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Prospects for Allelochemicals Utilization for Managing the Plant-Soil-Microbiome System in Phytostimulation Technologies

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Phytostimulation is an environment friendly, cost-effective phytoremediation technique based on mutualistic interactions between plants and rhizosphere microbiome capable of degrading hazardous pollutants. Allelochemicals found in plant root exudations, to a significant extent, shape the structure and functional state of the rhizosphere microbiome through direct and indirect effects. In this review, the various classes of allelochemicals (viz. organic acids, amino acids, phenolic acids, flavonoids, coumarins, tannins, triterpenoids, and benzoxazinoids) have been analyzed as to the character and physiological mechanisms of their effect on the populations of soil rhizobacteria and fungi taxonomical groups, promising as bioremediants.All considered classes of allelochemicals demonstrated selective activity in relation to different species of soil microorganisms. This allows using such compounds as markers of the "suitability" of plant species or cultivars as host plants in phytostimulation technologies. The possibility of controlling the bioremediation potential of the rhizosphere microbiome by including allelopathic plants into phytoremediation practices is considered. The implementation of an allelopathic approach in phytostimulation technology will allow to create stable associations of plants with bioremediating microorganisms, overcome the negative influence of biotic and abiotic factors on the soil microbiome and plants, improve the effectiveness of bioremediation technologies, and promote sustainable agricultural development.

Keywords: phytostimulation, allelochemicals, microbiome, rhizosphere

Introduction

Soil quality is the basis for food, economic, and environmental security. Approximately 33% of global soil resources are degraded due to erosion, pollution, compaction, salinization, acidification, dehumification, and other adverse processes associated with irrational management of soil resources (Poznyak, 2017). The most dangerous type of degradation from an environmental point of view is pollution with heavy metals, radioactive substances, as well as polycyclic aromatic hydrocarbons (Poznyak, 2017). According to expert estimates, the cleaning of soil contaminated with heavy metals, radionuclides, oil, or pesticides using bioremediation is only 5% of the costs of chemical remediation practices (Tsytsyura, et al. 2022).

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Phytostimulation (also referred to as rhizodegradation) is a novel bioremediation technique based on plant-supplied nutrients (exudates), enhancing the growth and remediating potential of the rhizosphere microbial communities capable of degrading hazardous pollutants into non-toxic products (Singh and Jain, 2004).Although this process requires a long period of time and is limited to the rhizosphere, it attracts the attention of many researchers due to its high effectiveness (potential complete mineralization of organic contaminants in-situ), cost-effectiveness, and safety to the environment (Singh and Jain, 2004; Tsytsyura, et al. 2022).

Bacteria and Fungi play key roles in the degradation of many organic pollutants. While plants creates a favorable environment for microorganisms-remediants in several ways:

1. root exudations containing sugars, carbohydrates, organic acids, amino acids etc. serve as nutrients for microbiome populations;
2. root systems bring oxygen to the rhizosphere, which ensures aerobic conditions;
3. foliar and root phytomass contribute to organic carbon accumulation;
4. endomycorrhizal fungi help to decompose some persistent organic pollutants that cannot be transformed solely by rhizobacteria (Birt et al., 2022; Wu et al., 2024).

The microbiome, in turn, promotes the host plant growth via nitrogen fixation, nutrient (i.e., phosphorus, potassium, sulfur, iron, zinc, etc.) mobilization, production of phytohormones, antibiotics, and detoxification of pollutants (Wu et al., 2024). Such allelopathic interactions between plants and microorganisms create a special biochemical environment that stimulates microbial activity, alters the availability of nutrients, physical and chemical soil characteristics, and affects the excretory activity of the plant`s roots (Birt et al., 2022). As a result, the microbiome formed in the rhizosphere and endorhizosphere could be markedly different from that in bulk soil. This phenomenon is referred to as the “rhizosphere effect” (Schneijderberg et al., 2020).

Plant species with high allelopathic potential, such as corn (*Zea mays* L.), bird‘s-foot trefoil (*Lotus corniculatus* L.), rye (*Secale cereal* L.), and alfalfa (*Medicago sativa* L.) exhibit strong rhizosphere effects, while other plant species, such as *Arabidopsis thaliana*, exhibit weak rhizosphere effects (Chase et al., 1991; Phillips et al., 2004; Cotton et al., 2019; Schneijderberg et al., 2020). The plant‘s ability to influence the soil microbiome is determined by the chemical composition and concentration of allelochemicals in its root exudates. The latter represent a unique composition of nutrients and biologically active compounds that can act as signaling molecules that mediate motility, chemotaxis, biofilm formation, and symbiotic relationships, influencing the growth and propagation of certain microbial populations (Chen and Liu, 2024).

On the other hand rhizosphere colonization process is influenced by the microorganism`s capacity to utilize or metabolize higher plant`s root exudates and regulate the metabolism and excretory function of higher plants. Moreover, researchers note that different taxonomic and ecotrophic groups of microorganisms exhibit different dietary preferences and the ability to metabolize components of root exudates (Chen and Liu, 2024). For example, cucurbitacins, the characteristic triterpenoids in Cucurbitacea, can serve as carbon sources for *Enterobacter* sp. and *Bacillus* sp., while inhibiting the fungal pathogen *Fusarium oxysporum* (Zhong et al., 2022). Root bacteria that can selectively metabolize the host plant`s allelochemicals as carbon sources have greater chances to colonize its rhizosphere. Successful colonization promotes closer associations between plants and microbes (Liu et al., 2016; Liu et al., 2019).

Numerous studies indicate the capacity of some allelochemicals to attract certain taxonomic groups of microorganisms and repel others, thus shaping specific microbiomes associated with the rhizosphere (Neal et al., 2012; Huanget al., 2019; Wang et al., 2020; Zhong et al., 2022). However, it remains unclear whether this is the result of nonspecific reactions of the soil microorganisms to biocidal or nutritious properties of phytochemicals or specific biochemical communication between plants and microorganisms takes place.

Although there is a huge amount of scientific information about the positive effects of root exudates on soil microbiota, the opposite trend may also occur: root exudates can negatively affect the rhizosphere environment, suppressing growthof beneficial bacteria and promoting phytopathogens, as well as their migration and spread in the rhizosphere, causing soil fatigue (Zhou et al., 2025).

In recent years, microbiome engineering has emerged as a promising approach to manage the plant-soil-microbiome system and increase crop productivity, create sustainable agroecosystems, reduce the use of synthetic agrochemicals, and contribute to ecological balance (Wankhade et al., 2025). However, the application of microbiome engineering to various crop growing systems remains underexploited, probably due to a poor understanding of the allelopathic interactions of the plant-soil-microbiome system. Understanding the ecophysiological mechanisms and ecological consequences of the latter will allow creating stable and effective, in terms of bioremediation, associations between plants and microorganisms-bioremediants.

In this review, we have analyzed scientific data on the nature and ecological and physiological mechanisms of the effects of different classes of allelochemicals on certain taxonomic groups of microorganisms that are promising in terms of bioremediation. The information presented in this review will allow us to identify biochemical markers for the selection of higher plant species capable of forming stable associations with bioremediating microorganisms, as well as to develop more effective phytostimulation technologies by involving allelopathic plant species or substances that will stimulate the colonization of the rhizosphere by beneficial microorganisms and repel unwanted ones.

Organic Acids

Organic acids are the most important compounds connecting plants and soil microbiocenosis. As part of the root exudates, they contribute to the assimilation of elements of mineral nutrition by plants, chelate some toxic metals, and regulate the pH of the soil. Organic acids are one of the main organic nutrients for rhizospheric microorganisms. At the same time, different taxonomic groups of microorganisms prefer organic acids with different chemical formulas. For example, representatives of the genus *Bacillus* spp. actively consume oxalic acid and malic acid (Yuan et al., 2015; Liu et al., 2019; Rudrappa et al., 2008), *Rhodobacter* spp. – succinic acid (Lee et al., 2011), nitrogen fixing *Azorhizobium* spp. – oxalic, malic, succinic, tartaric acids (Liu et al., 2019). In addition, organic acids can act as chemoattractants for certain microbes – bioremediants. In particular, malate, citrate, oxalate attract nitrogen-fixing representatives of the genus *Rhizobium* spp., mycorrhizal fungi, rhizobacteria *Enterobacter* spp., *Rhodococcus*, *Mycobacterium*. A free-living nitrogen-fixing *Azorhizobium caulinodans* demonstrated chemotaxis response to organic acids (succinate, citrate, tartrate, and malate), which were critical for nodulation and nitrogen fixation on the stems and roots of the host plant (Liu et al., 2019). *Pseudomonas putida* demonstrated chemotaxis response to acetate (Liu et al., 2019). Organic acids can contribute to the formation and stabilization of bacterial biofilms on the root surface, which is an important step in initiating and maintaining contact between a microorganism and a host plant, providing reliable attachment and protecting against stress factors (Yuan et al., 2015). On the other hand, organic acids can suppress unwanted microflora. In particular, some organic acids, such as acetic acid, lactic acid, propionic acid, and citric acid, could inhibit growth and toxin secretion in some fungi. In particular, acetic acid has been shown to inhibit growth and toxin secretion by *Aspergilus flavum*, *Penicillium purpurogenum*. Lactic acid inhibited toxin secretion by *Fusarium oxisporum*. Formic acid inhibited toxin secretion by *Rhizopus nigricans* (Hassan et al., 2015).

The antifungal activity of organic acids is associated with acidification of the cytoplasm, in combination with membrane damage and inhibition of enzymes. Some organic acids (for example, sorbic, propionic) can be incorporated into the lipid bilayer of the membrane of fungi. This increases the permeability of the membrane, leads to the leakage of ions and metabolites, and disrupts the osmotic balance. Anions of acids (for example, propionate, and sorbate) can bind to respiratory enzymes. This blocks the processes of oxidative phosphorylation and ATP synthesis, and the synthesis of cellular components. It is known that sorbic acid inhibits the formation of spores and the synthesis of lipids in fungi (Barbero-López et al., 2020).

The application of organic acids to soil stimulates the growth of certain strains of rhizobacteria, is neutral for others, and inhibits the growth of the rest. In particular, exogenicoxalic acid was shown to affect the association of a symbiont *Azorhizobium caulinodans*, with its host plant *Sesbania rostrata*, in an indirect way. It changed the chemotactic response of the symbiont chemoattractants: decreased toward acetate, succinate, and citrate, and increased chemotaxis toward lactate (Liu et al., 2019). While exogenic acetate (citric acid, lactic acid, succinic acid) promoted chemotaxis of *Pseudomonas putida* to citrate (Lopez-Farfan et al., 2017).

Many modern microbial biofertilizers, especially in liquid formulations, often include organic acids like lactic, citric, or acetic acid as stabilizers. Adding organic acids to biofertilizers enhances nutrient availability, supports beneficial microbe survival, regulates pH, suppresses pathogens, and boosts plant growth – making the biofertilizer more efficient and stable (Ammar et al., 2023). It is possible to regulate the pool of organic acids in the rhizosphere by planting allelopathic plants, such as for example, presented in Table 1, and also by using some fruit waste

Table 1 The effect of higher plants' allelochemicals on soil microorganisms, promising as bioremediants

Allelochemical	Effect on microorganisms	Plant species	Microorganism species	Reference
Carboxylic acids: **oxalic acid, malic acid**	induced the chemotaxis and biofilm formation	*Musa* spp.	*Bacillus amyloliquefaciens*	Yuan et al., 2015
oxalic, malic, succinic, tartaric acids	induced the chemotaxis and biofilm formation	*Sesbania rostrata*	*Azorhizobium caulinodans*	Liu et al., 2019
malic acids	carbon source, chemoattractants	*Arabidopsis thaliana*	*Bacillus subtilis*	Rudrappa et al., 2008
succinic acid	carbon source, chemoattractant	*Lolium multiflorum*	*Pseudomonas putida*	Kuiper et al., 2002
Aminoacids: **L-Tryptophane**	induce auxin biosynthetic pathways in bacteria	*Cucumis sativus*	*Bacillus amyloliquefaciens*	Liu et al., 2016
histidine, arginine, aspartic acid	Chemoattractants	*Sesbania rostrata*	*Azorhizobium caulinodans*	Liu et al., 2019
trimethylglycine	enhancing the bacterium's ability to cope with osmotic stress	*Triticum aestivum*	*Pseudomonas synxantha*	Bhattacharyya et al., 2025
Phenolic acids: **benzoic acid**	stimulation	*Arachis hypogaea*	*Trichoderma* spp. *Burkholderia*	Liu et al., 2017
Salicylic acid	significantly inhibit the growth, pigment accumulation, attachment to the plant`s roots, biofilm formation, and exoenzyme production	–	*Pseudomonas aeruginosa*	Prithiviraj et al., 2005
Ferulic acid chlorogenic acid	inhibited growth and indole acetic acid production inhibited growth	–	*Pseudomonas fluorescens*	Myszka et al., 2014
gallic acid, cinnamic acid	biocidal activity	–	*Pseudomonas* spp.	Dembińska et al., 2025
salicylic acid + siliceous mineral	Stimulated growth	–	ammonifying bacteria and actinomycetes	Zaimenko et al., 2021
	Inhibited growth	–	micromycetes	
_p_-coumaric, caffeic, protocatechuic, _p_-hydroxybenzoic, and phenyllactic acids	enhance growth	Legumes	*Bradyrhizobium* spp.	Pérez-Montaño et al., 2011
Flavonoids: **daidzein, luteolin-7xO-glucoside or quercetin-3-O-galactoside**	chemoattraction and induction of nodule formation	Legumes	*Sinorhizobium fredii*, *Rhizobium* spp., *Bradyrhizobium* spp.	Pérez-Montaño et al., 2011
naringenin and apigenin	significantly enhance cell multiplication		*Bradyrhizobium* spp.	Pérez-Montaño et al., 2011
baicalein and quercetin	inhibition of virulence	–	*Pseudomonas aeruginosa*	Paczkowski et al., 2017
quercetin, quercitrin	inducing of arbuscular mycorrhizalsymbiosis	*Triadica sebifera*	arbuscular mycorrhizalfungi	Tian et al., 2021
quercetin	increased relative abundance	–	*Pseudarthrobacter*, *Pseudomonas*	Schütz et al., 2021
isoflavonoids	antimicrobial activity	*Staudtia kamerunensis*	*Bacillus subtilis*, *Staphylococcus* spp.,epidermidis, *Mycobacterium* spp., *Staphylococcus* spp., *Enterobacter* spp., *Pseudomonas aeruginosa*	Tonga et al., 2022

First continuation of table 1

Allelochemical	Effect on microorganisms	Plant species	Microorganism species	Reference
apigenin, phloretin	In high concentrations suppress, in low promote biophilm formation enhanced the swarming motility and production of cellulose and curli		*Pseudomonas fluorescens*	Yu et al., 2020
rutin	promoted the biofilm formation	*Oryza sativa*	*Bacillus subtilis*	Singh, et al. 2016
apigenin	promoted the biofilm formation	*Oryza sativa*	*Gluconacetobacter diazotrophicus*	Yan et al., 2022
daidzein	selective promotion	*Glycine max*	Comamonadaceae	Okutani et al., 2020
Tannins: mixture of proanthocyanidins	Inhibition of growth andbiofilm formation, antimembrane activity	*Anadenanthera colubrina*, *Commiphora leptophloeos*, *Myracrodruon urundeuva*	*Pseudomonas aeruginosa*	Trentin et al., 2013
Ellagitannins	use as a carbon source	*Punica granatum*	*Aspergillus niger*	Ascacio-Valdés et al., 2014
Tannic acid	increase the relative abundance	*Morus* spp., *Stylosanthes guianensis*	*Weissella*, *Acinetobacter*, *Kosakonia* spp.	Wang et al., 2020
	reduce relative abundance		*Clostridium* spp.	
Condensed tannins	lower mycotoxin production and the associated microbiome. Increase relative abundance	*Dalea purpurea*	*Penicillium* spp., *Fusarium* spp., *Bacillus* spp.	Peng et al., 2018
Coumarins:	Inhibition of proliferation via a redox-mediated mechanism	*Arabidopsis thaliana*	*Pseudomonas* spp.	Voges et al., 2019
Scopoletin	Promotion of rhizosphere colonization	*Arabidopsis thaliana*	*Trichoderma asperellum*,*Trichoderma harzianum*, *Pseudomonas simiae*	Stringlis et al., 2018
Coumarin	Promotion of the rhizosphere colonization	*Lolium multiflorum*	*Geobacter* spp., *Polycyclovorans* spp., *Polycyclovorans* sp., *Ramlibacter* spp., *Geobacter* spp., *Massilia* spp. and *Neorhizobium*, *Pseudomonas* spp.	Yang et al., 2023
Benzoxazinoids:	attraction and recruitment of plant-beneficial rhizobacteria	*Zea mais*	*Pseudomonas putida*	Neal et al., 2012
2,2’-oxo-1,1’-azobenzene	carbon and nitrogen source, stimulation of rhizosphere colonization	*Secale cereale*	*Acinetobacter calcoaceticus*	Chase et al., 1991
DIBOA and DIMBOA	stimulation of rhizosphere colonization	*Zea mais*	Flavobacteriia	Cotton et al., 2019
Triterpenoids: pentacyclic triterpenes	quorum quencher and biofilm inhibitors	–	*Enterococcus* sp., *Staphylococcus* sp., *Pseudomonas aeruginosa*	Bhattacharya et al., 2023

Second continuation of table 1

Allelochemical	Effect on microorganisms	Plant species	Microorganism species	Reference
dammarane, apotirucallane	antibacterial	*Melia toosendan*	*Pseudomonas aeruginosa, Bacillus subtilis*	Shao et al., 2022
cycloalkane-type lanosterane-type schinortriterpenoids	antibacterial	*Schisandra sphenanthera*	*P. aeruginosa*, *B. subtilis*	Zhao et al., 2024
hopanoids	optimize plant-microbe symbioses, facilitate bacterial survival in soils and plant hosts	*Aeschynomene afraspera*	*Bradyrhizobium diazoefficiens*	Kulkarni et al., 2015
schitriterpenoids,schinortriterpenoids, isoanwuweizic acid, nigranoic acid, micrandilactone, lanci-fodilactone	controlling the feedback between the host plant and the endophytic microbial community	*Schisandra sphenanthera*	27 bacterial and 26 fungal isolates belonging to *Proteobacteria*, *Bacteroides*, *Actinobacteria*, *Firmicutes*.	You et al., 2021
thalianin, thalianyl fatty acid esters, and arabidin	direct the assembly and maintenance of microbiota	*Arabidopsis thaliana*	*Ascomycota*, *Basidiomycota*, *Zygomycota*	Huanget al., 2019
cucurbitacins	selectively stimulate	*Cucumis melo*, *Citrullus lanatus*	*Enterobacter* sp., *Bacillus* sp.	Zhong et al., 2022
pentacyclic triterpenoids	antimicrobial activity	*Staudtia kamerunensis*	*Bacillus subtilis*, *Staphylococcus* spp. *Mycobacterium* sp., *Enterobacter* spp.,*Pseudomonas aeruginosa*	Tonga et al., 2022
ursolic acid, oleanolic acid	antimicrobial activity	–	*Staphylococcus* spp.	Wrońska et al., 2022

as organic fertilizer (Ammar et al., 2023; Consoli et al., 2023). In modern organic agriculture, plant residues in various forms, such as powder, water extract, composts, or converted into biochar, are actively used. *Citrus* waste, apple, and grape pomace are a cheap source of organic fertilizers rich in organic acids, promising for use in phytostimulation technologies (Li et al., 2006; Consoli, et al., 2023). In particular, it is shown that the products of composting of citrus waste supplemented with calcium hydroxide (pH of 6.3) boosted the development of *Pseudomonas aeruginosa*, *P. fluorescens*, *P. luteola*, and *Serratia marcescens*, *Aspergillus* spp. Etc. (Heerden et al., 2002). Vermicomposting of grape marc derived from red winemaking stimulated the development of nitrogen-fixing species of Enterobacteriaceae, *Pseudomonas* spp., *Duganella* spp., *Allorhizobium* spp., *Neorhizobium* spp., *Pararhizobium* spp., and *Rhizobium* spp. (Gómez Brandón et al., 2019). Apple, grape, and beet wastes stimulated the growth of *Trichoderma* spp. (Zaimenko et al., 2020).

Thus, organic acids play an important role in the formation of symbiotic relationships between higher plants and the soil microbiome: they attract certain taxonomic groups of organisms and inhibit the development of others, promote the colonization process by involving them in the process of forming biofilms, nodules and fixing microorganisms on the root surface, regulate pH, bioavailability of mineral nutrients and toxic metals in the rhizosphere environment, regulate chemotactic responses of microorganisms. The specific selective activity of organic acids in relation to different rhizobacteria strains allows them to be used as a marker of the "suitability" of plant species as hosts in phytostimulation technologies. By regulating the pool of organic acids in the soil, it is possible to create stable and effective associations of plants with microorganisms-bioremediants.

Amino Acids

Amino acids are the main components of protein, energy, and nitrogen metabolism in higher plants and microbes. In addition, they are precursors for phytohormones, phytoalexines, and other secondary metabolites with specific biological activity. Recent findings indicate that amino acid metabolism is closely related to higher plants' interactions with the soil microbiome. First of all, amino acids are part of the organic pool of nitrogen in the soil, available to both plants and microbes (Moormann et al., 2022).

Amino acids can function as signaling molecules and defense compounds, interacting with the soil microbiota at different levels. While the protective function of phytoalexins derived from aromatic amino acids during pathogen attack is well established, their role in recruiting beneficial microbes is just beginning to become clear (Moormann et al., 2022).

It is known that amino acids are chemoattractants for many genera of beneficial microorganisms (viz. *Rhizobium*, *Azospirillum*, *Pseudomonas*, *Mycobacterium*, *Enterobacter* etc.), although a number of bacteria are repelled from certain amino acids (Matilla and Krell, 2024). Chemoattraction is preconditioned by the metabolic value of an amino acid as well as its signaling function and is species-specific (Matilla and Krell, 2024). For example, *Pseudomonas fluorescens* performed chemotaxis to all 20 proteinogenic amino acids (Matilla and Krell, 2024), *Pseudomonas putida*to gamma-aminobutyrate (Reyes-Darias et al., 2015), the nitrogen-fixing rhizobacterium *Sinorhizobium meliloti* – to all proteinogenic amino acids, except for aspartate,citrulline, cystine, gamma-aminobutyric acid, and ornithine (Webb et al., 2017), for other nitrogen-fixing rhizobacterium *Bradyrhizobium japonicum*, aspartate and glutamate are potent attractants (Althabegoiti et al., 2008).

In addition, such amino acids as tryptophan, cysteine, valine, and α-aminoadipic acid are substrates for the secondary metabolism of many soil microorganisms, including the synthesis of phytohormones, antibiotics, and siderophores (Fytlovitch et al., 1983; Liu et al., 2016). Application of these amino acids to the soil would allow regulation of rhizobacteria's secondary metabolism. For example, exogenous tryptophan stimulates the synthesis and excretion of auxins by *Bacillus amyloliquefaciens* (Liu et al., 2016).

The participation of amino acids in the symbiotic interactions between higher plants and *Rhizobium*, as well as mycorrhizae, is shown. Amino acids are involved in the transport and storage of nitrogen (glutamine, asparagine) by host plants, and serve as carbon, nitrogen, or sulfur sources, signals of cellular nitrogen status, and provide precursors of important metabolites for nitrogen-fixing microorganisms (Dunn, 2014).

Some amino acids and their derivative phytoalexins increase the resistance of plants to various stresses, including fungal infection (Soledade et al., 2015). It was also experimentally proven that plants can sense specific patterns in changes in amino acid metabolism and interpret them as a signal of a pathogen infestation (Moormann et al., 2022). In turn, rhizobacteria can stimulate the exudation of amino acids by plant roots. For example, it is shown that microbial products like phenazine or zearalenone, which are produced by common soil microorganisms such as *Pseudomonas*, significantly enhanced the net efflux of amino acids from roots of *Medicago sativa*, *Medicago truncatula*, and *Zea mays* (Phillips et al., 2004).

The traditional approach allowing enhancing the amount of amino acids in the soil is based on using legume crops as living plants or green manure. This approach has a very ancient history, dating back to the origins of agriculture. Today, legumes are widely used in crop rotations, intercropping, cover cropping, or as mulches to increase soil nitrogen reserves and improve the nitrogen cycle within agricultural ecosystems (Ma et al., 2024). In particular, the inclusion of legumes in crop rotation was shown to significantly enhance subsequent crops' productivity and yield quality as well as levels of certain secondary metabolites, involved in stress resistance (Ma et al., 2024). Long-term cereal-legume rotation resulted in a decrease in microbial diversity and richness but also led to the enrichment of beneficial bacteria, such as *Acinetobacter*, *Pseudomonas* (Zhang et al., 2017). The application of green manure consisting of a mixture of *Vicia sativa*, *Pisum sativum*, *Vicia faba*, *Secale cereal*e, and *Brassica napus* significantly increased the abundance of bacterial taxa involved in the soil nitrogen cycle, such as *Microvirga* spp., *Pontibacter* spp., and *Nitrospira* spp. in the rhizosphere of *Vitis vinifera* (Longa et al., 2017). The application of hairy vetch as green manure increased fungal biomass and diversity, including abundance of such promising bioremediant species as *Cladosporium* spp., *Arthrobacter* spp., *Variovorax* spp., *Pseudoxanthomonas*, *Glycomyces* capable of breaking down or neutralizing environmental contaminants (Ma et al., 2024).

Thus, amino acids are an important source of nutrition, and also perform a signaling function in the interactions between plants and rhizobacteria, especially symbiotic nitrogen fixers. Being precursors of phytohormones, phytoalexins, and other biologically active compounds, amino acids are involved in various signaling systems of communication at different levels – cell-to-cell signaling, quorum sensing, and "inter-kingdom" communication. By regulating the quantitative and qualitative composition of the amino acid pool in the rhizosphere, it is possible to influence the effectiveness of symbiotic relationships between plants and agronomically beneficial rhizobacteria, plant resistance to phytopathogens and other stress factors.

Phenolic Acids

Phenolic acids are an important group of allelochemicals involved in higher plants interactions with other plants, microorganisms, fungi, and animals. The biological activity of phenolic acids significantly exceeds that of the organic acids and amino acids. The accumulation of phenolic acids in the soil of the rhizosphere is associated with the phenomenon of soil sickness in monoculture crops such as peanuts, tobacco, ginseng, tea, lilac, etc. (Gorobets et al., 2005; Liu et al., 2017; Bao et al., 2022; Zhou et al., 2025). In addition to the direct phytotoxic effect on crops, the accumulation of phenolic acids in the rhizosphere soil can stimulate the growth of soil-borne pathogens (Liu et al., 2017; Bao et al., 2022; Zhou et al., 2025). For instance, *p*-hydroxybenzoic acid secreted by tobacco roots can enhance the growth of a soil-borne pathogen *Ralstonia solanacearum*, while ferulic and salicylic acids secreted by watermelon roots can stimulate the proliferation of *Fusarium oxysporum* (Zhou et al., 2025). Vanillic and *p*-hydroxybenzoic acids associated with the rhizosphere of *Panax notoginseng* promoted the growth of primary pathogenic bacteria of *Fusarium* spp., *Ilyonectria* spp., *Lelliottia* spp., and *Flavobacterium* spp. (Bao et al., 2022). Exogenous benzoic acid (0.1 mmol·L^{-1}) promoted the mycelia growth, sporulation capacity, and conidial germination of the peanut root rot pathogen *Fusarium* sp. *in vitro* and *in vivo* (Liu et al., 2017).

Accumulating in the rhizosphere soil in effective concentrations, phenolic acids can suppress the growth of many microorganisms, both agronomically useful and phytopathogenic. Significant antifungal and antibacterial activities demonstrate cinnamic, *p*-coumaric, salicylic, gallic, and tannic acids (Dembińska et al., 2025). Salicylic acid significantly inhibits the growth, pigment accumulation, attachment to the plant`s roots, and biofilm formation, exoenzyme production in *Pseudomonas aeruginosa* (Prithiviraj et al., 2005). Gallic acid in the concentration of 500 μg·mL^{-1} inhibited *P. aeruginosa*, causing irreversible changes in membrane properties, local ruptures with consequent leakage of intracellular constituents (Dembińska et al., 2025). Ferulic acid present in cucumber root`s exudates reduces bacterial diversity, and enhances fungal diversity (Zhou and Wu, 2012). Ferulic and chlorogenic acids at the concentration of 0.02 and 0.04 μg·ml^{-1} inhibit growth and indole acetic acid production in *Pseudomonas fluorescens* (Myszka et al., 2014).

Evidence suggests that bacteria associated with plants prone to accumulate significant amounts of phenol allelochemicals in the rhizosphere soil have evolved the ability to metabolise aromatic organic compounds (Bao et al., 2022). In particular, it was shown that the microbiome in the rhizosphere of a 3-year-old monoculture of *Panax notoginseng* exhibited a strong capacity to degrade four phenolic acids, secreted by *P. notoginseng* roots and rapidly (a half-life of less than 4.5 h) decrease their concentrations (Bao et al., 2022). Several beneficial rhizobacteria (viz. *Pseudomonas putida*, *Acinetobacter calcoaceticus*, *Agrobacterium tumefaciens*, *Rhodococcus erythropolis*) could detoxify phenolic acids and other aromatic compounds through the beta-ketoadipate pathway (Harwood and Parales, 1996). Some soil fungi, such as *Phanerochaete chrysosporium*, *Trametes versicolor*, *Aspergillus niger*, *Trichoderma reesei*, etc. produce ligninolytic enzymes, such as lignin peroxidases, phenoloxidase, and laccase, which transform and mineralize phenolic acids (Pointing 2001). Fungi, as a rule, have a higher level of enzymes capable of degrading phenolic acids compared to bacteria (Su et al., 2012).

Microorganisms adapted to metabolize phenolic allelochemicals as a rule are also capable of metabolising aromatic pollutants, such as aromatic hydrocarbons, naphthalene, toluene, and 2,4-dichlorophenoxyacetic acid, etc, and, therefore, are promising for cleaning soil from this kind of pollutants. The most studied are *Pseudomonas putida*, *Burkholderia* spp., *Coriolopsis* spp., *Trichoderma* spp., *Rhodococcus* spp., *Phanerochaete* spp., *Trametes* spp., *Pleurotus* spp. for which phenolic acids and their derivatives can also act as chemo-attractants (Pointing, 2001; Neal et al., 2012). For example, benzoate and 4-hydroxybenzoate were attractants for *Pseudomonas putida* strains capable of degrading many kinds of environmental pollutants (Parales and Harwood, 2002). *Pseudomonas pseudoalcaligenes*, a polychlorinated biphenyls (PCBs) degrader, demonstrated positive chemotactic response to biphenyl, benzoic acid, and chlorobenzoic acids (Tremaroli et al., 2010).

Although phenolic acids are quickly decomposed by soil microflora, their addition to the soil can significantly change the soil agrochemical characteristics and microbial community composition (Liu et al., 2017; Zaimenko et al., 2021; Su et al., 2023; Zhou et al., 2025). Phenolic allelochemicals are known to inhibit ammonia oxidation by nitrifying microorganisms and enhance the mobility of soil phosphorus. In high concentration, soil phenolics can chelate heavy metals (Misra et al., 2023).

Soil amending with benzoic acid increased the relative abundance of *Bionectria* spp. and *Trichoderma* spp. and decreased the relative abundance of *Metarhizium* spp. (Liu et al., 2017). Moreover, the character of the effect may vary depending on the concentration of the phenolic acid used. For example, it has been shown that application of salicylic acid and *p*-hydroxybenzoic в concentration 2 $mg{\cdot}g^{-1}$ negatively affected the availability of soil nutrients by acidifying the soil, as reflected in the low soil pH, but enhanced soil extracellular enzyme activity, especially in cellobiohydrolase, β-1,4-glucosidase, and β-xylosidase. In lower concentration (0.5 $mg{\cdot}g^{-1}$),these acids promoted soil nutrient availability and microbial diversity(Zaimenko et al., 2021; Zhou et al., 2025)

It is possible to regulate the concentration of phenolic acids in the rhizosphere soil by including allelopathic plants in the crop rotation (Table 1), cover cropping, or using them as green manure (Zaimenko et al., 2020; Gorobets et al., 2005). These compounds are relatively resistant to decomposition and are commonly found as breakdown products in soil. The main challenge is how to maintain the required level of these allelopathicals in the rhizosphere soil, preventing their accumulation in phytotoxic concentrations. Our previous studies have shown that the addition of natural siliceous minerals allows for the control of the phytotoxicity of phenolic allelochemicals for both plants and soil microflora (Zaimenko et al., 2021). Climatic factors were also shown to modulate the effect of phenolic allelochemicals on the soil microbiome. In particular, spruce forest soil phenolics stimulated fungi and cellulose hydrolyzers during winter, while it showed no effect on fungi, inhibited cellulose hydrolyzers, and stimulated ammonifiers in summer (Souto et al., 2000).

Thus, phenolic acids significantly affect the soil agrochemical characteristics and microbial community composition: inhibit the ammonia oxidation by nitrifying microorganisms, enhance the mobility of soil phosphorus, and chelate toxic metals. The main effect of these allelochemicals is the selective suppression of sensitive microorganisms, which contributes to the increase in the competitiveness of tolerant species, including rhizobacteria and fungi with bioremediating potential. For some species of bioremediant microorganisms capable of degrading organic aromatic pollutants, phenolic acids are chemoattractants. The nature of the effect of phenolic acids largely depends on their concentration, chemical structure, climatic and edaphic factors.

Flavonoids, Cumarins, and Tannins

Flavonoids, cumarins, and tannins are polyphenol secondary metabolites considered to be important mediators of the chemical communication between higher plants and microorganisms (Stringlis et al., 2019; Pébarthé-Courrouilh et al., 2025).In particular, their role in chemical defense against phytopathogens has been demonstrated by many authors (Soledade et al., 2015; Stringlis et al., 2019; Pébarthé-Courrouilh et al., 2025). A number of the compounds mentioned above have been shown to function as phytoanticipins or phytoalexines in specific plant species (Trentin et al., 2013; Soledade et al., 2015; Tonga et al., 2022; Pébarthé-Courrouilh et al., 2025).

The polyphenols like flavonoids, cumarins, tannins enter the rhizosphere in the composition of the rainfall foliar leachates, root exudation, and litter decay products. Estimates of the polyphenol inputs into soils range from 1–85 $kg{\cdot}ha^{-1}{\cdot}y^{-1}$ for temperate meadow and forest vegetation to 479–1,710 $kg{\cdot}ha^{-1}{\cdot}y^{-1}$ in tropical ecosystems (Schmidt et al., 2013).

Soil polyphenols affect soil microbiome by serving as a carbon source for some microorganisms and inhibiting others (Okutani et al., 2020; Ghitti, et al., 2022; Tonga et al., 2022). Multivariate analysis of soil microbial diversity in several soils with long-term fertilizer treatments showed that the polyphenol concentration in the dissolved organic carbon fraction in the soil was the most important variable correlated to bacterial community diversity (Schmidt et al., 2013; Okutani et al., 2020). There are several evidences that polyphenols influence the pools and fluxes of inorganic and organic soil nutrients (Hättenschwiler & Vitousek, 2000). The most studied is the polyphenol`s regulation of soil nitrogen cycle. In particular, they were shown to inhibit nitrification as well as ammonification processes, decomposition of soil organic matter (Hättenschwiler and Vitousek, 2000; Schmidt et al., 2013; Zaimenko et al., 2025b), and either suppress or stimulate the symbiotic nitrogen (N_2)-fixing bacteria (Hättenschwiler and Vitousek, 2000). There are numerous scientific evidences indicating the potential of phenolic allelochemicals as inhibitors of soil bacteria but stimulators of microfungi and actinomycetes (Zaimenko et al., 2025b).

The antibacterial effects of polyphenols are due to their interruption of multiple bacterial processes, including the cell membrane and cell wall synthesis, nucleic acid synthesis, and energy metabolism. They can also potentiate other antibacterial compounds by inhibiting efflux pumps. The polyphenols could bind to microbial enzymes, altering nutrient cycles and soil respiration (Pébarthé-Courrouilh et al., 2025). According to the toxicity to microorganisms, polyphenols can be arranged in the following order: flavonoids <tannins <coumarins (Dehghanian et al., 2022; Yang et al., 2023). The presence of methyl and methoxy groups, as well as the formation of quinone forms, increases the toxicity of polyphenols for microorganisms.

Certain flavonoids have been shown to regulate the legume-rhizobia symbiosis by attracting nitrogen-fixing rhizobia and activating the transcription of bacterial genes coding for Nod factors affecting root morphogenesis and nodule formation (Pérez-Montaño et al., 2011; Okutani et al., 2020; Ghitti et al., 2022). Flavonoids also promote arbuscular mycorrhizal fungi spore germination, hyphal growth, and root colonization efficiency (Tian et al., 2021; Tonga et al., 2022; Ghitti et al., 2022). Flavonoids can affect microbial traits involved in rhizocompetence, such as motility and chemotaxis, or induce specialized pathways, such as the expression of the bph operon involved in the bioremediation of recalcitrant xenobiotics (Ghitti et al., 2022). The plant-derived flavonoids apigenin and phloretin have been shown to act as signalling molecules strengthening mutualistic interactions between plants and non-symbiotic beneficial rhizobacteria of *Pseudomonas fluorescens* (Yu et al., 2020). Exogenous rutin (in the concentration of 1 pM) was shown to promote the biofilm formation in *Bacillus subtilis* (Singh et al., 2016). Apigenin promoted the biofilm formation in the N_2-fixing bacterium *Gluconacetobacter diazotrophicus*, associated with the rhizosphere of rice plants (Yan et al., 2022).

Certain beneficial rhizobacteria, such as *Bacillus* sp., *Pseudomonas* sp., and endophytic fungi (*Paraconiothyrium* sp.), manifested good capacity to metabolize some flavonoids (viz. quercetin, naringin, naringenin, daidzein, and apigenin) as carbon sources. Naringenin-mediated chemotaxis was displayed by *Aeromonas* sp. (Ghitti et al., 2022). The treatment of soils with flavonoids (daidzein and quercetin) has been shown to modulate the soil microbiome: significantly reduce alpha diversity but increase relative abundance of tolerant *Proteobacteria*, in particular *Pseudarthrobacter* and *Pseudomonas strains* (for quercetin) and Comamonadaceae(for daidzein) (Okutani et al., 2020; Schütz et al., 2021). Inoculation of the host plant with *Pseudomonas*, *Bacillus*, *Rhizobium*, and *Azospirillum* has been shown to enhance the biosynthesis of polyphenols, especially flavonoids and tannins in plants (Jakubowska et al., 2025).

Exogenous tannins have been shown to suppress the development of a wide range of microbes and filamentous fungi in pure culture, with the least inhibitory doses ranging from 0.5–20.0 $g \cdot l^{-1}$ for bacteria and as low as 0.012 $g \cdot l^{-1}$ for fungi (Dehghanian et al., 2022). Antibacterial effects of tannins are due in large part to their ability to complex and precipitate bacterial proteins, associated with virulence and sporulation, such as pectinases, cellulases, amylases, β-galactosidases, lipases, proteases, laccases, etc. (Dehghanian et al., 2022; Pébarthé-Courrouilh et al., 2025), anti-membrane activity, inhibition of biofilm formation, and bacterial adhesion to the host cells (Trentin et al., 2013). Some *Staphylococcus*, *Klebsiella*, and *Bacillus* species, and certain fungal species (*Aspergillus niger*) have been shown to use tannin as a carbon source due to their capacity to produce tannase, an enzyme that breaks down complex tannins, releasing gallic acid and glucose (Dehghanian et al., 2022).

Plants excrete coumarins into the rhizosphere soil to facilitate iron uptake and shape their root microbiome by selectively inhibiting the growth of pathogenic microbes (Moormann et al., 2022). Certain species of beneficial rhizobacteria have been shown not only to tolerate this allelochemical but also to stimulate coumarin biosynthesis in roots and their excretion into the rhizosphere. In particular, it was shown that coumarin scopoletin regulates *Arabidopsis thaliana* – *Pseudomonas simiae* system induced systemic resistance and iron-uptake responses. It was found to be a dominant metabolite that is produced in the roots and excreted into the rhizosphere, where it manifested selective antimicrobial activity: inhibited soil-borne fungal pathogens and stimulated colonization of *Arabidopsis thaliana* by *Pseudomonas simiae*, a beneficial rhizobacteria such as *Trichoderma asperellum*, *Trichoderma harzianum*, which were tolerant to this compound (Stringlis et al., 2018).

Application of exogenous coumarin (in the concentration of 200 $mg \cdot kg^{-1}$) had a negligible effect on the annual ryegrass (*Lolium multiflorum* Lam.) rhizosphere soil bacterial species, but exhibited a significant effect on the abundance of certain bacteria in the rhizospheric microbial community. In particular, this increased abundance of beneficial nitrite-oxidizing (Nitrospiraceae), hydrocarbon-degrading *Polycyclovorans* sp., *Ramlibacter* sp., *Geobacter* sp., while other decomposers of organic pollutants, such as *Massilia* sp. and *Neorhizobium* sp., were inhibited (Yang et al., 2023).

The polyphenol pool in the rhizosphere soil can be managed by sowing allelopathic plants (Table 1), as well as by applying organic fertilizers containing plant waste rich in polyphenols, such as spent coffee ground, pomegranate peel, citrus fruit wastes, date palm leaves, etc. (Li et al., 2006; Chilosi et al., 2020; Consoli et al., 2023; Zaimenko et al., 2025). In particular, it was shown that soil amendment with spent coffee grounds could suppress certain phytopathogenic microorganisms (viz. *Sclerotinia sclerotiorum* and *Phytophthora nicotianae*) and provide a natural carrier for beneficial *Trichoderma* spp. (Chilosi et al., 2020). Application of biofertilizers containing plant material rich in polyphenols has been shown to boost phenolic levels in the treated agricultural crops when compared to chemical farming (Ammar et al., 2023; Consoli et al., 2023). High solar radiation in a semiarid environment favors the synthesis of phenolic derivatives (Trentin et al., 2013; Dehghanian et al., 2022).

As a component of bioremediation technology, polyphenols could play an important role due to their high biological activity and relative resistance to degradation by soil microbiota. In plant-microbe interactions, polyphenols, particularly flavonoids, play major roles in communication between plants and microbes: symbiotic signaling, triggering, or amplifying plant immune responses to phytopathogens. Flavonoids can affect microbial traits involved in rhizocompetence, such as motility and chemotaxis, or induce specialized pathways, such as the expression of the bph operon involved in the bioremediation of recalcitrant xenobiotics. High tannin levels in roots or litter can modify rhizosphere microbial communities, which in turn influence root signaling networks and nutrient cycling.Cumarins modulate root microbial communities, favoring some taxonomical groups of microbes and inhibiting others. They also act as signals of the plant's nutritional state to the microbial community.

Benzoxazinoids

Benzoxazinoids are indole-derived defense compounds characteristic of Poaceae species, though some dicot plants could also synthetise ones (Schullehner et al., 2008; Hu et al., 2018). These secondary metabolites are responsible for the allelopathic effects of the world`s economically important crops, such as maize, wheat, rye, and barley (Schullehner et al., 2008). During the last decades, they received close attention from many researchers as important herbivore and pathogen resistance factors (Hu et al., 2018). Recent studies demonstrated the important role of these allelochemicals in shaping the rhizosphere microbiome. Benzoxazinoids defend grasses from phytopathogens and could also act as chemoattractants for beneficial rhizobacteria, mycorrhizal fungi, and other soil fungi. In particular, benzoxazinoids have been shown to promote rhizosphere colonization by *Pseudomonas putida* (Neal et al., 2012), *Flavobacteria*, and Methylophilaceae (Cotton et al., 2019), and inhibit host recognition and virulence of the phytopathogens such as *Agrobacterium tumefaciens* (Maresh et al., 2006) and *Ralstonia solanacearum* (Thoenen et al., 2023).

Benzoxazinoids are not stable, and commonly are degraded by soil microorganisms within days to weeks after release. However, their breakdown products (MBOA and AMPO) are much more persistent, being detectable in soil for months to years, and could cause irreversible changes in the soil microbiome, which affect the productivity of subsequent crops during the next growing seasons (Hu et al., 2018; Thoenen et al., 2023).

Certain species of bioremediants capable of degrading hydrocarbons, aromatic compounds, and heavy metals, such as *Acinetobacter calcoaceticus* (Chase et al., 1991), *Pseudomonas putida* (Neal et al., 2012), *Chaetosphaeria* spp. (Zikmundová et al., 2002), *Bacillus mojavensis* (Bacon et al., 2007), *Pantoea* sp., *Rhizobium* spp. (Thoenen et al., 2023) can use benzoxazinoids as carbon/nitrogen sources and reduce their toxicity in soil. For *Pseudomonas putida*, benzoxazinoids acted as recruitment signals (Neal et al., 2012). Lactonase was identified as an enzyme that mediated metabolic specialisation of rhizobacteria to benzoxazinoids (Thoenen et al., 2024). The cell wall structure was also shown to be involved in the tolerance patterns of the different bacteria to benzoxazinoids and aminophenoxazinones (Thoenen et al., 2023).

The molecular mechanisms of benzoxazinoids' effects on microorganisms are largely unknown. Some authors consider benzoxazinoids' toxicity to be due to intercalation with DNA, chelation, and disruption of cell wall function (Thoenen et al., 2023). The antimicrobial activities of the different benzoxazinoid compounds were shown to be highly selective. In particular, it was shown that bacterial tolerance to 6-methoxy-benzoxazolin-2-one (MBOA), the most abundant and selective antimicrobial metabolite in the maize rhizosphere, depended on the thickness of the peptidoglycan layer. Tolerant strains belonged to the gram-positive Bacillaceae, while gram-negative Xanthomonadaceae and Rhizobiaceae were generally susceptible to MBOA (Thoenen et al., 2023).

The amounts of benzoxazinoids in the soil could be managed using intercropping and crop rotation with cereals (Table 1), or applying grain post-harvest residues as green manure.

Thus, benzoxazinoids are selective antibiotics that shape the rhizobacterial communities. Like many other specialized exometabolites of plants, benzoxazinoids have dual functions – suppressing phytopathogens and recruiting beneficial rhizobacteria, helping plants to form an optimal root microbiome. The extent to which benzoxazinoids shape the associated rhizosphere microbiome, as well as the molecular mechanisms of their effects, is still largely unexplored.

Triterpenoids

Triterpenoids are secondary metabolites produced by plants, bacteria, fungi, and marine organisms from the 2,3-oxidized squalene, manifesting a wide range of biological activities (Zhong et al., 2025). They play a prominent role in the higher plants' adaptation to biotic stress factors such as competing plants, phytopathogens, and herbivores (Wrońska et al., 2022). Multiple studies have revealed that triterpenoids secreted by higher plants and soil microbiota are involved in the formation of the rhizosphere microbiome by promoting or inhibiting the growth of specific microbial taxa (Luo et al., 2020; Zhong et al., 2022; Nakamura et al., 2025). A number of natural triterpenoids are documented for their antibiotic activity due to their destructive effects on the microbial cell membranes and cell walls, disrupting their barrier function, affecting the expression of genes involved in biofilm formation, peptidoglycan metabolism, glycolysis, synthesis of fatty acids, amino acids, peptidoglycans, and cell autolysis (Wrońska et al., 2022; Bhattacharya, et al., 2023; Spaggiari et al., 2024). Some triterpenois were shown to enhance bacterial susceptibility to other antibacterial compounds through disrupting the normal barrier function of the bacterial cell membrane(Spaggiari et al., 2024) and potentiate antibacterial effects of other allelochemicals and synthetic antibiotics (Kurek et al., 2012; Tonga et al., 2022; Wrońska et al., 2022).

Recent studies have shown that plant triterpenoids can influence the composition of endophytic microorganisms, stimulating or inhibiting certain species, while endophytic bacteria and fungi, in turn, promote host plant root growth and synthesis of triterpenoids (You et al., 2021). The selective effect of triterpenoids on free-living rhizobacteria has been shown in a number of works, indicating selective inhibition of phytopathogens andstimulation of beneficial microbes(Huang et al., 2019; Zhong et al., 2022; Nakamura et al., 2025).

Rhizobacteria associated with allelopathic plants have evolved the ability to metabolize aromatic compounds of both plant origin and anthropogenic aromatic pollutants, such as naphthalene, toluene, and 2,4-dichlorophenoxyacetic acid (Neal et al., 2012). Selective positive effect of triterpenoids on beneficial microbiota associated with their ability to inhibit antagonistic bacteria, as well as their participation in adaptation to various stress conditions (high temperature, low pH, high osmolarity, bile salts, oxidative stress, and antimicrobial peptides) (Kulkarni et al., 2015). Besides, many triterpenoid compounds have positive environmental effects. In particular, they can spontaneously assemble into stable hydrogel systems under specific experimental conditions without the need for additional crosslinking agents or any chemical modification, which optimizes soil physical and chemical properties, waterholding capacity, and prevents the leaching of mineral elements (Zhong et al., 2025). The functional groups present in triterpenoids, such as hydroxyl, carboxyl, and carbonyl groups, can interact with metal ions (e.g., Na^+, K^+, Ag^+, Mn^{2+}, Mg^{2+}, Zn^{2+}, Cu^{2+}, Fe^{2+}, Sr^{2+}, and Ga^{3+}, which play crucial roles in the structural integrity and functional regulation of the metal ion-complexed triterpenoid hydrogel (Zhong et al., 2025).

Microorganisms also synthesize and release triterpenoids into the environment, which regulate their interactions with higher plants. The most studied in this regard are hopanoids – pentacyclic triterpenoids, widespread lipid components of bacterial and microalgal membranes. Hopanoids provide mechanical rigidity to membranes and protect cells from numerous stresses, including acidic or alkaline pH, high temperature, high osmolarity, oxidative stress, toxic metals, antibiotics, etc. (Kulkarni et al., 2015). It has been shown that hopanoids play an important role in the formation cf the symbiotic system comprising the nitrogen-fixing bacteriaand the legumes (Kulkarni et al., 2015; Belin et al., 2018).

Based on the results of metagenomic analysis of soil microbiota, Ricci et al. (2014) established a significant positive correlation between the ability of bacteria and blue-green algae to synthesize 2-methylhopanoids and their association with the rhizosphere of higher plants. In particular, 43 and 63% of microorganisms with hpnP sequences were identified as bacteria, with commensal or mutualistic symbiotic types of interaction with higher plants. The application of hopanoids and hopanoid-producing nitrogen fixers to soil has been proposed and patented as a biofertilizer technique that increases environmental resistance of plant-associated microbial symbionts, including nitrogen-fixing bacteria that are essential for transforming atmospheric nitrogen to soluble forms available to crops (Newman et al., 2020).

Thus, the analysis of the scientific literature confirms the crucial role of triterpenoids of plant and bacterial origin in regulating the species diversity and ecological functional structure of the root microbiota. The application of these allelochemicals in agricultural practice may provide new methods for regulating the rhizosphere microbiome in the future. In particular, natural triterpenoids can be used to establish closer relationships between plants and agronomically beneficial microorganisms, which will contribute to a better manifestation of the desired ecological functions of the latter.

Conclusions

Allelochemicals play an important role in regulating the relationship between higher plants and the soil microbiome: they attract certain taxonomic groups of organisms and inhibit the development of others. Analysis of the literature reveals a wide range of ecological mechanisms of the observed effects of allelochemicals on soil microbiota. Allelochemicals affect the permeability of cell membranes, the integrity of cell walls, and are involved in various signaling systems of communication at different levels – cell-to-cell signaling, quorum sensing, and “inter-kingdom“ communication, can stimulate or inhibit the process of biofilm formation, nodules, and fixation of microorganisms on the root surface. They can also act on the number of rhizobacteria and fungi indirectly, through changes in pH, nitrogen and phosphorus cycles, bioavailability of mineral nutrients, and toxic metals. The character and size of allelochemicals’ effect on the soil microbiome depends on their chemical nature, concentration, edaphic and climatic conditions. For all considered in this review classes of allelochemicals (viz., organic acids, amino acids, phenolic acids, flavonoids, coumarins, tannins, triterpenoids, benzoxazinoids) selective activity was recorded in relation to various strains of rhizobacteria and fungi, which allows them to be used as a marker of the “suitability“ of plant species as host organisms in phytostimulation technologies. By regulating the pool of allelochemicals in the soil, it is possible to influence the species diversity and ecological functional structure of the root microbiota. The implementation of these allelochemicals in bioremediating practice can provide new methods for rhizosphere microbiome regulation. In particular, natural organic acids, amino acids, flavonoids, and triterpenoids can be used to establish closer links between plants and agronomically useful nitrogen-fixing microorganisms, which will contribute to a better manifestation of the desired ecological functions of the latter.

Conflicts of Interest

The authors declare no conflict of interest.

Ethical Statement

This article doesn’t contain any studies that would require an ethical statement.

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