its ability to produce siderophores that chelate heavy metals (Zaynab et al., 2022; Shi et al., 2017), as well as rhamnolipids or surfactants that improve the solubility and mobility of hydrocarbons and heavy metals (Soberón-Chávez et al., 2021; Wu et al., 2019; Vilasó-Cadre et al., 2017; Agnello et al., 2016), as *P. puteola* and *P. stutzeri*. It has been reported that *Pseudomonas* species can degrade oil by the production of rhamnolipids (Ossai et al., 2020). These findings highlight the potential of *Pseudomonas* species in the bioremediation of contaminated soils, particularly those impacted by hydrocarbons and heavy metals.

2.2. Heavy metals chelation and soil bioremediation

Pollution of agricultural soils by heavy metals is a major concern causing ecological and environmental issues. Improving plant tolerance to heavy metal stress ought to enable crop growth with minimal or zero accumulation of heavy metals in edible parts of plants that fulfill the safe food requirements for a rapidly growing world population (Etesami, 2018). Plant growth-promoting rhizobacteria or PGPRs, such as *Pseudomonas*, are bacteria inhabiting the rhizosphere, an area around plant roots (Santoyo et al., 2021). The aforementioned is also recognized for promoting plant

Table 1. Tolerance to heavy metals by different *Pseudomonas* species; in the case of *P. reptilivora*, it has not yet been determined whether they tolerate the metals shown.

Organism	Heavy metals								Reference
	Cd	Cr	Hg	Cu	Pb	As	Mn	U	
P. aeruginosa	+	+	+	+	-	-	+	+	Choudhary and Sar (2011)
P. putida	+	-	+	+	-	-	+	-	Hussein et al. (2005)
P. fluorescens	+	-	-	-	-	-	-	-	Yang et al. (2018)
P. reptilivora	NA	NA	NA	+	NA	NA	+	NA	Yeğin et al. (2020)

NA = Not available, (+) can tolerate, (-) can't tolerate/inhibit growth.

growth by supplying nutrients, producing hormones, and protecting plants from pathogens (Sun et al., 2021; Morales-Cedeño et al., 2021). Additionally, it has also been found that PGPRs are effective in remediating contaminated soils (Feng et al., 2022; Anuroopa et al., 2021; Pandey and Gupta, 2020), and the ability of some PGPRs to produce organic acids such as gluconic acid has been described (Sun et al., 2020). The function of gluconic acid in heavy metal chelation is to bind to metal ions and form a more stable complex than the metal ion itself. Formation of this complex decreases the bioavailability of the metal ions by making them less toxic to plants and other organisms (Jain et al., 2020; Kour et al., 2019).

Figure 1 shows the benefits produced by different species of *Pseudomonas*), i.e., *P. aeruginosa* was able to bind 900 mg/L of Cd^{+2} at when added to a growth medium (Chellaiah, 2018), also *P. fluorescens* gim-3 could solubilize and dissolve 75.315 mg/L of Cd^{+2} found in soil (1.952 ± 0.084 mg/kg) using GA (Yang et al., 2018).

Gluconic acid is one of many metabolites produced by *Pseudomonas,* that could help to reduce the contamination of heavy metals in polluted soils. In summary, harnessing the abilities of PGPRs, particularly *Pseudomonas*, offers a promising avenue for mitigating the ecological and environmental impacts of heavy metal pollution in agricultural soils. By facilitating safe and sustainable crop growth, these beneficial bacteria contribute to the global effort to ensure food security while safeguarding our environment, Table 2 shows different heavy metals solubilized by different *Pseudomonas*.

2.3. Pseudomonas in sustainable agriculture, their capacity for disease biocontrol and plant growth

Pseudomonas spp. are effective biocontrol agents due to their catabolic adaptability, their ability to colonize roots, and their production of antifungal metabolites (Das et al., 2020). Fluorescent *Pseudomonas* are particularly adept at counteracting phytopathogens and stimulating disease resistance in host plants (Raio and Puopolo, 2021; Tienda et al., 2020; Mohammed et al., 2020); among these species, *P. aeruginosa*, *P. putida*, *P. cichori*, and *P. chlororaphis* are commonly found; these protect plants against pathogens by efficiently consuming root exudates and resisting predation by soil predators through antipredatory mechanisms such as toxicity and production of secondary metabolites, which reduce bacterial resistance (Kang et al., 2020; Arrebola et al., 2019). *Pseudomonas* relies on their ability to efficiently consume root exudates (substances released by plant roots) and resist being devoured by soil predators like nematodes and protozoa to defend themselves against these predators.

2.4. Pathogen suppresion

Pseudomonas spp. have developed several antipredator mechanisms, such as the production of secondary metabolites, which interact with predators in a complex way by affecting their physiology and behavior. Depending on the specific metabolite, it can act as a repellent, stressor, or toxin. The production of these secondary metabolites

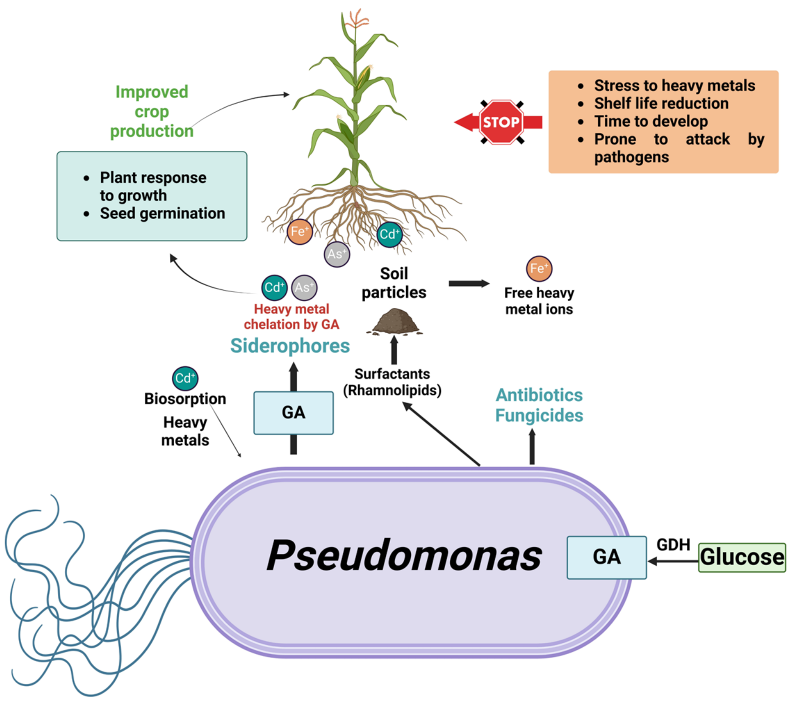

Figure 1. *Pseudomonas* is a beneficial bacteria that can improve the soil quality and plant growth in polluted environments. It produces various substances, such as siderophores, rhamnolipids, antibiotics, fungicides, and organic acids, that can help plants cope with stress from heavy metals and pathogens, improving crop production. For example, gluconic acid (GA) which is produced by an enzymatic reaction between glucose and glucose dehydrogenase (GDH) that when combined with rhamnolipids can bind to heavy metals and reduce their toxicity, (taken and modified from Singh et al., 2019, created with BioRender, 2023).

Table 2. Various heavy metals that were solubilized by different *Pseudomonas* species (taken and modified from Fakhar et al., 2020).

Heavy metal	Effects in plants or humans	Species	BE	Reference
Cadmium (Cd)	Affects seed development, inhibits DNA-mediated transformation, and alters the functions of enzymatic activities.	*P. aeruginosa*	900 mg/L	Abbas et al. (2017)
		P. fluorescens	94%	
Crome (Cd)	Decreases growth and disrupts enzyme activity.	*P. stutzeri*	25.6 mg/g	Yaashikaa et al. (2019)
		P. alcaliphilia	200 mg/L	El-Naggar et al. (2020)
		P. putida	1000 mg/L	
		Pseudomonas sp.	32%	
Cobalt (Co)	Causes cell membrane instability, readily oxidizes lipids, inhibits oxidative phosphorylation, and denatures proteins.	*P. alcaphilia*	96.32%	Elsayed et al. (2022)
		P. aeruginosa	100 mg/L	Al-Dhabi et al. (2020)
Mercury (Hg)	A leading cause of cancer and leukemia in humans. Alters DNA and damages cell walls.	*P. aeruginosa*	99.70%	Imron et al. (2021)
		P. putida	98%	Xue et al. (2022)
Uranium (U)	In humans causes respiratory disease and nephrotoxicity (mostly cell necrosis).	*P. aeruginosa*	275 mg/g (95%)	Choudhary and Sar (2011)

BE = Bioremediation Efficiency.

by biocontrol bacteria such as *Pseudomonas* spp. serves multiple functions, including plant protection against pathogens and enhancement of bacterial resistance. This was demonstrated in a study by Kang et al. (2020), in which they found that *P. koreensis* and *P. entomophilia* possess traits as nitrogen fixation, phosphate solubilization, heavy metal chelation (Kang et al., 2020), and phytohormone production that directly facilitate the proliferation of their plant hosts (Zboralski and Filion, 2023).

P. aeruginosa acts as a biocontrol agent in potatoes, tomatoes, and taro presenting various biologically active metabolites with the capacity to be used against different fungi and bacteria, facilitating the solubilization of nutrients so the plant assimilates them, thus increasing the size of the root, leaves and chlorophyll levels (Ghadamgahi et al., 2022). On the other hand, *P. parahaemolyticus* affects bacterial pustules in soybean plants by using production through the VILS2 lipopeptide pathway (Kakembo and Lee, 2019). Indeed *P. aeruginosa* isolated from the soil rhizosphere (part of the soil immediate to the roots) had a fungicidal effect against *Penicillium citreosulfuratum*, *P. citrinum* and *Stromatinia gladioli* pathogens of safranine (*Crocus satvus* L.), with inhibition percentages of 23.16%, 49.17%, and 79.76% respectively (Hu et al., 2021).

2.5. Drought tolerance

Drought tolerance refers to a plant's ability to resist dehydration and maintain it's physiological functions even under water-deficient conditions (Ilyas et al., 2020). Droughts associated with low rainfall are currently one of the most important factors affecting agricultural production and are expected to increase further in the future, posing major challenges to mankind., it has been reported that many agricultural regions are affected from drought up to 50%, and could even lose more however some strains of *Pseudomonas* can improve drought tolerance and crop production (Uzma et al., 2022), and different gene expression and induced drought tolerance (Humaira et al., 2020), on the other hand, other *Pseudomonas* have been shown to showed effective plant growth promotion and antifungal activity under drought stress conditions (Vurukonda et al., 2022), *P. putida* favors drought tolerance in tomato plants and promotes yields (Saglam et al., 2022).

2.6. Salt stress tolerance

Soil salinity has emerged as a great threat to the agricultural ecosystems, presence of water-soluble salts in excess negatively impacts plants physiological processes including seed germination, photosynthesis, membrane transport, antioxidants and ethylene production (Chang et al., 2014). The application of salt-tolerant plant growth promoting bacteria has shown remarkable success in enchanting productivity of saline soils (Arora et al., 2020). According to Do et al. (2022), two *Pseudomonas* (strain ND06 and ND09) showed potential in promoting peanut growth under salinity conditions, the study concluded that ND09 may be used as a biological ecofriendly agent in agriculture practices, it has also been reported that *P. pseudoalcaligenes* ismore effective in reducing salt stress soybean (Humaira et al., 2020). According to Lu et al. (2021), *P. aerugionsa* can alleviate the effects of the salt stress on plants and induce accumulation of free proline, simengly *P. simiae* showed increases in proline production when subjected to salt stress (Vaishnav and Choudhary, 2018). There before, soil salinity would be an important factor in the modern agriculture.

2.7. Limitations of using Pseudomonas

Unlike the studies discussed previously, it is important to mention that there are certain restrictions of using *Pseudomonas*. For example, they can slow root growth if the strains excrete high concentrations of indole-3-acetic acid, a plant hormone that can regulate plant growth and development and can promote phytopathogenic disease if used with *P. fluorescens* and *P. syringae* (Djami-Tchatchou et al., 2022; Xie et al., 1996). On the other hand, *P. aeruginosa* is an opportunistic pathogen that causes severe infections such as bloodstream, skin infections, and pneumonias, these infections can lead to high mortality of hosts or patients with suppressed immunity, therefore, caution is recommended with this strain (Reynolds and Kollef, 2021). Some *Pseudomonas* can produce cyanide which may cause an inhibitory effect on pathogens., however, cyanide has an inhibitory effect on plant growth like lettuce (Saharan and Nehra, 2011; Parikh and Jha 2012).

Overall, *Pseudomonas* shows promise as a biocontrol agent in modern agriculture, with its ability to defend plants against soil-borne phytopathogens but depends on the specific species and their interactions with plants and the environment. Therebefore, it's important to know which strain of *Pseudomonas* that could be chosen for its use in agricultural fields, contrasting with the risk on human health (see Table 3).

3. *Pseudomonas* Beyond Earth

NASA plans to launch the Artemis II mission in 2024, which will orbit the lunar surface and establish a sustainable base of operations. This base will play a crucial role in simulating the growth of plants and microorganisms in microgravity, providing valuable insights for future missions to Mars. The findings from these experiments will serve as prototypes for the establishment of the first human colony on the red planet in 2033 (Koehle et al., 2023). Whether bacteria can survive in space is a novel topic that still requires research. A bacterial species that has had positive effects on space radiation is *Deinoccocus radiodurans*, which has been able to survive the harmful effects of radiation for a 3-year period (Ott et al., 2020; Canganella and Bianconi, 2007). Research has also been carried out on the survival of *Pseudomonas* in space on the International Space Station (ISS). In a study conducted by Boyle et al. (1990), the potential survival of *P. aeruginosa* and *S. aureus* in harsh growth conditions was investigated. The findings indicated that *Pseudomonas* has the ability to endure nutrient deprivation in water, a capability not shared by *Staphylococcus* strains.

3.1. The potential use of Pseudomonas on the planet Mars

As outlined in the study "Grand Challenges for Synthetic Biology in Space" by Menezes et al. (2015), bacteria in

Table 3. Commonly applied biotechnological potential in *Pseudomonas*.

Organism	BSL	Dangerous to humans	¿Has it been studied for use in agriculture?	Benefit	Reference
P. aeruginosa	2	Yes	Yes	It produces various antibiotics, antifungals, rhamnolipids. Increases root size and produces antibiotics.	LaBauve and Wargo (2012)
P. putida	1	No	Yes		Clark and Pazdernik (2015)
P. reptilivora	1	No (highly pathogen to reptiles)	No, but it could be used in outer-space environments	It has not been studied for field use, however, degrades nitrogen compounds, heavy metals, produces antibiotics, and tolerates high salinity.	Yeğin et al. (2020)
P. syringae	2	No (highly pathogen to plants)	Yes	Produces highly destructive molecules against phytopathogens	Xin et al. (2018)
P. stutzeri	1	No	Yes	Promotes seed germination	Lami et al. (2020)
P. fluorescens	1	No	Yes	Efficient biocontrol, some strains use NO_3 instead of O_2	O'Callaghan (2016)
P. chlororaphis	1	No	Yes	Provides protection against fungal phytopathogens.	Galloway et al. (2011)
P. chloropaphis sub. Aurantiaca	1	No	Yes	Antifungal activity, plant growth promotion Mehnaz et al. (2020)	Hu et al. (2014)
P. protogens	1	No	Yes	Biocontrol agent against diseases Vesga et al. (2020)	Murthy et al. (2021)

BSL = Biosafety level.

general are needed to produce food, drugs, clean water, air, building materials, carbon, nitrogen, and light. This is done by using the resources available on Mars without needing to be brought from Earth (which otherwise may result in high transportation costs). The core issue of Martian soil is the amount of perchlorate lying in the soil (approximately 0.5 to 1%), which was detected by NASA's Phoenix probe in 2008, and since then, perchlorate has been found in multiple areas of the red planet (Qu et al., 2022). Nevertheless, although perchlorate increases the chances of finding microorganisms, these are highly toxic to humans and pose a health risk for future explorations. The main advantage of its use is the production of O_2 (Dávila et al., 2013). *P. stuzeri* USD1 has been shown to metabolize medium concentrations of perchlorates (≥ 1 mM to 10 mM) with 100% solubilization, making them more accessible to plants and other microorganisms, although in lower yield than *Azospirillum brasilense* (Sunilkumar and Lal, 2021).

Based on the chemical analysis performed on the rocks, different atoms have been detected that are beneficial for *Pseudomonas* growth, like Fe^{+2}, Mg^{+2}, Al^{+2}, Ca^{+2}, K^{+}, and O_2, as well as boron in the Gale crater with a concentration of 0.05% w/v, which is an element that could support life on Mars (Gasda et al., 2017). The challenge of growing plants on Mars involves providing the essential resources for their development, such as sunlight, oxygen, water, and nutrients. The issue is that ultraviolet radiation is far more dangerous than on Earth due to the lack of atmospheric ozone, so specialized greenhouses are needed (Sadler and Giacomelli, 2002). The radiation that plants would receive on Mars would be 17 times higher than that received on Earth, so there would be damage to plant leaves (Tack et al., 2021). Likewise, biomass produced in the simulated Martian soil is very similar to that in the terrestrial soil and bacteria are needed for plant growth due to the presence of many heavy metals in Martian soil (see Figure 2) (Tack et al., 2021; Wamelink et al., 2014). In addition, one of the limiting factors is the lack of nitrogen, an essential nutrient for optimal plant growth and performance. However, most *Pseudomonas* species are known to fix atmospheric nitrogen and convert it into soluble nitrogen. (Maggi et al., 2018; Mylona et al., 1995), for example many *Pseudomonas* can produce nitrogen by the degradation of urea, a compound that is commonly found in human urine (Tang et al., 2022; Liu et al., 2021; Ralphs et al., 2015; Putnam, 1971).

The quest for sustaining life in extraterrestrial environments, such as Mars, hinges on the availability of essential resources like water. Previous discoveries have found evidence of liquid water on Mars, however Martian soil does present challenges due to its low organic carbon content and limited water retention capacity, innovative approaches are being explored to overcome these hurdles, this can be improved by using *Pseudomonas* strains that produces polysaccharides or adhesives proteins that bind soul particles thereby increasing he moisture of soil (Ralphs et al., 2015; Maggi and Pallud, 2010) such biotechnological advancements could pave the way for future agricultural endeavors on the Red Planet, marking a significant milestone in the human pursuit of interplanetary habitation. Another crucial factor is energy, microbial energy production has gained much interesting in the last decade, according to Billi et al. (2019), many scientists have turned toward the use of microbial fuel cells (MFC). MFCs have indeed become a focal point in sustainable energy research due to their ability to harness the power of microorganisms, known as electrogens, to convert organic compounds into electricity as a sustainable energy source on Earth.

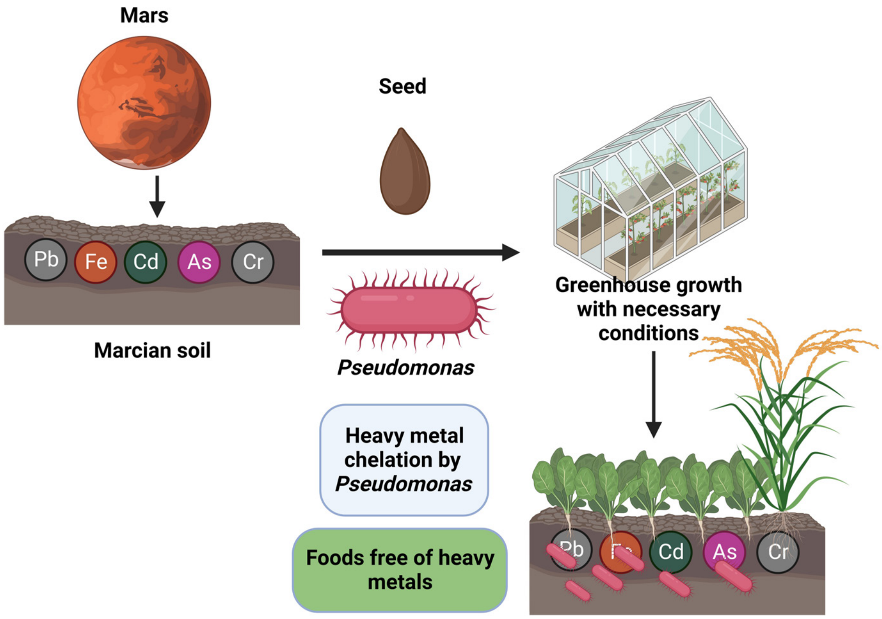

Figure 2. Theoretical growth of plants in Martian soil where *Pseudomonas* chelate heavy metals by being left in soil and the plant free of toxic pollutants (adapted and modified from Wamelink et al., 2014, created with BioRender, 2023).

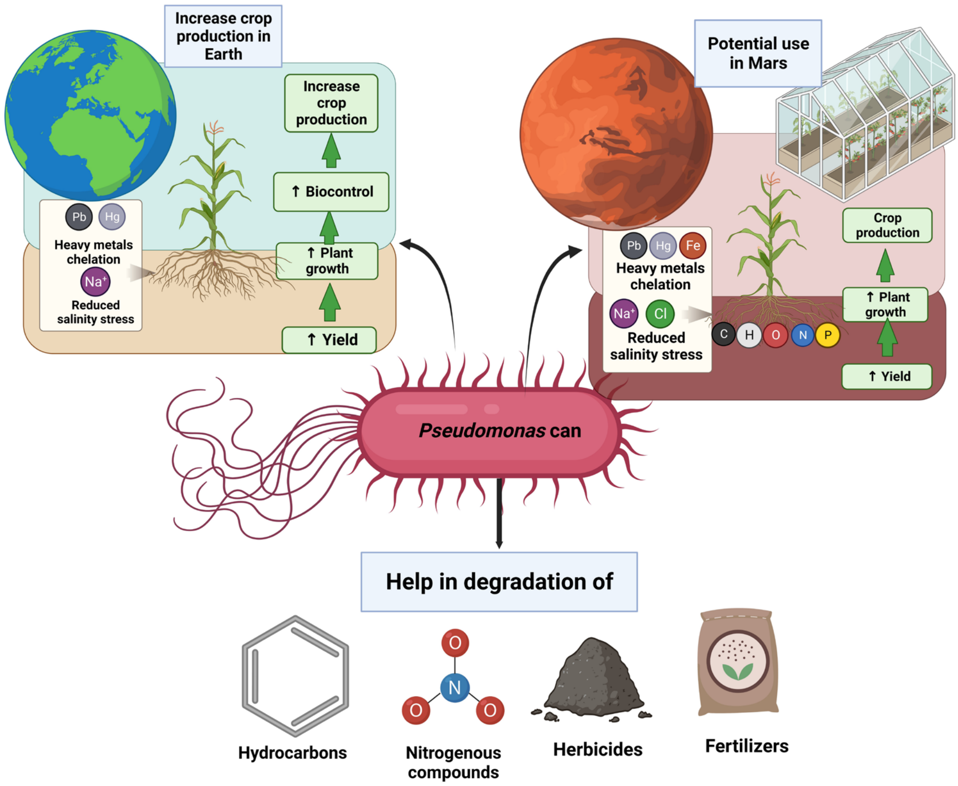

Figure 3. *Pseudomonas* species are versatile bacteria that can degrade various pollutants, such as hydrocarbons, heavy metals, herbicides, and fertilizers. They can also produce useful compounds, such as biosurfactants, biopolymers and biofuels.

For instance, *P. aeruginosa*, an electrogenic bacteria, has shown promise in electricity generation, highlighting the potential of MFCs in renewable energy applications (Arkatkar et al., 2021), however, since *P. aeruginosa* is harmful to humans more research is need by using other *Pseudomonas* like *P. putida* or *P. reptilivora*.

According to Trapero et al. (2017) and Ren et al. (2016), MFC's can produce up to 5.61 W/m^2 and can be used for waste management and bioremediation (Bose et al., 2020; Zhang et al., 2019; Cao et al., 2015). As research continues, the scalability and economic viability of MFCs remain key areas of focus, with the goal of transitioning from laboratory-scale models to real-world applications that can sustainably meet the growing energy demands.

In summary, *Pseudomonas* is a genus of bacteria that can adapt to various environments and perform diverse metabolic functions. Some of its species have been shown to degrade organic pollutants, produce biofuels, and synthesize biopolymers. These capabilities make *Pseudomonas* a potential candidate for bioremediation and bioengineering applications, especially in the context of terraforming Mars. By introducing *Pseudomonas* to the Martian soil, it may be possible to enhance its fertility, increase its nitrogen and oxygen content, reduce its toxicity, increase moisture of the soil, and produce energy. Therefore, *Pseudomonas* can be regarded as a powerful microorganism in the need to terraform Mars (see Figure 3).

These characteristics make them potential candidates for bioremediation and biotechnology applications on Earth and Mars.

4. Conclusions

Pseudomonas genera are found in most soils also play a role in a wide range of biotechnological processes, including enhancing plant growth, controlling diseases or pathogens, cycling nutrients, fixing nitrogen, or bioremediating heavy metals. *Pseudomonas* are important for modern agriculture and have been shown to protect plants from pathogens, toxic herbicides, or fertilizers. Without a doubt, *Pseudomonas* is a key bacterium for removing heavy metals from terrestrial soil and has the potential to be used in Martian soil.

By 2025 or 2026, it is expected that the Artemis missions will be working to establish a base of operations on the Moon as well as Mars. Thus, it is vital for space exploration to seek biotechnological alternatives such as *Pseudomonas* assistance to meet the objectives set for human survival in space. That is, by boosting the growth and development of plants with the aid of microorganisms, the planet Mars may be colonized in the future.

Pseudomonas in extreme substrate conditions can help resolve the environmental impact generated by pollutants, such as heavy metals. Our team has focused on the use of *P. reptilivora* B-6bs as a biotechnological producer of different primary metabolites, such as amino acids L-proline and L-glutamic acid using urea as a substrate; organic acids, such as gluconic acid, 2-ketogluconic acid and 5-ketogluconic acid; the generation of polyhydroxyalkanoates; and different antibiotics. Conversely, our team has observed that *P. reptilivora* B-6bs can withstand heavy metals like copper, iron, manganese, and cobalt, in a culture medium, producing various antibiotics. Last, as a team, we emphasize that *Pseudomonas* (in general) and *P. reptilivora* B-6bs can be exploited both on Earth and in outer space. In addition, perhaps in the future, on another planet like Mars.

Acknowledgements

To the National Council of Humanities, Sciences, and Technology (CONAHCYT) for the support granted during the doctoral program at the Tecnológico Nacional de México/Instituto Tecnológico de Morelia. Partial donations from the Tecnológico Nacional México call 2023 and 2024 (Convocatorias de Investigación Científica, Desarrollo Tecnológico e Innovación). And Instituto de Ciencia, Tecnología e Innovación del Estado de Michoacán de Ocampo call (FCCHTl22-ME004 and FCCHTI23_ME-4.1.-0001).

References

ABBAS, S.Z., RAFATULLAH, M., HOSSAIN, K., ISMAIL, N., TAJARUDIN, H.A. and ABDUL KHALIL, H.P.S., 2017. A review on mechanism and future perspectives of cadmium-resistant bacteria. *International Journal of Environmental Science and Technology*, vol. 15, no. 1, pp. 243-262. http://doi.org/10.1007/s13762-017-1400-5.

ADEDIBU, P.A., 2023. Ecological problems of agriculture: impacts and sustainable solutions. *ScienceOpen Preprints*. In press. http://doi.org/10.14293/PR2199.000145.v1.

AGNELLO, A.C., BAGARD, M., VAN HULLEBUSCH, E.D., ESPOSITO, G. and HUGUENOT, D., 2016. Comparative bioremediation of heavy metals and petroleum hydrocarbons co-contaminated soil by natural attenuation, phytoremediation, bioaugmentation and bioaugmentation-assisted phytoremediation. *The Science of the Total Environment*, vol. 563-564, pp. 693-703. http://doi.org/10.1016/j.scitotenv.2015.10.061. PMid:26524994.

AL-DHABI, N.A., ESMAIL, G.A. and VALAN ARASU, M., 2020. Sustainable conversion of palm juice wastewater into extracellular polysaccharides for absorption of heavy metals from Saudi Arabian wastewater. *Journal of Cleaner Production*, vol. 277, pp. 124252. http://doi.org/10.1016/j.jclepro.2020.124252.

ALEGRÍA-TORRES, J.A., PÉREZ-RODRÍGUEZ, R.Y., GARCÍA-TORRES, L., COSTILLA-SALAZAR, R. and ROCHA-AMADOR, D.O., 2020. Exposure to arsenic and lead in children from Salamanca México, effects on telomeric lengthening and mitochondrial DNA. *Environmental Science and Pollution Research International*, vol. 27, no. 6, pp. 6420-6428. http://doi.org/10.1007/s11356-019-07108-4. PMid:31873895.

ANUROOPA, N., RAM, A., RANADEV, P., DJ, B. and ASHWIN, R., 2021. *Pseudomonas* species in soil as a natural resource for plant growth promotion and biocontrol characteristics: an overview. *Madras Agricultural Journal*, vol. 108, pp. 1-13. http://doi.org/10.29321/MAJ.10.000571.

ARKATKAR, A., MUNGRAY, A.K. and SHARMA, P., 2021. Study of electrochemical activity zone of *Pseudomonas aeruginosa* in microbial fuel cell. *Process Biochemistry*, vol. 101, pp. 213-217. http://doi.org/10.1016/j.procbio.2020.11.020.

ARORA, M., SAXENA, P., ABDIN, M.Z. and VARMA, A., 2019. Interaction between *Piriformospora indica* and *Azotobacter chroococcum* diminish the effect of salt stress in *Artemisia annua* L. by enhancing enzymatic and non-enzymatic antioxidants. *Symbiosis*, vol. 80, no. 1, pp. 61-73. http://doi.org/10.1007/s13199-019-00656-w.

ARORA, N.K., FATIMA, T., MISHRA, J., MISHRA, I., VERMA, S., VERMA, R., VERMA, M., BHATTACHARYA, A., VERMA, P., MISHRA, P. and BHARTI, C., 2020. Halo-tolerant plant growth promoting rhizobacteria for improving productivity and remediation of saline soils. *Journal of Advanced Research*, vol. 26, pp. 69-82. http://doi.org/10.1016/j.jare.2020.07.003. PMid:33133684.

ARREBOLA, E., TIENDA, S., VIDA, C., DE VICENTE, A. and CAZORLA, F.M., 2019. Fitness features involved in the biocontrol interaction of *Pseudomonas chlororaphis* with host plants: the case study of PcPCL1606. *Frontiers in Microbiology*, vol. 10, pp. 719. http://doi.org/10.3389/fmicb.2019.00719. PMid:31024497.

BACKER, R., ROKEM, J.S., ILANGUMARAN, G., LAMONT, J., PRASLICKOVA, D., RICCI, E., SUBRAMANIAN, S. and SMITH, D.L., 2018. Plant growth-promoting rhizobacteria: context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. *Frontiers in Plant Science*, vol. 9, pp. 1473. http://doi.org/10.3389/fpls.2018.01473. PMid:30405652.

BILLI, D., VERSEUX, C., FAGLIARONE, C., NAPOLI, A., BAQUÉ, M. and DE VERA, J., 2019. A desert cyanobacterium under simulated Mars-like conditions in low earth orbit: implications for the habitability of Mars. *Astrobiology*, vol. 19, no. 2, pp. 158-169. http://doi.org/10.1089/ast.2017.1807. PMid:30742497.

BIORENDER [online], 2023 [viewed 25 January 2023]. Available from: https://www.biorender.com/

BOSE, D., SANTRA, M., SANKA, R.V.S.P. and KRISHNAKUMAR, B., 2020. Bioremediation analysis of sediment- microbial fuel cells for energy recovery from microbial activity in soil. *International Journal of Energy Research*, vol. 45, no. 4, pp. 6436-6445. http://doi.org/10.1002/er.6163.

BOYLE, M., FORD, T., MITCHELL, R. and MAKI, J.S., 1990. *Survival of pathogenic bacteria under nutrient starvation conditions.* Warrendale: SAE International. SAE Technical Paper Series. http://doi.org/10.4271/901381.

CANGANELLA, F. and BIANCONI, G., 2007. Survival of microorganisms representing the three Domains of life inside the International Space Station. *Microgravity Science and Technology*, vol. 19, no. 5-6, pp. 148-153. http://doi.org/10.1007/BF02919471.

CAO, X., SONG, H., YU, C. and LI, X., 2015. Simultaneous degradation of toxic refractory organic pesticide and bioelectricity generation using a soil microbial fuel cell. *Bioresource Technology*, vol. 189, pp. 87-93. http://doi.org/10.1016/j.biortech.2015.03.148. PMid:25864035.

CASTRO-GONZÁLEZ, N.P., CALDERÓN-SÁNCHEZ, F., PÉREZ-SATO, M., SONÍ-GUILLERMO, E. and REYES-CERVANTES, E., 2019. Health risk due to chronic heavy metal consumption via cow's milk produced in Puebla, Mexico, in irrigated wastewater areas. *Food Additives & Contaminants. Part B, Surveillance*, vol. 12, no. 1, pp. 38-44. http://doi.org/10.1080/19393210.2018.1520742. PMid:30277127.

CHANG, P., GERHARDT, K.E., HUANG, X., YU, X., GLICK, B.R., GERWING, P.D. and GREENBERG, B.M., 2014. Plant growth-promoting bacteria facilitate the growth of barley and oats in salt-impacted soil: implications for phytoremediation of saline soils. *International Journal of Phytoremediation*, vol. 16, no. 7-12, pp. 1133-1147. http://doi.org/10.1080/15226514.2013.821447. PMid:24933907.

CHELLAIAH, E.R., 2018. Cadmium (heavy metals) bioremediation by *Pseudomonas aeruginosa*: a minireview. *Applied Water Science*, vol. 8, no. 6, pp. 154. http://doi.org/10.1007/s13201-018-0796-5.

CHOUDHARY, S. and SAR, P., 2011. Uranium biomineralization by a metal resistant *Pseudomonas aeruginosa* strain isolated from contaminated mine waste. *Journal of Hazardous Materials*, vol. 186, no. 1, pp. 336-343. http://doi.org/10.1016/j.jhazmat.2010.11.004. PMid:21112694.

CLARK, D.P. and PAZDERNIK, N.J., 2015. *Biotechnology: academic cell*. San Diego: Elsevier, 345 p.

DAS, K., ABROL, S., VERMA, R., ANNAPRAGADA, H., KATIYAR, N. and SENTHILKUMAR, M., 2020. *Pseudomonas*. In: N. AMARESAN, M. SENTHIL KUMAR, K. ANNAPURNA, K. KUMAR and A. SANKARANARAYANAN, eds. *Beneficial microbes in agro-ecology bacteria and fungi.* Amsterdam: Elsevier, pp. 133-148. http://doi.org/10.1016/B978-0-12-823414-3.00008-3.

DÁVILA, A.F., WILLSON, D., COATES, J.D. and MCKAY, C.P., 2013. Perchlorate on Mars: a chemical hazard and a resource for humans. *International Journal of Astrobiology*, vol. 12, no. 4, pp. 321-325. http://doi.org/10.1017/S1473550413000189.

DE WERRA, P., PÉCHY-TARR, M., KEEL, C. and MAURHOFER, M., 2009. Role of gluconic acid production in the regulation of biocontrol traits of *Pseudomonas fluorescens* CHA0. *Applied and Environmental Microbiology*, vol. 75, no. 12, pp. 4162-4174. http://doi.org/10.1128/AEM.00295-09. PMid:19376896.

DJAMI-TCHATCHOU, A., LI, Z.A., STODGHILL, P., FILIATRAULT, M.J. and KUNKEL, B.N., 2022. Identification of Indole-3-acetic acid-regulated genes in *Pseudomonas syringae* pv. tomato strain DC3000. *Journal of Bacteriology*, vol. 204, no. 1, e0038021. http://doi.org/10.1128/JB.00380-21. PMid:34662236.

DO, Q.T., LUU, A., DAO, M.T., HOANG, Q.N. and NGUYEN, T.T., 2022. Isolation of salt-tolerant Pseudomonas strains with potential for alleviation of salt stress in peanut plant (*Arachis hypogaea* L.). *Acta Agriculturae Slovenica*, vol. 118, no. 3. http://doi.org/10.14720/aas.2022.118.3.2626.

EL-NAGGAR, N.E., EL-KHATEEB, A.Y., GHONIEM, A.A., EL-HERSH, M.S. and SABER, W.I.A., 2020. Innovative low-cost biosorption process of Cr^{6+} by *Pseudomonas alcaliphila* NEWG-2. *Scientific Reports*, vol. 10, no. 1, pp. 14043. http://doi.org/10.1038/s41598-020-70473-5. PMid:32820181.

ELSAYED, A., MOUSSA, Z., ALRDAHE, S.S., ALHARBI, M.M., GHONIEM, A.A., EL-KHATEEB, A.Y. and SABER, W.I.A., 2022. Optimization of heavy metals biosorption via artificial neural network: A case study of cobalt (II) sorption by *Pseudomonas alcaliphila* NEWG-2. *Frontiers In Microbiology*, vol. 13.https://doi.org/10.3389/fmicb.2022.893603.

ETESAMI, H., 2018. Bacterial mediated alleviation of heavy metal stress and decreased accumulation of metals in plant tissues: mechanisms and future prospects. *Ecotoxicology and Environmental Safety*, vol. 147, pp. 175-191. http://doi.org/10.1016/j.ecoenv.2017.08.032. PMid:28843189.

FAKHAR, A., GUL, B., GURMANI, A.R., KHAN, S.M., ALI, S., SULTAN, T., CHAUDHARY, H.J., RAFIQUE, M. and RIZWAN, M., 2020. Heavy metal remediation and resistance mechanism of *Aeromonas, Bacillus*, and *Pseudomonas*: a review. *Critical Reviews in Environmental Science and Technology*, vol. 52, no. 11, pp. 1868-1914. http://doi.org/10.1080/10643389.2020.1863112.

FENG, Y., LIU, Q., CHEN, S., ZHANG, S., WANG, M., MUNIR, M.A.M., FENG, Y., HE, Z. and YANG, X., 2022. Roles of exogenous plant growth regulators on phytoextraction of Cd/Pb/Zn by *Sedum alfredii* Hance in contaminated soils. *Environmental Pollution*, vol. 293, pp. 118510. http://doi.org/10.1016/j.envpol.2021.118510. PMid:34793909.

GALLOWAY, W.R.J.D., HODGKINSON, J.T., BOWDEN, S.D., WELCH, M. and SPRING, D.R., 2011. Quorum sensing in Gram-Negative bacteria: Small-Molecule modulation of AHL and AI-2 quorum sensing pathways. *Chemical Reviews*, vol. 111, no. 1, pp. 28-67. http://doi.org/10.1021/cr100109t. PMid:21182299.

GASDA, P.J., HALDEMAN, E.B., WIENS, R.C., RAPIN, W., BRISTOW, T.F., BRIDGES, J.C., SCHWENZER, S.P., CLARK, B.C., HERKENHOFF, K.E., FRYDENVANG, J., LANZA, N., MAURICE, S., CLEGG, S.M., DELAPP, D., SANFORD, V.L., BODINE, M. and MCINROY, R.E., 2017. In situ detection of boron by ChemCam on Mars. *Geophysical Research Letters*, vol. 44, no. 17, pp. 8739-8748. http://doi.org/10.1002/2017GL074480.

GHADAMGAHI, F., TARIGHI, S., TAHERI, P., SARIPELLA, G.V., ANZALONE, A., KALYANDURG, P.B., CATARA, V., ORTÍZ, R. and VETUKURI, R.R., 2022. Plant growth-promoting activity of *Pseudomonas aeruginosa* FG106 and its ability to act as a biocontrol agent against potato, tomato and taro pathogens. *Biology*, vol. 11, no. 1, pp. 140. http://doi.org/10.3390/biology11010140. PMid:35053136.

GUTIÉRREZ-ALBANCHEZ, E., GARCÍA-VILLARACO, A., LUCAS, J.A., HORCHE, I., RAMOS-SOLANO, B. and GUTIÉRREZ-MAÑERO, F.J., 2021. *Pseudomonas palmensis* sp. nov., a novel bacterium isolated from *Nicotiana glauca* microbiome: draft genome analysis and biological potential for agriculture. *Frontiers in Microbiology*, vol. 12, pp. 672751. http://doi.org/10.3389/fmicb.2021.672751. PMid:34489881.

HU, S., WANG, X., SUN, W., WANG, L. and LI, W., 2021. In vitro study of biocontrol potential of rhizospheric *Pseudomonas aeruginosa* against pathogenic fungi of saffron (*Crocus sativus* L.). *Pathogens*, vol. 10, no. 11, pp. 1423. http://doi.org/10.3390/pathogens10111423. PMid:34832579.

HU, W., GAO, Q., HAMADA, M., DAWOOD, D.H., ZHENG, J., CHEN, Y. and MA, Z., 2014. Potential of *Pseudomonas chlororaphis* subsp. *aurantiaca* strain Pcho10 as a biocontrol agent against *Fusarium graminearum. Phytopathology*, vol. 104, no. 12, pp. 1289-1297. http://doi.org/10.1094/PHYTO-02-14-0049-R. PMid:24941327.

HUMAIRA, Y., SANA, N. and MURK, B., 2020. Halotolerant rhizobacteria *Pseudomonas pseudoalcaligenes* and *Bacillus subtilis* mediate systemic tolerance in hydroponically grown soybean (*Glycine max* L.) against salinity stress. *PLoS One*, vol. 15, no. 4, e0231348. http://doi.org/10.1371/journal.pone.0231348. PMid:32298338.

HUSSEIN, H., FARAG, S., KANDIL, K.M. and MOAWAD, H., 2005. Tolerance and uptake of heavy metals by *Pseudomonas. Process Biochemistry*, vol. 40, no. 2, pp. 955-961. http://doi.org/10.1016/j.procbio.2004.04.001.

ILYAS, M., NISAR, M., KHAN, N., ALI, H., KHAN, A.H., HAYAT, K., FAHAD, S., KHAN, A. and ULLAH, A., 2020. Drought tolerance strategies in plants: a mechanistic approach. *Journal of Plant Growth Regulation*, vol. 40, no. 3, pp. 926-944. http://doi.org/10.1007/s00344-020-10174-5.

IMRON, M.F., KURNIAWAN, S.B. and ABDULLAH, S.R.S., 2021. Resistance of bacteria isolated from leachate to heavy metals and the removal of Hg by *Pseudomonas aeruginosa* strain FZ-2 at different salinity levels in a batch biosorption system. *Sustainable Environment Research*, vol. 31, no. 1, pp. 14. http://doi.org/10.1186/s42834-021-00088-6.

JAIN, D., KOUR, R., BHOJIYA, A.A., MEENA, R.H., SINGH, A., MOHANTY, S.R., RAJPUROHIT, D. and AMETA, K.D., 2020. Zinc tolerant plant growth promoting bacteria alleviates phytotoxic effects of zinc on maize through zinc immobilization. *Scientific Reports*, vol. 10, no. 1, pp. 13865. http://doi.org/10.1038/s41598-020-70846-w. PMid:32807871.

KAKEMBO, D. and LEE, Y.H., 2019. Analysis of traits for biocontrol performance of *Pseudomonas parafulva* JBCS1880 against bacterial pustule in soybean plants. *Biological Control*, vol. 134, pp. 72-81. http://doi.org/10.1016/j.biocontrol.2019.04.006.

KANG, S., ASAF, S., KHAN, A.L., LUBNA., KHAN, A., MUN, B.G., KHAN, M.A., GUL, H. and LEE, I.J., 2020. Complete genome sequence of *Pseudomonas psychrotolerans* CS51, a plant growth-promoting bacterium, under heavy metal stress conditions. *Microorganisms*, vol. 8, no. 3, pp. 382. http://doi.org/10.3390/microorganisms8030382. PMid:32182882.

KIKI, M.J., 2022. Effects of pyocyanin pigment on the chemical and physical characteristics of agricultural soils. *Applied Ecology and Environmental Research*, vol. 20, no. 4, pp. 3117-3127. http://doi.org/10.15666/aeer/2004_31173127.

KIM, W., TENGRA, F.K., YOUNG, Z.D., SHONG, J., MARCHAND, N., CHAN, H.K., PANGULE, R.C., PARRA, M., DORDICK, J.S., PLAWSKY, J.L. and COLLINS, C.H., 2013. Spaceflight promotes biofilm formation by *Pseudomonas aeruginosa. PLoS One*, vol. 8, no. 4, e62437. http://doi.org/10.1371/journal.pone.0062437. PMid:23658630.

KOEHLE, A.P., BRUMWELL, S.L., SETO, E., LYNCH, A.M. and URBANIAK, C., 2023. Microbial applications for sustainable space exploration beyond low Earth orbit. *NPJ Microgravity*, vol. 9, no. 1, pp. 47. http://doi.org/10.1038/s41526-023-00285-0. PMid:37344487.

KOUR, R., JAIN, D., BHOJIYA, A.A., SUKHWAL, A., SANADHYA, S., SAHEEWALA, H., JAT, G., SINGH, A. and MOHANTY, S.R., 2019. Zinc biosorption, biochemical and molecular characterization of plant growth-promoting zinc-tolerant bacteria. *3 Biotech*, vol. 9, no. 11, pp. 421. http://doi.org/10.1007/s13205-019-1959-2.

LABAUVE, A.E. and WARGO, M.J., 2012. Growth and laboratory maintenance of *Pseudomonas aeruginosa. Current Protocols in Microbiology*, vol. 25, no. 1, pp. Unit 6E.1. http://doi.org/10.1002/9780471729259.mc06e01s25. PMid:22549165.

LAGHLIMI, M., BAGHDAD, B., HADI, H.E. and BOUABDLI, A., 2015. Phytoremediation mechanisms of heavy metal contaminated soils: a review. *Open Journal of Ecology*, vol. 5, no. 8, pp. 375-388. http://doi.org/10.4236/oje.2015.58031.

LAMI, M.J., ADLER, C., SANTO, M.C.C., ZENOFF, A.M., CRISTÓBAL, R., ESPINOSA-URGEL, M. and VINCENT, P., 2020. *Pseudomonas stutzeri* MJL19, a rhizosphere-colonizing bacterium that promotes plant growth under saline stress. *Journal of Applied Microbiology*, vol. 129, no. 5, pp. 1321-1336. http://doi.org/10.1111/jam.14692. PMid:32367524.

LI, W., WILKES, R.A. and ARISTILDE, L., 2021. Effects of phosphonate herbicides on the secretions of plant-beneficial compounds by two plant growth-promoting soil bacteria: a metabolomics investigation. *ACS Environmental Au*, vol. 2, no. 2, pp. 136-149. http://doi.org/10.1021/acsenvironau.1c00030. PMid:37101584.

LIU, Y., CUI, S., REN, Y., GUO, L., LIU, H., ZHANG, Z., TU, L., WANG, J. and LI, X., 2021. Nitrogen removal and aggregation characteristics of *Pseudomonas aeruginosa* YL and its application capacity for ammonium-rich wastewater treatment. *Journal of Water Process Engineering*, vol. 43, pp. 102260. http://doi.org/10.1016/j.jwpe.2021.102260.

LU, Q., GE, G., SA, D., WANG, Z., HOU, M. and JIA, Y.S., 2021. Effects of salt stress levels on nutritional quality and microorganisms of alfalfa-influenced soil. *PeerJ*, vol. 9, e11729. http://doi.org/10.7717/peerj.11729. PMid:34316396.

MAGGI, F. and PALLUD, C., 2010. Martian base agriculture: the effect of low gravity on water flow, nutrient cycles, and microbial biomass dynamics. *Advances in Space Research*, vol. 46, no. 10, pp. 1257-1265. http://doi.org/10.1016/j.asr.2010.07.012.

MAGGI, F., TANG, F.H.M., PALLUD, C. and GU, C., 2018. A urine-fuelled soil-based bioregenerative life support system for long-term and long-distance manned space missions. *Life Sciences in Space Research*, vol. 17, pp. 1-14. http://doi.org/10.1016/j.lssr.2018.01.003. PMid:29753408.

MEDIĆ, A. and KARADŽIĆ, I., 2022. *Pseudomonas* in environmental bioremediation of hydrocarbons and phenolic compounds-key catabolic degradation enzymes and new analytical platforms for comprehensive investigation. *World Journal of Microbiology & Biotechnology*, vol. 38, no. 10, pp. 165. http://doi.org/10.1007/s11274-022-03349-7. PMid:35861883.

MEHNAZ, S., BECHTHOLD, A. and GROSS, H., 2020. Draft genome sequence of *Pseudomonas chlororaphis* subsp. *aurantiaca* ARS-38, a bacterial strain with plant growth promotion potential, isolated from the rhizosphere of cotton in Pakistan. *Microbiology Resource Announcements*, vol. 9, no. 3, e01398-19. http://doi.org/10.1128/MRA.01398-19. PMid:31948966.

MENEZES, A.A., MONTAGUE, M., CUMBERS, J., HOGAN, J.A. and ARKIN, A.P., 2015. Grand challenges in space synthetic biology. *Journal of the Royal Society, Interface*, vol. 12, no. 113, pp. 20150803. http://doi.org/10.1098/rsif.2015.0803. PMid:26631337.

MISRA, P., ARCHANA, UNIYAL, S. and SRIVASTAVA, A., 2022. *Pseudomonas* for sustainable agricultural ecosystem. In: R.P. SINGH, G. MANCHANDA, K. BHATTACHARJEE and H. PANOSYAN, eds. *Microbial syntrophy-mediated eco-enterprising: a volume in developments in applied microbiology and biotechnology.* Singapore: Elsevier, pp. 209-223. http://doi.org/10.1016/B978-0-323-99900-7.00012-2

MOHAMMED, A.F., OLOYEDE, A.R. and ODESEYE, A.O., 2020. Biological control of bacterial wilt of tomato caused by *Ralstonia solanacearum* using *Pseudomonas* species isolated from the rhizosphere of tomato plants. *Archiv für Phytopathologie und Pflanzenschutz*, vol. 53, no. 1-2, pp. 1-16. http://doi.org/10.1080/03235408.2020.1715756.

MORALES-CEDEÑO, L.R., DEL CARMEN OROZCO-MOSQUEDA, M., LARA, P.D.L., PARRA-COTA, F.I. and DE LOS SANTOS-VILLALOBOS, S., 2021. Plant growth-promoting bacterial endophytes as biocontrol agents of pre- and post-harvest diseases: fundamentals, methods of application and future perspectives. *Microbiological Research*, vol. 242, pp. 126612. http://doi.org/10.1016/j.micres.2020.126612. PMid:33059112.

MULLAEVA, S.A., DELEGAN, Y.A., STRELETSKII, R., САЗОНОВА, O.N., PETRIKOV, K., IVANOVA, A.A., DYATLOV, I.A., SHEMYAKIN, I.G., BOGUN, A.G. and VETROVA, A., 2022. *Pseudomonas veronii* strain 7–41 degrading medium-chain n-alkanes and polycyclic aromatic hydrocarbons. *Scientific Reports*, vol. 12, no. 1, pp. 20527. http://doi.org/10.1038/s41598-022-25191-5. PMid:36443410.

MURTHY, K.N., KRISHNAMURTHY, S., UDAYASHANKAR, A.C., SRINIVAS, C. and JOGAIAH, S., 2021. Biocontrol potential of plant growth-promoting rhizobacteria (PGPR) against *Ralstonia solanacearum*: current and future prospects. In: S. JOGAIAH, ed. *Biocontrol agents and secondary metabolites: applications and immunization for plant growth and protection.* Duxford: Woodhead Publishing, pp. 153-180. http://doi.org/10.1016/B978-0-12-822919-4.00007-7.

MYLONA, P., PAWLOWSKI, K. and BISSELING, T., 1995. Symbiotic nitrogen fixation. *The Plant Cell*, vol. 7, no. 7, pp. 869-885. http://doi.org/10.2307/3870043. PMid:12242391.

O'CALLAGHAN, M., 2016. Microbial inoculation of seed for improved crop performance: issues and opportunities. *Applied Microbiology* *and Biotechnology*, vol. 100, no. 13, pp. 5729-5746. http://doi.org/10.1007/s00253-016-7590-9. PMid:27188775.

OSMAN, M.A., YANG, F. and MASSEY, I.Y., 2019. Exposure routes and health effects of heavy metals on children. *Biometals*, vol. 32, no. 4, pp. 563-573. http://doi.org/10.1007/s10534-019-00193-5. PMid:30941546.

OSSAI, I.C., AHMED, A., HASSAN, A. and HAMID, F.S., 2020. Remediation of soil and water contaminated with petroleum hydrocarbon: a review. *Environmental Technology and Innovation*, vol. 17, pp. 100526. http://doi.org/10.1016/j.eti.2019.100526.

OTT, E., KAWAGUCHI, Y., KÖLBL, D., RABBOW, E., RETTBERG, P., MORA, M., MOISSL-EICHINGER, C., WECKWERTH, W., YAMAGISHI, A. and MILOJEVIC, T., 2020. Molecular repertoire of *Deinococcus radiodurans* after 1 year of exposure outside the International Space Station within the Tanpopo mission. *Microbiome*, vol. 8, no. 1, pp. 150. http://doi.org/10.1186/s40168-020-00927-5. PMid:33121542.

PANDEY, S. and GUPTA, S., 2020. Evaluation of *Pseudomonas* sp. for its multifarious plant growth promoting potential and its ability to alleviate biotic and abiotic stress in tomato (*Solanum lycopersicum*) plants. *Scientific Reports*, vol. 10, no. 1, pp. 20951. http://doi.org/10.1038/s41598-020-77850-0. PMid:33262413.

PARIKH, K. and JHA, A., 2012. Biocontrol features in an indigenous bacterial strain isolated from agricultural soil of Gujarat, India. *Journal of Soil Science and Plant Nutrition*, vol. 12, no. 2, pp. 245-252. http://doi.org/10.4067/S0718-95162012000200004.

PRASHAR, P. and SHAH, S., 2016. Impact of fertilizers and pesticides on soil microflora in agriculture. In: E. Lichtfouse, ed. *Sustainable Agriculture Reviews*. Springer, pp. 331-361. https://doi.org/10.1007/978-3-319-26777-7_8.

PUTNAM, D.F., 1971 [viewed 25 January 2023]. *Composition and concentrative properties of human urine* [online]. Washington, D.C.: NASA. NASA Technical Reports Server (NTRS). Available from: https://ntrs.nasa.gov/citations/19710023044

QU, S., ZHAO, Y., CUI, H., YIN, X., JACKSON, W.A., NIE, X., WU, Z., WANG, J., ZHOU, D., QI, C., LI, X. and LIU, J., 2022. Preferential formation of chlorate over perchlorate on Mars controlled by iron mineralogy. *Nature Astronomy*, vol. 6, no. 4, pp. 436-441. http://doi.org/10.1038/s41550-021-01588-6.

RAHMAN, M.M., KHAN, I., FIELD, D.L., TECHATO, K. and ALAMEH, K., 2022. Powering agriculture: present status, future potential, and challenges of renewable energy applications. *Renewable Energy*, vol. 188, pp. 731-749. http://doi.org/10.1016/j.renene.2022.02.065.

RAIO, A. and PUOPOLO, G., 2021. *Pseudomonas chlororaphis* metabolites as biocontrol promoters of plant health and improved crop yield. *World Journal of Microbiology & Biotechnology*, vol. 37, no. 6, pp. 99. http://doi.org/10.1007/s11274-021-03063-w. PMid:33978868.

RALPHS, M., FRANZ, B., BAKER, T.W. and HOWE, S., 2015. Water extraction on Mars for an expanding human colony. *Life Sciences in Space Research*, vol. 7, pp. 57-60. http://doi.org/10.1016/j.lssr.2015.10.001. PMid:26553638.

REN, H., TIAN, H., GARDNER, C.L., REN, T. and CHAE, J., 2016. A miniaturized microbial fuel cell with three-dimensional graphene macroporous scaffold anode demonstrating a record power density of over 10 000 W m−3. *Nanoscale*, vol. 8, no. 6, pp. 3539-3547. http://doi.org/10.1039/C5NR07267K. PMid:26804041.

REYNOLDS, D. and KOLLEF, M.H., 2021. The Epidemiology and pathogenesis and treatment of *Pseudomonas aeruginosa* infections: an update. *Drugs*, vol. 81, no. 18, pp. 2117-2131. http://doi.org/10.1007/s40265-021-01635-6. PMid:34743315.

SADLER, P.D. and GIACOMELLI, G.A., 2002. Mars inflatable greenhouse analog: life support and biosphere science. *International Journal of Earth Space*, vol. 8, no. 2, pp. 115-123.

SAGLAM, A., DEMIRALAY, M., ÇOLAK, D.N., PEHLIVAN, N., PEHLIVAN, N., BASOK, O. and KADIOĞLU, A., 2022. *Pseudomonas putida* KT2440 induces drought tolerance during fruit ripening in tomato. *Bioagro*-, vol. 34, no. 2, pp. 139-150. http://doi.org/10.51372/bioagro342.4.

SAHARAN, B. and NEHRA, V., 2011. Plant growth promoting rhizobacteria: a critical review. *International Journal of Statistics in Medical Research*, vol. 21, pp. 1-30.

SANTOYO, G., URTIS-FLORES, C.A., LOEZA-LARA, P.D., OROZCO-MOSQUEDA, M.D.C. and GLICK, B.R., 2021. Rhizosphere colonization determinants by Plant Growth-Promoting Rhizobacteria (PGPR). *Biology*, vol. 10, no. 6, pp. 475. http://doi.org/10.3390/biology10060475. PMid:34072072.

SHAHID, I., MALIK, K.A. and MEHNAZ, S., 2018. A decade of understanding secondary metabolism in Pseudomonas spp. for sustainable agriculture and pharmaceutical applications. *Environmental Sustainability*, vol. 1, no. 1, pp. 3-17. http://doi.org/10.1007/s42398-018-0006-2.

SHI, P., XING, Z., ZHANG, Y. and CHAI, T., 2017. Effect of heavy metal on synthesis of siderophores by *Pseudomonas aeruginosa* ZGKD3. *IOP Conference Series*, vol. 52, pp. 012103. http://doi.org/10.1088/1742-6596/52/1/012103.

SINGH, S.K., SINGH, P.P., GUPTA, A., SINGH, A. and KESHRI, J., 2019. Tolerance of heavy metal toxicity using PGPR strains of *Pseudomonas species*. In: A.K. SINGH, A. KUMAR and P.K. SINGH, eds. *PGPR amelioration in sustainable agriculture: food security and environmental management.* Duxford: Elsevier, pp. 239-252. http://doi.org/10.1016/B978-0-12-815879-1.00012-4.

SOBERÓN-CHÁVEZ, G., GONZÁLEZ-VALDEZ, A., SOTO-ACEVES, M.P. and COCOTL-YAÑEZ, M., 2021. Rhamnolipids produced by *Pseudomonas*: from molecular genetics to the market. *Microbial Biotechnology*, vol. 14, no. 1, pp. 136-146. http://doi.org/10.1111/1751-7915.13700. PMid:33151628.

STREETER, K. and KATOULI, M., 2016. *Pseudomonas aeruginosa*: a review of their pathogenesis and prevalence in clinical settings and the environment. *Infection Epidemiology and Medicine*, vol. 2, no. 1, pp. 25-32. http://doi.org/10.18869/modares.iem.2.1.25.

SUN, X., SHAO, C., CHEN, L., JIN, X. and HÓNG, N., 2020. Plant growth-promoting effect of the chitosanolytic phosphate-solubilizing bacterium *Burkholderia gladioli* MEL01 after fermentation with chitosan and fertilization with rock phosphate. *Journal of Plant Growth Regulation*, vol. 40, no. 4, pp. 1674-1686. http://doi.org/10.1007/s00344-020-10223-z.

SUN, X., XU, Z., XIE, J., HESSELBERG-THOMSEN, V., TAN, T., ZHENG, D., STRUBE, M.L., DRAGOŠ, A., SHEN, Q., ZHANG, R. and KOVÁCS, Á.T., 2021. *Bacillus velezensis* stimulates resident rhizosphere *Pseudomonas stutzeri* for plant health through metabolic interactions. *The ISME Journal*, vol. 16, no. 3, pp. 774-787. http://doi.org/10.1038/s41396-021-01125-3. PMid:34593997.

SUNILKUMAR, U. and LAL, S., 2021. Perchlorate reducing bacteria and their insight towards astrobiology. *International Journal of Research and Analytical Reviews*, vol. 8, no. 1. http://doi.org/10.13140/RG.2.2.26997.70880.

TACK, N., WAMELINK, G., DENKOVA, A., SCHOUWENBURG, M., HILHORST, H., WOLTERBEEK, H. and GOEDHART, P., 2021. Influence of Martian radiation-like conditions on the growth of *Secale cereale* and *Lepidium sativum. Frontiers in Astronomy and Space Sciences*, vol. 8, pp. 665649. http://doi.org/10.3389/fspas.2021.665649.

TANG, Y., DONG, W., AI, W., ZHANG, L., LI, J., YU, Q., GUO, S. and LI, Y., 2022. Design and establishment of a large-scale controlled ecological life-support system integrated experimental platform. *Life Sciences in Space Research*, vol. 31, pp. 121-130. http://doi.org/10.1016/j.lssr.2021.08.001. PMid:34689944.

TIENDA, S., VIDA, C., LAGENDIJK, E., DE WEERT, S., LINARES, I., GONZÁLEZ-FERNÁNDEZ, J., GUIRADO, E., DE VICENTE, A. and CAZORLA, F.M., 2020. Soil application of a formulated biocontrol rhizobacterium, *Pseudomonas chlororaphis* PCL1606, induces soil suppressiveness by impacting specific microbial communities. *Frontiers in Microbiology*, vol. 11, pp. 1874. http://doi.org/10.3389/fmicb.2020.01874. PMid:32849458.

TRAPERO, J.R., HORCAJADA, L., LINARES, J.J. and LOBATO, J., 2017. Is microbial fuel cell technology ready? An economic answer towards industrial commercialization. *Applied Energy*, vol. 185, pp. 698-707. http://doi.org/10.1016/j.apenergy.2016.10.109.

UZMA, M., IQBAL, A. and HASNAIN, S., 2022. Drought tolerance induction and growth promotion by indole acetic acid producing *Pseudomonas aeruginosa* in *Vigna radiata*. *PLoS One*, vol. 17, no. 2, e0262932. http://doi.org/10.1371/journal.pone.0262932.

VAISHNAV, A. and CHOUDHARY, D.K., 2018. Regulation of drought-responsive gene expression in *Glycine max* L. Merrill is mediated through *Pseudomonas simiae* strain AU. *Journal of Plant Growth Regulation*, vol. 38, no. 1, pp. 333-342. http://doi.org/10.1007/s00344-018-9846-3.

VELIVELLI, S.L.S., DE VOS, P., KROMANN, P., DECLERCK, S. and PRESTWICH, B.D., 2014. Biological control agents: from field to market, problems, and challenges. *Trends in Biotechnology*, vol. 32, no. 10, pp. 493-496. http://doi.org/10.1016/j.tibtech.2014.07.002.

VESGA, P., FLURY, P., VACHERON, J., KEEL, C., CROLL, D. and MAURHOFER, M., 2020. Transcriptome plasticity underlying plant root colonization and insect invasion by *Pseudomonas protegens*. *The ISME Journal*, vol. 14, no. 11, pp. 2766-2782. http://doi.org/10.1038/s41396-020-0729-9. PMid:32879461.

VILASÓ-CADRE, J.E., RODRÍGUEZ GÁMEZ, O. and ÁBALOS RODRÍGUEZ, A., 2017. Extracción de petróleo en suelo contaminado empleando ramnolípidos producidos por *Pseudomonas aeruginosa* ORA9. *Revista Internacional de Contaminación Ambiental*, vol. 33, no. 3, pp. 485-493. http://doi.org/10.20937/RICA.2017.33.03.11.

VURUKONDA, S.S.K.P., VARDHARAJULA, S. and ZULFIKAR, A.S., 2022. In vitro assessment of *Pseudomonas sp*. strain FCBB-2 for effective plant growth promotion and antifungal activity under drought stress. *Asian Plant Research Journal*, vol. 9, no. 2, pp. 13-27. http://doi.org/10.9734/aprj/2022/v9i230200.

WAMELINK, G., FRISSEL, J., KRIJNEN, W., VERWOERT, M.R. and GOEDHART, P.W., 2014. Can plants grow on Mars and the Moon: a growth experiment on Mars and Moon soil simulants. *PLoS One*, vol. 9, no. 8, e103138. http://doi.org/10.1371/journal.pone.0103138. PMid:25162657.

WU, J., ZHANG, J., ZHANG, H., GAO, M., LIU, L. and ZHAN, X., 2019. Recycling of cooking oil fume condensate for the production of rhamnolipids by *Pseudomonas aeruginosa* WB505. *Bioprocess and Biosystems Engineering*, vol. 42, no. 5, pp. 777-784. http://doi.org/10.1007/s00449-019-02081-1. PMid:30741355.

XIE, H., PASTERNAK, J. and GLICK, B.R., 1996. Isolation and characterization of mutants of the plant growth-promoting rhizobacterium *Pseudomonas putida* GR12-2 that overproduce indoleacetic acid. *Current Microbiology*, vol. 32, no. 2, pp. 67-71. http://doi.org/10.1007/s002849900012.

XIN, X., KVITKO, B.H. and HE, S.Y., 2018. *Pseudomonas syringae*: what it takes to be a pathogen. *Nature Reviews. Microbiology*, vol. 16, no. 5, pp. 316-328. http://doi.org/10.1038/nrmicro.2018.17. PMid:29479077.

XUE, Y., QIU, T., SUN, Z., LIU, F. and YU, B., 2022. Mercury bioremediation by engineered *Pseudomonas putida* KT2440 with adaptationally optimized biosecurity circuit. *Environmental Microbiology*, vol. 24, no. 7, pp. 3022-3036. http://doi.org/10.1111/1462-2920.16038. PMid:35555952.

YAASHIKAA, P., KUMAR, P.S., BABU, V.P., DURGA, R.K., MANIVASAGAN, V., SARANYA, K. and SARAVANAN, A., 2019. Modelling on the removal of Cr (VI) ions from aquatic system using mixed biosorbent (*Pseudomonas stutzeri* and acid treated Banyan tree bark). *Journal of Molecular Liquids*, vol. 276, pp. 362-370. http://doi.org/10.1016/j.molliq.2018.12.004.

YANG, P., ZHOU, X., WANG, L., LI, Q., ZHOU, T., CHEN, Y., ZHAO, Z. and HE, B., 2018. Effect of Phosphate-Solubilizing bacteria on the mobility of insoluble cadmium and metabolic analysis. *International Journal of Environmental Research and Public Health*, vol. 15, no. 7, pp. 1330. http://doi.org/10.3390/ijerph15071330. PMid:29941813.

YEĞIN, S., SAHA, B.C., KENNEDY, G.J., BERHOW, M. and VERMILLION, K.E., 2020. Efficient bioconversion of waste bread into 2-keto-d-gluconic acid by *Pseudomonas reptilivora* NRRL B-6. *Biomass Conversion and Biorefinery*, vol. 10, no. 2, pp. 545-553. http://doi.org/10.1007/s13399-020-00656-7.

YU, J., JIN, B., JI, Q. and WANG, H., 2023. Detoxification and metabolism of glyphosate by a *Pseudomonas* sp. via biogenic manganese oxidation. *Journal of Hazardous Materials*, vol. 448, pp. 130902. http://doi.org/10.1016/j.jhazmat.2023.130902. PMid:36731313.

ZAYNAB, M., AL-YAHYAI, R., AMEEN, A., SHARIF, Y., ALI, L., FATIMA, M., KHAN, K.A. and LI, S., 2022. Health and environmental effects of heavy metals. *Journal of King Saud University. Science*, vol. 34, no. 1, pp. 101653. http://doi.org/10.1016/j.jksus.2021.101653.

ZBORALSKI, A. and FILION, M., 2023. *Pseudomonas* spp. can help plants face climate change. *Frontiers in Microbiology*, vol. 14, pp. 1198131. http://doi.org/10.3389/fmicb.2023.1198131. PMid:37426009.

ZHANG, J., YUAN, H., DENG, Y., ABU-REESH, I. M., HE, Z., and YUAN, C., 2019. Life cycle assessment of osmotic microbial fuel cells for simultaneous wastewater treatment and resource recovery. *The International Journal of Life Cycle Assessment,* vol. 24, no. 11, pp. 1962-1975. https://doi.org/10.1007/s11367-019-01626-6.