FROM SOIL TO SURVIVAL: PGPB-TRIGGERED DEFENSE AND ADAPTATION IN PLANTS

Natalija Atanasova-Pancevska[1*], Daniela Todevska[2]
[1]Ss. Cyril and Methodius University in Skopje, Faculty of Natural Sciences and Mathematics – Skopje, Institute of Biology, Department of Microbiology and Microbial Biotechnology, Skopje, North Macedonia
[*]corresponding author: natalijaap@gmail.com, natalija@pmf.ukim.mk
[2] Goce Delcev University, Stip, Faculty of Agriculture, Department for Plant Production, Stip, Republic of North Macedonia

ABSTRACT

Plants and beneficial soil bacteria engage in dynamic and reciprocal interactions that influence plant development, nutrient acquisition, and stress resilience. Among these, plant growth-promoting bacteria (PGPB) have garnered considerable attention due to their ability to support plant health through a range of biochemical and physiological mechanisms. These bacteria produce a variety of bioactive compounds that enhance plant stress tolerance, improve nutrient availability, and offer protection against phytopathogens.

PGPB influence plant performance through both direct and indirect mechanisms. Direct pathways include the biosynthesis of phytohormones (such as indole-3-acetic acid), solubilization of essential nutrients like phosphate, zinc, and potassium, ammonia production, and atmospheric nitrogen fixation. Indirectly, they contribute by secreting siderophores, lytic enzymes, hydrogen cyanide, and antibiotics, which suppress harmful microorganisms and enhance plant immunity.

These functional traits position PGPB as valuable components in sustainable agriculture, especially for the development of bioformulants including biofertilizers, biopesticides, and biofungicides. Such alternatives reduce dependency on chemical inputs and contribute to environmentally responsible crop management. Nonetheless, despite the expanding repertoire of beneficial strains, the practical implementation of PGPB in agriculture remains challenging. Factors such as microbial survival, strain specificity, plant-microbiome compatibility, and fluctuating environmental conditions can influence their efficacy in field applications.

This review explores recent advances in understanding PGPB-mediated plant adaptations to abiotic and biotic stressors, with emphasis on molecular mechanisms, signaling pathways, and metabolite production. It also discusses formulation strategies and delivery systems designed to maximize their stability and performance. Ultimately, leveraging PGPB potential requires a deeper integration of microbiology, plant physiology, and environmental science to ensure their consistent and scalable use in sustainable agricultural systems.

Keywords: Plant Growth-Promoting Bacteria, stress tolerance, sustainable agriculture, biocontrol

INTRODUCTION

As part of the soil ecosystem, microorganisms have a major impact on the nitrogen cycle, soil fertility management, and plant diversity preservation. According to Zhou et al. (2020), a crucial area for important biological interactions between plants and microorganisms is the rhizosphere, a tiny area that surrounds the plant roots. Microorganisms such as bacteria, actinobacteria, fungus, algae, and protozoa aggressively compete for food and space in this productive area (Manghwar et al., 2023). Both the host and the microorganisms benefit from the ability of the plant growth promoting microorganism (PGPM) to live in and interact with plant roots; a population of rhizospheric bacteria and fungi may also serve as a home for other microbes (dos Lopes et al., 2021). The most prevalent of all the helpful microorganisms are bacteria, which are followed by fungus and actinobacteria (Poria et al., 2021).

Food security is threatened by the world's population growth, which increases the demand for fertilizers based on inorganic chemicals, which is detrimental to the environment and human health (Mitter et al., 2021). Because of the numerous environmental stressors that also contribute to low crop yields, organic farming that relies on microflora such as PGPM guarantees food availability while improving crop quality, productivity, and environmentally friendly farming practices (Jalal, et al., 2023). Therefore, by reducing the use of chemical fertilizers, crop production using PGPM provides sustainability and protects soil biodiversity (dos Lopes et al., 2021).

The majority of plant growth-promoting bacteria (PGPB) are proteobacteria. It includes genera like Pantoea, Thiobacillus, Pseudomonas, Micrococcus, Rhodococcus, Azospirillum, Azotobacter, Acinetobacter, Acetobacter, Klebsiella, Enterobacter, Alcaligenes, Arthrobacter, Burkholderia, Azorhizobium, Achromobacter, Serratia, Bradyrhizobium, Flavobacterium, Mesorhizobium, Microrhizobium, Streptomyces, Bacillus, Azoarcus, Aeromonas, Azoarcus, Caulobacter, Chromobacterium, Delftia, Frankia, Flavobacterium, Gluconacetobacter, Paenibacillus, Rhizobium and Streptomyces (Table 1).

Table 1. Plant growth promoting bacteria and their common host plant family (from Fanai et al., 2024).

Family	Plant	Plant growth-promoting bacteria
Fabaceae	Phaseolus vulgaris	*Rhizobium acidosoli, R. endophyticum, R. esperanzae, R. etli, R. hidalgoense, R. mesoamericanum, R. tropici, Acinetobacter* sp.
Poace	Rice, wheat, maize, soirghum, sugarcane	Azospirillum sp.
Asteraceae	Puticaria	*Bacillus cereus, Agrobacterium fabrum, Brevibacillus brevis, Bacillus subtilis, Paenibacillus* sp., *Acinetobacter radioresistant, Burkholderia* sp.
Solanaceae	Artemisia annua	*Brevibacillus* sp., *Bacillus* sp., *Pseudomonas* sp., *Azospirillum* sp., *Klebsiella* sp., *Enterobacter* sp., *Alcaligenes* sp., *Azotobacter* sp., *Streptomyces* sp., *Pantoea* sp., *Bacteroides* sp., *Proteobacteria* sp., *Radiobacter* sp., *Stenotrophomonas* sp.
Brassicaceae	Brasica oleraceae	*Pseudomonas* sp., *Enterobacter* sp., *Arthrobacter* sp., *Pantoea* sp.
Crasulaceae	Echevari laui	*Erwinia* sp., *Pantoea* sp.

In addition to helping plants tolerate a variety of biotic and abiotic stressors, the PGPB also promotes plant growth by promoting the solubility of various inorganic mineral nutrients, fixing nitrogen, releasing plant growth regulators, and producing a number of other biochemicals that either directly or indirectly increase plant productivity. Figure 1

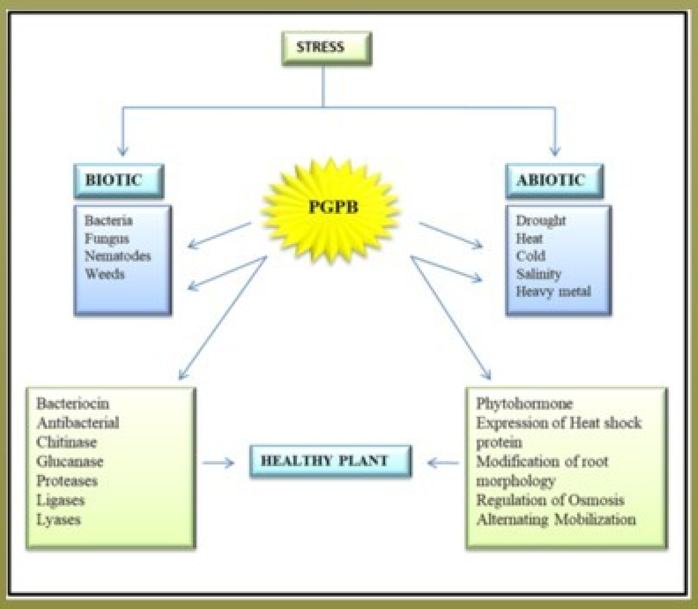

Figure 1. Functions that plant growth-promoting bacteria provide. The impacts of both biotic (caused by living things) and abiotic (induced by environmental variables) stress on plants demonstrate how PGBP helps to lessen the effects of stress. Through processes including siderophores, lytic enzymes, HCN, antibiotics & nitrogen fixation, hormone synthesis, etc., PGBP improve plant development, nutrient absorption, and stress tolerance (from Fanai et al., 2024).

ABIOTIC AND BIOTIC STRESS FACTORS

Continuously subjecting plants to biotic and abiotic stressors has a negative effect on their growth and development, which lowers yield and quality (Singh et al., 2021). With the help of a naturally occurring PGPB that increases resistance against different phytopathogens by generating biochemicals and improving soil fertility, plants subsequently develop particular kinds of defense mechanisms for stress response (Leontidou et al., 2020). Figure 2

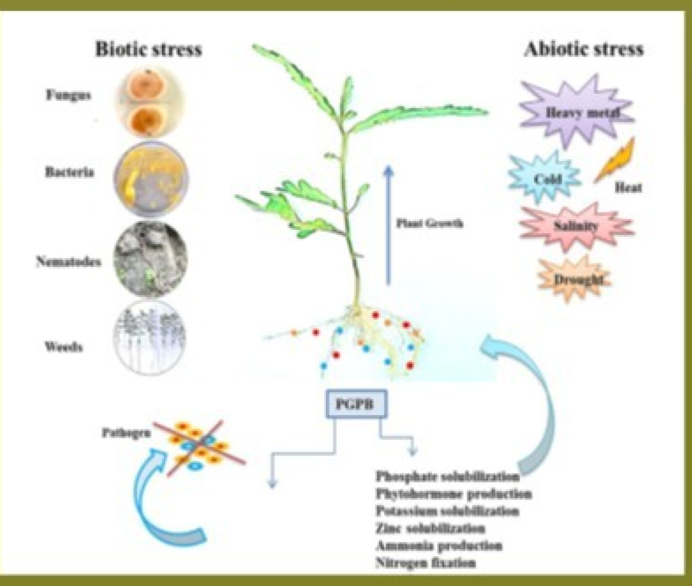

Figure 2. Various stressors and bacteria that support plant growth react to provide plant growth promotion. The impacts of both biotic (caused by living things) and abiotic (induced by environmental variables) stress on plants demonstrate how PGBP helps to lessen the effects of stress. By means of processes like nitrogen fixation, hormone synthesis, and biocontrol, PGBP improve plant growth, nutrient absorption, and stress tolerance (from Fanai et al., 2024).

Drought stress is categorized into hydrological, socio-economic, meteorological, and agricultural types, each leading to soil moisture deficits and the accumulation of reactive oxygen species that damage plant structure and function (Ahluwalia et al., 2021). By contrast, plant growth-promoting bacteria (PGPB) enhance drought tolerance through improved water uptake, root architecture modification, and production of protective phytochemicals (Khan and Bano, 2019). For example, inoculation with Bacillus pumilus and Pseudomonas putida improved maize drought resilience and nutrient acquisition (Kálmán et al., 2024), while Bacillus subtilis and Azospirillum brasilense increased osmolyte synthesis to support wheat germination under water deficit (Ilyas et al., 2020).

A rise in average global temperatures poses a significant abiotic challenge for crop productivity (Desaint et al., 2021). Heat-tolerant microbes—including Bacillus cereus, Serratia liquefaciens, Pseudomonas putida, P. fluorescens (Mitra et al., 2021), Burkholderia phytofirmans, Curvularia protuberata (Rana et al., 2021), Paraburkholderia phytofirmans, and various Bacillus and Pseudomonas spp. (Ahmad et al., 2023)—mitigate thermal damage by modulating plant hormone levels (e.g., cytokinins, ACC deaminase) and activating antioxidant enzymes that control water uptake and induce heat-shock protein expression (Moumbock et al., 2021). Exogenous application of specific amino acids further alleviates heat-stress effects by enhancing stress-responsive pathways (Santos et al., 2022).

Soil salinization, driven by water scarcity and the accumulation of NaCl-rich compost from sewage and waste treatment, and the build-up of soluble ions—bicarbonate, magnesium, sodium, chloride, sulfate, carbonate, and calcium—alters soil composition, diminishes fertility, impairs germination, and disrupts chloroplast structure, leading to reduced pigment synthesis, ion toxicity, and osmotic imbalance (Ahmed et al., 2020; Krishnamoorthy et al., 2022). Salinity stress further reduces plant development, fruit yield, biomass, stomatal conductance, and water movement (Ansari et al., 2019). Plant growth-promoting bacteria counteract these adverse effects by inducing stress-responsive pathways that lower reactive oxygen species production, synthesizing Na^+-binding exopolysaccharides, and producing phytohormones to enhance root growth and water uptake (Subramaniam et al., 2020).

DIRECT AND INDIRECT MECHANISMS OF PGPB IN ENHANCING PLANT PERFORMANCE

Indirect mechanisms

Siderophore production: Bacteria secrete ferric-specific ligands (hydroxamates, phenolates, carboxylates) to solubilize iron for themselves and host plants, enhancing root colonization and outcompeting pathogens; common producers include *Bacillus, Chryseobacterium, Phyllobacterium*, and *Pseudomonas* spp. (Bhatt et al., 2019).

Protease secretion: Microbial proteases (alkaline, acidic, neutral)—notably from *Bacillus* spp.—hydrolyze pathogen proteins and generate antifungal metabolites (e.g., serine proteases, subtilisins), serving as an indirect plant defense; activity is screened on skim-milk agar by clear halo formation (Castaldi et al., 2021).

Catalase activity: Catalase-positive strains (e.g., *Bacillus marinus, B. sphaericus, Staphylococcus aureus*) detoxify H_2O_2 at root interfaces, mitigating oxidative damage under stress; detected by bubble formation in 3% H_2O_2 (Talaiekhozani, 2022).

Amylase production: Alpha-amylases from endophytes like *Bacillus amyloliquefaciens* and *B. licheniformis* degrade pathogen cell walls and contribute to industrial applications (detergents, stain removal); screened on starch agar via iodine-stained halos (Ismail et al., 2021).

Urease activity: Ureolytic bacteria hydrolyze urea into plant-available ammonium and nitrates, supporting nitrogen nutrition and biomineralization (soil enrichment, concrete repair); measured by pH-dependent color change in urea broth (Cui et al., 2022).

Hydrogen cyanide (HCN) release: Rhizobacteria (mostly *Pseudomonas* and *Bacillus* spp.) emit HCN to inhibit fungi, nematodes, insects, and weeds without harming the host plant; detected via alkaline-picrate colorimetric assay (Alemu, 2016).

Direct mechanisms

Phytohormone production: Plant growth–promoting bacteria (PGPB) synthesize cytokinins, gibberellins, and especially indole-3-acetic acid (IAA), which regulate cell division, root initiation, and stress responses. Strains such as *Paenibacillus polymyxa, Rhizobium leguminosarum, Pseudomonas fluorescens* produce cytokinins (Mekureyaw et al., 2022), while *Bacillus pumilus* and *B. licheniformis* generate multiple gibberellins (Gutiérrez-Mañero et al., 2001). IAA producers, including *Azospirillum, Arthrobacter, Bradyrhizobium, Pantoea, Rahnella*, and *Enterobacter*, enhance root elongation and nutrient uptake (Rehman et al., 2020).

Phosphate solubilization: PSB release organic acids (citric, gluconic) that chelate cations and convert insoluble phosphates (tricalcium, rock phosphate) into bioavailable forms. Key taxa include *Pseudomonas putida, Azospirillum lipoferum, Bacillus firmus, B. polymyxa, Serratia marcescens*, and *Arthrobacter aureofaciens*. PSB inoculation boosts phosphorus availability and activates stress-responsive genes in crops like potato and sugarcane (Lin et al., 2023).

Ammonia production: Ammoniagenic PGPB such as *Pseudomonas putida, Klebsiella* spp., and *Enterobacter asburiae* generate NH_3, raising soil pH to suppress pathogens and supply inorganic nitrogen, which enhances root/shoot growth and biomass (Gohil et al., 2022).

Nitrogen fixation: Symbiotic genera (*Bradyrhizobium, Mesorhizobium, Sinorhizobium, Azorhizobium, Neorhizobium*) and free-living diazotrophs (*Azotobacter, Azospirillum, Burkholderia, Pseudomonas*, cyanobacteria) convert atmospheric N_2 into plant-available forms, supporting growth and yield (Basile and Lepek, 2021). Microbial consortia of *B. subtilis* and *A. brasilense* enhance root/shoot development, gas exchange, and grain yield in wheat, while co-inoculation of *Bradyrhizobium* and *Bacillus* improves nodulation and *Vigna unguiculata* productivity (Galindo et al., 2024; Gaspareto et al., 2023).

Zinc solubilization: Zinc is a vital enzyme co-factor, with optimal plant tissue levels at 30–100 mg·kg^{-1}; deficiency impairs growth and causes necrotic lesions. Zinc-solubilizing bacteria secrete organic acids and iron-chelating enzymes to lower rhizosphere pH and release Zn^{2+} (Eshaghi et al., 2019). Key taxa include *Pseudomonas aeruginosa, Gluconacetobacter diazotrophicus, P. striata, P. fluorescens, Burkholderia cenocepacia, Serratia liquefaciens, S. marcescens, Bacillus thuringiensis, B. aryabhattai, B. subtilis, Thiobacillus thioxidans*, and cyanobacteria. *Rhizobium, Pseudomonas*, and *Bacillus* spp. enhance Zn translocation and grain biofortification, improving wheat quality via exopolysaccharide and siderophore production (Jalal et al., 2024). Co-inoculation of *B. subtilis* or *P. fluorescens* with foliar ZnO further boosts maize chlorophyll, amino acids, glutelin, and prolamin content. Bacterial Zn nanoparticles inhibit biofilm

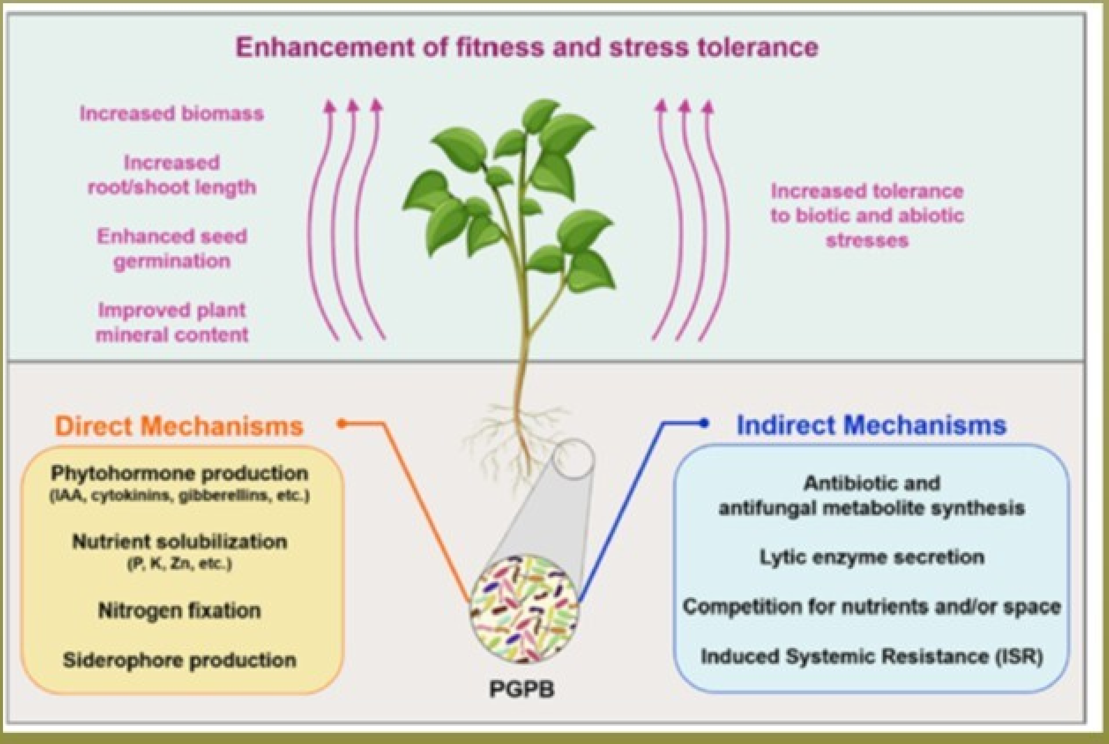

Figure 3. Overview of the main mechanisms used by PGPB to improve plant growth (from Vuolo et al., 2022)

CONCLUSION

Plant growth–promoting bacteria represent a cornerstone of sustainable agriculture by naturally supplying key metabolites—phytohormones, siderophores, lytic enzymes, hydrogen cyanide, and ammonia—and by solubilizing essential nutrients (P, Zn, K) or fixing atmospheric nitrogen. Their multifaceted modes of action not only enhance crop yield and quality under both biotic and abiotic stresses but also reduce reliance on synthetic agrochemicals, thereby protecting soil health and the broader environment.

To translate this promise into practice, future work must prioritize the development and field-ready formulation of robust biofertilizers and biocontrol agents tailored to specific crops and stress conditions. Equally critical is the systematic evaluation of PGPB–host compatibility to safeguard beneficial traits during root colonization, as well as the design of microbial consortia whose members coexist synergistically without compromising individual functionality. Addressing these challenges will pave the way for precision applications of PGPB, driving both productivity gains and ecological resilience in modern farming.

REFERENCES

- Bhatt, P., Huang, Y., Zhan, H. and Chen, S. 2019. Insight into microbial applications for the biodegradation of pyrethroid insecticides. *Frontiers in Microbiology*, *10*, p.1778. DOI 10.3389/fmicb.2019.01778.
- Cappellari, L.D.R., Chiappero, J., Palermo, T.B., Giordano, W. and Banchio, E. 2020. Volatile organic compounds from rhizobacteria increase the biosynthesis of secondary metabolites and improve the antioxidant status in Mentha piperita L. grown under salt stress. *Agronomy*, *10*(8), p.1094. DOI 10.3390/AGRONOMY10081094.
- Castaldi, S., Petrillo, C., Donadio, G., Piaz, F.D., Cimmino, A., Masi, M., Evidente, A. and Isticato, R. 2021. Plant growth promotion function of Bacillus sp. strains isolated from salt-pan rhizosphere and their biocontrol potential against Macrophomina phaseolina. *International journal of molecular sciences*, *22*(7), p.3324. DOI 10.3390/ijms22073324.
- Cui, M.J., Teng, A., Chu, J. and Cao, B. 2022. A quantitative, high-throughput urease activity assay for comparison and rapid screening of ureolytic bacteria. *Environmental research*, *208*, p.112738. DOI 10.1016/j.envres.2022.112738.
- Gohil, R.B., Raval, V.H., Panchal, R.R. and Rajput, K.N. 2022. Plant growth-promoting activity of Bacillus sp. PG-8 isolated from fermented panchagavya and its effect on the growth of Arachis hypogea. *Frontiers in Agronomy*, *4*, p.805454. DOI 10.3389/fagro.2022.805454.
- Gutiérrez-Mañero, F.J., Ramos-Solano, B., Probanza, A.N., Mehouachi, J., R. Tadeo, F. and Talon, M. 2001. The plant-growth-promoting rhizobacteria Bacillus pumilus and Bacillus licheniformis produce high amounts of physiologically active gibberellins. *Physiologia Plantarum*, *111*(2), pp.206-211. DOI 10.1034/j.1399-3054.2001.1110211.x.
- Ilyas, N., Mumtaz, K., Akhtar, N., Yasmin, H., Sayyed, R.Z., Khan, W., Enshasy, H.A.E., Dailin, D.J., Elsayed, E.A. and Ali, Z. 2020. Exopolysaccharides producing bacteria for the amelioration of drought stress in wheat. *Sustainability*, *12*(21), p.8876. DOI 10.3390/su12218876
- Ismail, M.A., Amin, M.A., Eid, A.M., Hassan, S.E.D., Mahgoub, H.A., Lashin, I., Abdelwahab, A.T., Azab, E., Gobouri, A.A., Elkelish, A. and Fouda, A. 2021. Comparative study between exogenously applied plant growth hormones versus metabolites of microbial endophytes as plant growth-promoting for Phaseolus vulgaris L. *Cells*, *10*(5), p.1059. DOI 10.3390/cells10051059.
- Jalal, A., da Silva Oliveira, C.E., Galindo, F.S., Rosa, P.A.L., Gato, I.M.B., de Lima, B.H. and Teixeira Filho, M.C.M. 2023. Regulatory mechanisms of plant growth-promoting rhizobacteria and plant nutrition against abiotic stresses in Brassicaceae family. *Life*, *13*(1), p.211. DOI 10.3390/life13010211.
- Khan, N., Bano, A., Ali, S. and Babar, M.A. 2020. Crosstalk amongst phytohormones from planta and PGPR under biotic and abiotic stresses. *Plant Growth Regulation*, *90*(2), pp.189-203. DOI 10.1007/S10725-020-00571-X.
- Krishnamoorthy, R., Roy Choudhury, A., Walitang, D.I., Anandham, R., Senthilkumar, M. and Sa, T. 2022. Salt stress tolerance-promoting proteins and metabolites under plant-bacteria-salt stress tripartite interactions. *Applied Sciences*, *12*(6), p.3126. DOI 10.3390/APP12063126.
- Leontidou, K., Genitsaris, S., Papadopoulou, A., Kamou, N., Bosmali, I., Matsi, T., Madesis, P., Vokou, D., Karamanoli, K. and Mellidou, I. 2020. Plant growth promoting rhizobacteria isolated from halophytes and drought-tolerant plants: Genomic characterisation and exploration of phyto-beneficial traits. *Scientific reports*, *10*(1), p.14857. DOI 10.1038/s41598-020-71652-0.
- Lopes, M.J.D.S., Dias-Filho, M.B. and Gurgel, E.S.C. 2021. Successful plant growth-promoting microbes: inoculation methods and abiotic factors. *Frontiers in Sustainable Food Systems*, *5*, p.606454. DOI 10.3389/FSUFS.2021.606454.
- Lin, Y., Yang, L., Chen, Z., Gao, Y., Kong, J., He, Q., Su, Y., Li, J. and Qiu, Q. 2023. Seasonal variations of soil bacterial and fungal communities in a subtropical Eucalyptus plantation and their responses to throughfall reduction. *Frontiers in Microbiology*, *14*, p.1113616. DOI 10.3389/fmicb.2023.1113616.
- Manghwar, H., Jalal, A., Da CE, Oliveira, S., Aparecida. P., Rosa, L, Galindo, FS., Carvalho, M., Filho, MT. 2023. Beneficial microorganisms improve agricultural sustainability under climatic extremes. Life 13(5):1102 DOI 10.3390/life13051102.
- Mekureyaw, M.F., Pandey, C., Hennessy, R.C., Nicolaisen, M.H., Liu, F., Nybroe, O. and Roitsch, T. 2022. The cytokinin-producing plant beneficial bacterium Pseudomonas fluorescens G20-18 primes tomato (*Solanum lycopersicum*) for enhanced drought stress responses. *Journal of Plant Physiology*, *270*, p.153629. DOI 10.1016/j.jplph.2022.153629
- Mitra, D., Rodriguez, A.M.D., Cota, F.I.P., Khoshru, B., Panneerselvam, P., Moradi, S., Sagarika, M.S., Anđelković, S., de los Santos-Villalobos, S. and Mohapatra, P.K.D. 2021. Amelioration of thermal stress in crops by plant growth-promoting rhizobacteria. *Physiological and Molecular Plant Pathology*, *115*, p.101679.DOI 10.1016/j.pmpp.2021.101679.
- Mitter, E.K., Tosi, M., Obregón, D., Dunfield, K.E. and Germida, J.J. 2021. Rethinking crop nutrition in times of modern microbiology: innovative biofertilizer technologies. *Frontiers in Sustainable Food Systems*, *5*, p.606815. DOI 10.3389/fsufs.2021.606815.