



Available online at www.sciencedirect.com

ScienceDirect



REVIEW

The rhizosphere microbial complex in plant health: A review of interaction dynamics



Oluwaseyi Samuel OLANREWAJU, Olubukola Oluranti BABALOLA

Food Security and Safety Focus Area, Faculty of Natural and Agricultural Sciences, North-West University, Mmabatho 2735, South Africa

Abstract

Climate change, urbanization, and population increase limit food availability. To sustain human existence, there is the need to increase food and agricultural production to mitigate the impact of these factors. Scientists have been working for years on ways to increase food production. From plant breeding techniques to soil science, scientists have made tremendous progress. The rhizobiome has been proven to be important to crop production, and the impact of the rhizobiome on plant health cannot be overemphasized. Being rich in diverse complex microbial interactions, the rhizosphere has become a major force in recent plant growth promotion studies. The upsurge in next-generation sequencing applications with the various “omics” technologies is helping to unearth information relating to rhizosphere impact on plant growth. Explaining the complex interactions between and across microbial species present in the rhizosphere is important to further enhance our understanding of their mechanistic and mutualistic functions. Knowledge from this can be used in rhizosphere biome engineering for improved plant growth and yield in the face of the various biotic and abiotic challenges.

Keywords: below-ground interactions, climate change, plant growth promotion, plant microbiome, root exudation

1. Introduction

The world population is increasing at an alarming rate such that it seems almost impossible to meet human food demand. With the population set to eclipse 10 billion by 2050, there is an increased pressure on researchers to

find lasting solutions to the looming food shortage that will be experienced. Plant biologists especially have been feeling the weight of the responsibility of finding lasting solutions. Climate change and urbanization are important contributing factors (Tiwari *et al.* 2016) to the slow progress seen in the improvement of food production. Increased temperature, salinity, and drought are among the effects of climate change on the environment. Climate change affects crop growth and development (Knox *et al.* 2012), hence disrupting yield and food availability. There is therefore a dire need to find lasting solutions to improve crop production to sustain human existence.

The soil is composed of diverse species of microorganisms (Olanrewaju 2016). Organisms ranging from prokaryotes to eukaryotes are present in the soil (Lee *et al.* 2017). These organisms can either be

Received 21 April, 2021 Accepted 19 August, 2021
Correspondence Olubukola Oluranti BABALOLA, E-mail: olubukola.babalola@nwu.ac.za

© 2022 CAAS. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).
doi: 10.1016/S2095-3119(21)63817-0

beneficial or pathogenic in nature. Beneficial organisms play fundamental roles either as single organisms (Egamberdiyeva 2007; Esitken *et al.* 2010) or collectively as a consortium (Wang *et al.* 2012; Shilev *et al.* 2020) of organisms to promote plant health through disease suppression and growth promotion (Olanrewaju 2016; Olanrewaju and Babalola 2019a). Many researches have affirmed the role of microorganisms, especially bacteria and fungi, in plant growth promotion (Jeon *et al.* 2003; Richardson *et al.* 2009; Ortiz *et al.* 2015; Bakhshandeh *et al.* 2020). These microorganisms are termed plant growth-promoting microorganisms (PGPM) (Olanrewaju *et al.* 2018). Various mechanisms by which PGPM aid plant health have been studied (Beneduzi *et al.* 2012; Ahemad and Kibret 2014; Glick 2014; Olanrewaju *et al.* 2017; Backer *et al.* 2018), however, a full understanding of these mechanisms, especially at the molecular level, has not been well established yet. Research in understanding how plants respond to or recruit PGPM to their root systems is still at the early stage. Interactions between the PGPM are relatively unknown. This knowledge will be fundamental for the development and use of rhizobiome engineering. Plants recruit PGPM by exuding compounds through their roots that act as signal molecules (Beneduzi *et al.* 2012; Olanrewaju *et al.* 2018). Various factors can trigger the release of these exudates by plants (Olanrewaju 2016). PGPM in turn, respond to the signal sent and accumulated in the rhizosphere forming the rhizosphere microbial community. Thus, the plants shape their rhizobiome (Berendsen *et al.* 2012) and each plant has a distinct rhizobiome which depends on the exudates released. The plant's rhizobiome can vary depending on the developmental stage (Zhao *et al.* 2012). Plants release exudates in the form of metabolites and volatile compounds; however, it is unknown whether the exudates are non-specific, attracting all microbes, or are specific to the genus or species of the microbes they attract. Further, it is not known if a form of chain reaction of attractions and recruitment occurs based on the released exudates. Additionally, there are both beneficial and non-beneficial microorganisms present in the soil, but it is not known how (or if) exudates differentiate between them when microbes are recruited to the rhizobiome. All of these are key points that need to be resolved to improve our understanding of the below-ground interactions that affect plant health.

Many microbes establish beneficial interactions with plants including endophytes (Kumari and Bharat 2018). In this review, we focused on plant responses (pattern-triggered and effector-triggered responses) to pathogen attack and use of root exudates to recruit beneficial

microbes. We also reviewed the interactions between beneficial, pathogenic, and mutualistic microbes in the rhizobiome that could improve plant disease resistance.

2. Pattern-triggered responses

Plants rely on the immunity of each cell and the signals emanating from sites of pathogen attack for defense from pathogen invasion (Salguero-Linares and Coll 2019). The plant immune system consists of regulatory proteins working alone or in cooperation to exert control against disease infestations (Nimchuk *et al.* 2003).

One branch of the plant immune system uses pattern recognition receptors (PRRs) (Jones and Dangl 2006). PRRs respond to microbe-associated molecular patterns (MAMPs) or pathogen-associated molecular patterns (PAMPs) (Newman *et al.* 2013) such as flagellin and chitin. The second branch of the immune system acts inside the cell. It uses the nucleotide-binding leucine rich repeat (NB-LRR) proteins, which are encoded by most R genes (Eitas and Dangl 2010). They are related to the animal CATERPILLER/NOD/NLR protein 7 and STAND ATPases (Jones and Dangl 2006). The NB-LRR proteins recognize the different effector molecules from various pathogens and activate the defense responses. Although NB-LRR proteins are effective against obligate biotrophs, they are, however, not effective against pathogens acting at the site of host colonization, i.e., the necrotrophic pathogens (Jones and Dangl 2006).

For pathogens to access nutrients from host plants and proliferate, they must damage plant cells (Doughari 2015). Sugar, which is the main nutrient sought by pathogens (Mercier and Lindow 2000), is located within the apoplastic space (Naseem *et al.* 2017). Therefore, pathogens must degrade plant cellular materials before they can get it. However, this is not so simple because pathogens must overcome the first layer of plant immunity, PAMP-triggered immunity (PTI), which is triggered on pathogen invasion (Gupta *et al.* 2020). If it can overcome the PAMP-triggered immunity, then the second phase of the plant immune system, effector-triggered immunity (ETI), is activated (Nguyen *et al.* 2021).

2.1. PAMP-triggered immunity

Plant response to invaders differs from the way mammals and invertebrates respond because plants do not have acquired immune systems, which might have allowed them to recognize external-invaders to elicit pathogen-specific responses. Plants depend on immune receptors on plasma membranes, which sense PAMPs and MAMPs

(Wan *et al.* 2019). Detection of PAMPs triggers a change in the cell which is activated by PRRs and these lead to a cascade of responses through the recognition of the conserved microbial molecules which leads to resistance from the plants. ETI is activated as soon as pathogens overcome the PTI defense system (David *et al.* 2019).

2.2. Effector-triggered immunity

Failure of PTI to stop pathogen invasion activates the release of effectors by pathogens. Different effectors have different ways of carrying out their actions, for example, some effectors are injected into the host cell cytosol by Type III proteins while some make use of haustoria (Xu *et al.* 2020). Haustoria connected to the host cell plasma membrane serve in carrying effectors from the pathogen. When the NB-LRR proteins in the host cell cytoplasm recognize these pathogenic proteins, there is an activation of the plant's second immunity, which is the ETI (Khan *et al.* 2020a). NB-LRRs are specific in their binding interactions because of their richness in leucine.

Along with the plant's inbuilt mechanisms to fight off invading pathogens, plants also rely on the support of its rhizobiome. The plant's rhizosphere community has been said to be its second genome (Berendsen *et al.* 2012). Any change in the plant because of pathogen invasion or negative environmental factors causes an action from the rhizobiome.

3. Unifying diversities in the rhizosphere: Role of root exudates

Although rhizosphere microorganisms differ in traits and phylogeny, they co-exist and operate together despite their divergencies. The complexity of the soil and its richness in nutrients makes it a favorable environment for various forms of life to exist. Microorganism interactions, co-existence, and “divergence-overlook” in the rhizosphere are controlled by signals released from plants through the roots into the rhizosphere (Berendsen *et al.* 2012; Olanrewaju *et al.* 2018). These signaling compounds are called exudates. The root systems of plants acquire water and nutrients from the soil while also releasing low and high-weight molecular compounds (Olanrewaju 2016).

Root exudates which include secondary metabolites, volatile organic compounds, sugars, hormones, and primary metabolites among others (Rolfe *et al.* 2019), act as catalysts or activators of interactions in the rhizosphere thereby shaping the rhizosphere microbial communities (Olanrewaju *et al.* 2018; Rolfe *et al.* 2019). These

exudates are not always passively released and release activators such as pathogen attack, and nutrient and water deficiency may stimulate the release of exudates. Although research into the molecular mechanism of root exudate release is on-going, it is believed that these exudates are crucial to the recruitment of the rhizobiome. The means by which exudates diffuse through the soil and target required microbes remains unresolved. Further, it is not yet established how exudates signal the appropriate microbes to meet the plant's needs. For example, there are microbes that are good biocontrol agents, but inefficient growth promoters and *vice versa*. In a situation where exudates are released because of pathogen attack, the question of how the signals attract appropriate biocontrol agents to help the plant in suppressing the pathogens arises. Such questions require answers before a full understanding of plant–microbe interactions is achieved.

Root exudates majorly serve as signals to recruit microbes to the rhizosphere irrespective of microbe species. The only requirement of the exudates is that the plant's needs are met. Different conditions lead to the release of different exudates from plant roots. The microbes are unified in their response to the exudates to help the plant (Fig. 1). The plant in turn provides nutrients for the microbes for their survival (Olanrewaju *et al.* 2017). Signal molecules that plants use in seeking help from the rhizosphere microbes have been reported in some studies (Korenblum *et al.* 2020). Studies on this aspect of plant growth promotion by microorganisms are still in its early stage. The signals are in the form of flavonoids, jasmonic acids, strigolactones and hormones such as auxins and gibberellic acids.

4. Rhizobiome response to plant signals

Individual organisms each play a unique role in the rhizobiome that can be beneficial or detrimental (Fig. 1). Beneficial roles promote microorganism abundance and coexistence, whereas harmful roles promote discriminating and parasitological reactions, such as the formation of bacteriophages by viruses and bacteria (Sharma *et al.* 2019). Some bacteria are killed, while others are rendered obsolete; in either case, these bacteria no longer have control over their actions and, as a result, cannot have a positive impact (Argov *et al.* 2017).

Different signaling molecules are transmitted to the soil and are specific for the beneficial microbes they attract to the rhizosphere. This synergistic effect along with the various PGPM mechanisms of plant protection

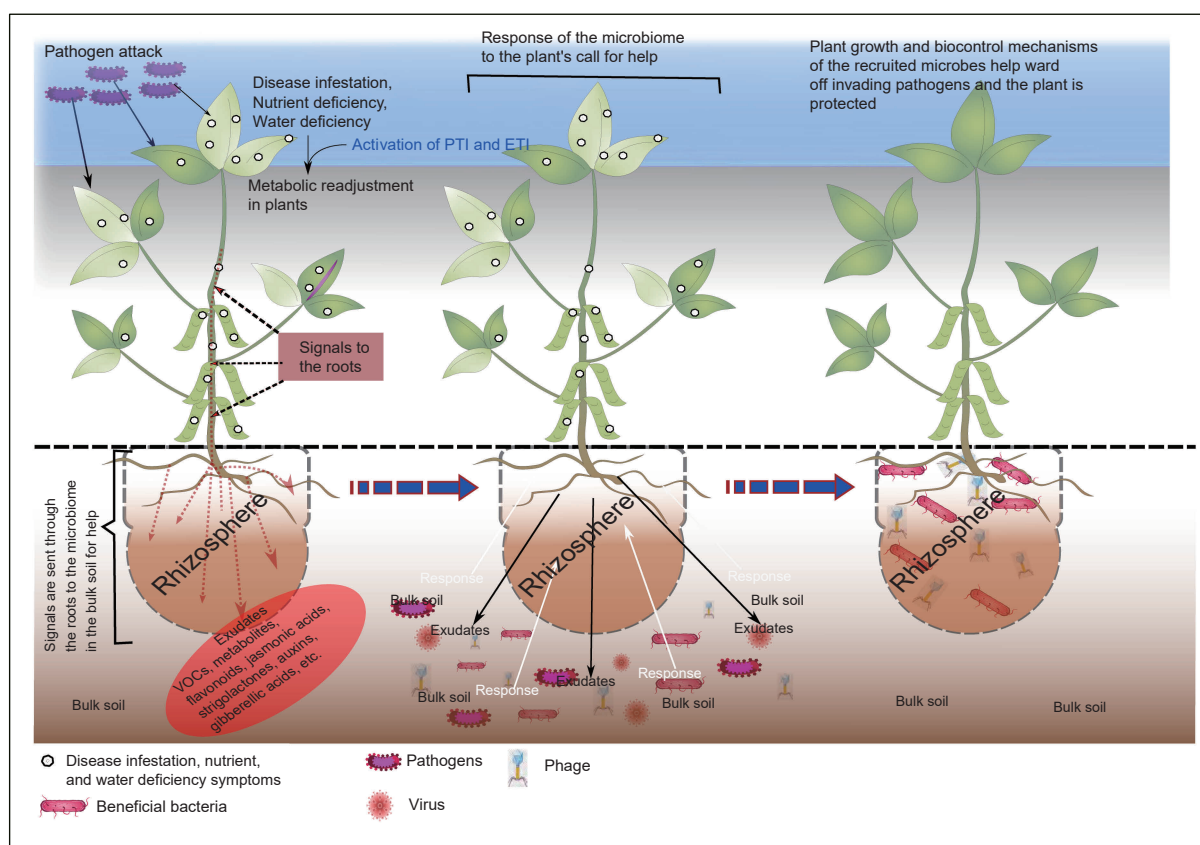


Fig. 1 Soil microbiome response to plant signals. Left panel, plant signals to the soil microbiome arising from pathogen attack, nutrient, or water deficiency; centre panel, the response of the various microorganisms to the exudates released by the plant; right panel, plant growth response to biocontrol mechanisms provided by recruited microbes. There is a positive response as pathogens do not respond to the signals.

is one means of reducing the number of pathogens in the rhizosphere. The ability of PGPM to outnumber the pathogens is very crucial for their successful colonization and dominance of the rhizosphere to effectively eradicate pathogens, thereby protecting their host plant.

4.1. Positive interactions

The role of individual microbes and consortia groups in mutual protection cannot be overlooked. This however directly or indirectly affects plant growth through various plant growth-promoting mechanisms (Olanrewaju 2016; Olanrewaju *et al.* 2017). Individual microbes in their way portray traits that either allow for co-existence with other microbes, or dominance such as that expressed by phages on some bacteria, which suppresses the activities of other microbes. Positive interactions, therefore, allow for co-existence among individual microbes because of mutual relationships developed. Protists are another class of microbes that aid the plants in fighting pathogen attacks (Xiong *et al.* 2020). They have been well studied

in aquatic ecosystems but not well studied in the soil, partly because of the difficulty in extracting them (Gao *et al.* 2019).

4.2. Negative interactions

Microbes fight for dominance and survival to establish themselves in the rhizosphere. They fight for nutrients, and produce toxic compounds against other microbes. The toxic products suppress the activities of these other microbes or kill them off completely. Production of antibiotics (Minden *et al.* 2017), volatile organic compounds (Olanrewaju 2016; Olanrewaju *et al.* 2018), and siderophores (Babalola *et al.* 2019), are common mechanisms employed by these microbes to achieve dominance. This type of interaction has negative impacts on the survival of other microbes in the rhizosphere.

4.3. Phage interactions

Recently, phage diversity, types, phylogeny, morphology,

roles in the rhizosphere, and evolutionary relationships have been extensively reviewed by Dion *et al.* (2020), and Pratama *et al.* (2020). Phages are present in all environments, including aquatic and extreme environments. They used to be regarded as having small genomes, but the advancement in genomic tools have shown phages with a wider range of genome sizes, with some regarded as jumbo phages (Yuan and Gao 2017). Phages attack bacteria and take over their host genome. This interaction can be parasitic or mutualistic as some phages kill their host while some do not. In the rhizobiome, phage interactions may reduce the bacteria community through infection (Suttle 2007). It is beneficial to the rhizobiome if the phages are not pathogenic, as they can fight off invading pathogens. However, if the phages take up pathogenic bacteria the phages become pathogenic. Depletion of beneficial bacteria that help the plant can also occur because of the actions of the phages. This ultimately reduces the ability of the rhizobiome to protect their host. Phages are highly specific in their choice of host bacteria (Peng *et al.* 2020) as well as plant genotype (Morris *et al.* 2020). Phages have long been considered as antibacterial agents. Therefore, phage-bacteria interaction is an area that needs focused attention from researchers. This is an outstanding interaction that has not been explored in plant health.

5. Complex interactions in the rhizobiome that improve plant health

The rhizobiome harbors many complex interacting organisms that drive functional activities that have a positive impact on plant health. Although not considered because they are out of the scope of this review, plant-plant interactions, which involve allelochemicals, are one of the predominant interactions in the soil. It is worthwhile mentioning that allelopathy originates in the rhizosphere through the roots of one plant impacting the roots of another plant. These interactions are exclusive between plants alone. We will consider other important interactions that are specific to the rhizobiome such as interactions between the various microbes that exist in the rhizosphere. Bacteria, fungi, viruses, and archaea, among others, are present in the rhizosphere. These organisms interact together and their interaction has an effect on the rhizobiome (Fig. 1).

Quorum signaling/sensing (QS) involves the communication and coordination of microbe activities using molecules that act as signals. These molecules must be at a sufficient concentration to induce a response from the receiving microbe(s). Signaling can occur between pathogen-beneficial microbes, pathogen-

pathogen microbes, and beneficial-beneficial microbes. QS is required for successful adaptation by both beneficial and non-beneficial microbes to the host environment. Among the key mediators of QS, especially in gram-negative bacteria, are *N*-acyl-L-homoserine lactones (AHLs). They are produced by bacteria and diffuse through the membranes into the rhizosphere, and plants have been reported to produce metabolites that mimic the actions of AHLs (Hassani *et al.* 2019). Canavanine, a toxic arginine analogue to many bacteria except rhizobia, is present in root exudates of some legumes (Worst *et al.* 2015). It is used for selective purposes by legumes to control their rhizosphere bacterial populations (Swamy *et al.* 2016). They use it to select for beneficial rhizobia and remove other bacteria genera from their rhizosphere (Swamy *et al.* 2016). Another mimicking compound that is secreted by *Combretum albiflorum* is catechin, which is reported to interfere with the signaling of *Pseudomonas aeruginosa* PAO1 (Vandeputte *et al.* 2010). Catechin is a flavonoid used by the plant as the first line of defense against invading pathogens. Some PGPM use this mechanism of signal disruption in controlling pathogens. By disrupting the signaling between pathogens, they can disrupt the expression of virulence genes. In addition, rhizosphere QS can be disrupted by abiotic factors such as alkaline pH (Rana *et al.* 2020). The secretion of AHLs by PGPM can also induce systemic resistance in the host plants. For example, *Serratia liquefaciens* MG1 and *Pseudomonas putida* IsoF secrete AHLs that initiate induced systemic resistance (ISR) against *Alternaria alternata* in tomato plants using the SA and ethylene-dependent pathways (Schuhegger *et al.* 2006).

For PGPM to exert their effects on host plants, they must be able to successfully colonize their host plants (Olanrewaju 2016; Olanrewaju *et al.* 2017) and the activities of these PGPMs are influenced by the exudates from the roots which is termed the 'rhizosphere effect' (Bais *et al.* 2006). Plants provide a carbon source which informs a chain of signals for the microbes and subsequently for microbe colonization.

6. Plant growth promoting bacteria (PGPB) in plant health and stress alleviation

The rhizobiome plays an important role in improving plant health by helping in the control of pathogens, stimulation of plant growth, nutrient acquisition, and alleviation of biotic and abiotic stress. The roles played by the rhizobiome are key to plant survival. Beneficial microbes employ several mechanisms to carry out their plant growth promoting activities. These mechanisms

can act directly on the plants (through the production of direct-acting compounds and making nutrients available) or indirectly through control of pathogens by producing metabolites against these pathogens (Ahemad and Kibret 2014). They are also directly or indirectly involved in abiotic stress mitigation. The mechanisms of action and their role in stress alleviation, plant growth, and pathogen control have been extensively covered in various reviews (Saharan and Nehra 2011; Beneduzi *et al.* 2012; Kaushal and Wani 2016; Turan *et al.* 2016; Ilangumaran and Smith 2017; Olanrewaju *et al.* 2017; Ojuederie *et al.* 2019; Zhu *et al.* 2020), therefore, we will only present an overview in the present review.

6.1. Modulation of plant hormones

In plants, phytohormones function as chemical messengers playing key role in plant physiology and development. These hormones include auxin, gibberellins, ethylene, cytokinins, and abscisic acids (Müller 2021). Others are jasmonic acid, brassinosteroids, and salicylic acid (Olanrewaju *et al.* 2018). Some rhizosphere microbes produce phytohormones that promote plant growth and development (Beneduzi *et al.* 2012; Ahemad and Kibret 2014; Olanrewaju 2016; Turan *et al.* 2016; Backer *et al.* 2018; Ojuederie *et al.* 2019).

Indole acetic acid (IAA) is the most well characterized form of auxin produced by bacteria and plants. It promotes apical dominance, cell division and elongation, seed germination, and root development. It is important for photosynthesis, stress resistance, and metabolite synthesis (Khan *et al.* 2020b; Teklić *et al.* 2021). More than 80% of rhizosphere bacteria synthesize IAA. The three main pathways of IAA biosynthesis are discussed in other studies (Di *et al.* 2016; Olanrewaju *et al.* 2017; Morffy and Strader 2020), hence it will not be a focus in this study.

Auxin producing PGPB modulate plant response by increasing IAA synthesis. This was reported in the study of Liu *et al.* (2016) on cucumber inoculated with *Bacillus amyloquefaciens* strain SQR9 in which inoculation resulted in an increase in tryptophan and subsequently in IAA synthesis. As a result of the increased IAA synthesis, the cucumber growth was improved. Similar reports of increased growth promotion through auxin synthesis by IAA have been reported by Prashanth and Mathivanan (2010), Dey *et al.* (2004) and Castaldi *et al.* (2021).

Auxin-producing PGPB are involved in mitigation of deleterious effects of biotic and abiotic stresses (Kaushal and Wani 2016; Ilangumaran and Smith 2017). They mitigate the impacts of these stresses on crop growth and development. Drought stress affects nutrient and mineral

transport in plants (da Silva *et al.* 2011) and hence slows plant development or in some cases causes plant death. The ability of auxin-producing PGPB to mitigate the effect of these stresses on plants improves plant health and production (Guo *et al.* 2021). Salt stress on the other hand inhibits the synthesis of phytohormones (Figueiredo *et al.* 2008), therefore IAA-producing PGPB can be effective in mitigating the impact of salt stress on plants.

Cytokinins are involved in apical dominance, nodule formation, seed germination, root elongation, and vascular development (Osugi and Sakakibara 2015), while gibberellins are involved in flowering, leaf expansion stem elongation, embryogenesis, and fruit ripening (Gaba 2005). Synthesis of cytokinin in the rhizosphere by cytokinin-producing PGPB increases cytokinin concentration in the soil resulting in plant growth stimulation. Plant growth stimulation by cytokinin and gibberellin produced by PGPB has been shown in various studies.

6.2. PGPB in nutrient acquisition

Macro- and micro-nutrients are involved in important physiological and biochemical processes such as cell division, cell development, respiration, fruit quality, grain quality, enzyme functioning, and biosynthesis of macromolecules (Hakim *et al.* 2021). Phosphorus, zinc, iron, and nitrogen are all essential for plant physiological and biochemical processes. Phosphorus and nitrogen are important constituents of nucleic acids. In addition, phosphorus is an integral part of the cell energy carrier molecules viz ATP, ADP, NADP, and NADPH (Fredeen *et al.* 1990). Phosphate solubilizing bacteria present in the soil are actively involved in the solubilization process of inorganic phosphates, thereby making them available for plant use (Alori *et al.* 2017). Several phosphate solubilizing bacteria genera have been reported such as *Bacillus*, *Pseudomonas*, *Enterobacter*, *Klebsiella*, and *Xanthomonas*. Plant growth promotion by phosphate solubilizing bacteria has been extensively reviewed (Rodríguez and Fraga 1999; Zaidi *et al.* 2009; Billah *et al.* 2019). Valetti *et al.* (2018) reported the increase in rapeseed yield upon inoculation with phosphate solubilizing bacteria.

Nitrogen can be taken up by plants only in the form of ammonium and nitrate. Free living and symbiotic nitrogen fixing bacteria convert atmospheric nitrogen to ammonia for plant use (Babalola *et al.* 2017). *Rhizobium*, *Bradyrhizobium*, *Ensifer*, *Azorhizobium*, and *Frankia* are symbiotic nitrogen fixing bacteria genera in association with selected plant species such as legumes. Free-living non-symbiotic bacteria genera include *Arthrobacter*,

Azoarcus, *Azospirillum*, *Azotobacter*, *Enterobacter*, *Mitsuaria*, and *Pseudomonas* (Mahmud et al. 2020). Inoculation with nitrogen-fixing bacteria promote growth and yield of many legume species (Xu et al. 2018a; Ke et al. 2019). Furthermore, PGPB stimulating the upregulation of nitrate transporter genes for effective uptake of nitrate was reported in *Arabidopsis* (Kechid et al. 2013). They reported upregulation of nitrate transport genes *NRT2.5* and *NRT2.6* when *Arabidopsis* was inoculated with *Phyllobacterium brassicaearum* upregulated nitrate transport genes *NRT2.5* and *NRT2.6* (Kechid et al. 2013). Similar findings were reported by Lee et al. (2020) upon inoculation of *Arabidopsis* was inoculated with *Bacillus subtilis* strain L1. In addition, they reported growth promotion in *Arabidopsis*, *Lactuca*, and *Triticum* upon inoculation with *Bacillus subtilis* strain L1 (Lee et al. 2020).

6.3. PGPB as biocontrol agents

Pathogens are a threat to global crop production leading to high use of pesticides and fungicides for their control. Application of pesticides and fungicides has contaminated the soil and waterways (Hakim et al. 2021) and their usage is not sustainable for the environment or for human health. Application of PGPB for pathogen control is environmentally friendly and sustainable. PGPB help plants fight pathogens through various ways such as ACC-deaminase production, siderophore production, lytic enzyme production, antibiosis, and induced systemic resistance (Glick 2014; Olanrewaju et al. 2017; Backer et al. 2018).

Production of ACC-deaminase Pathogen infection stimulates increased ethylene concentrations in plants leading to oxidative stress, nutrient deficiency, decreased metabolism, and death (Verma et al. 2021). PGPB with 1-aminocyclopropane-1-carboxylate (ACC) deaminase production potential confer resistance to ethylene-triggered stress conditions in plants. In a conducive environment, ethylene regulates normal cell function and development but during pathogen infestation, ethylene level increases, leading to chlorosis, senescence, and plant growth inhibition (Gupta and Pandey 2019). ACC deaminase producing PGPB prevents the production of ethylene from ACC by degrading ACC into ammonia and α -ketobutyrate, thereby alleviating the effect of stress responses caused by increase in ethylene concentration (Honma and Shimomura 1978). Several studies have reported the benefit of ACC producing PGPB on plant defense and stress alleviation (Nascimento et al. 2013; Glick 2014; Gamalero et al. 2017).

Production of siderophores Siderophores are iron-chelating compounds that have the potential to provide

iron for plant use. PGPB that can produce siderophores enhance plant growth and development through the scavenging of iron and other nutrients in the soil for plant use (Olanrewaju et al. 2017). The scavenging of these nutrients limits their availability for use by pathogens in the rhizosphere, endosphere, or phyllosphere of plants. Unavailability of nutrients for the pathogens effectively reduces their activity and might consequently lead to their death. Several siderophore producing bacteria that improve plant growth through pathogen control have been reported (Olanrewaju 2016; Ferreira et al. 2019). Kumar et al. (2018) reported growth promotion in wheat upon inoculation with siderophore producing rhizobacteria and Ghavami et al. (2017) also reported that inoculating canola and maize with siderophore-producing *Micrococcus yunnanensis* and *Stenotrophomas chelatiphaga* increased growth and iron content.

Antibiosis Antibiotic production is one of the most effective mechanisms for biocontrol used by PGPB. These antibiotics are secondary metabolites produced by PGPB in response to plant exudates, low nutrient, or pathogen attack (Olanrewaju et al. 2018). Lipopeptides produced by *Bacillus* and *Pseudomonas* have been investigated for their potential for use in the biocontrol of various plant pathogens (Olorunleke et al. 2017; Mejri et al. 2018; Dunlap et al. 2019; Liu et al. 2020). These lipopeptides help in the control of fungal, bacteria, protozoa, and nematode pathogens. Different genera of PGPB produce different antimicrobial compounds that act against various pathogens. 2,4-Diacetylphloroglucinol (DAPG), produced mainly by pseudomonads, is one of the most extensively studied antibiotics. DAPG acts on pathogens such as *Pythium* sp. by damaging their membranes and preventing zoospore formation (Pal and Gardener 2006).

Lytic enzyme production Lytic or cell-wall degrading enzymes destroy the integrity and stability of pathogen cell walls, thereby preventing the development of the pathogens. Lytic enzymes produced by PGPB include lipases, phosphatases, proteases, glucanase, and chitinases (Olanrewaju et al. 2017), and through the actions of these enzymes, PGPB protect plants against major pathogens such as *Sclerotium rolfsii*, *Botrytis cinerea*, *Fusarium oxysporum*, *Pythium ultimum*, *Phytophthora* sp., and *Rhizoctonia solani* (Wahyudi et al. 2011; Olanrewaju and Babalola 2019a). Bacteria isolates *Pseudomonas aeruginosa* JO and JO7 have been found to inhibit the growth of the pathogens *Fusarium oxysporum* f. sp. lycopersici and *Alternaria solani* on tomato plant (Paramanandham et al. 2017). Dukare and Paul (2021) reported that *Pseudomonas* sp. NS-1, which produces various cell wall degrading enzymes, inhibited the growth of *Fusarium udum*. Streptomyces

strains have also been reported to produce cell wall degrading enzymes that inhibit growth of plant pathogens (Olanrewaju and Babalola 2019b; Wonglom *et al.* 2019).

Another important biocontrol mechanism of PGPB is ISR. The mechanisms used by PGPB in ISR are reported in the studies cited in Section 6.0 above.

6.4. Role of PGPB in stress alleviation

Drought stress alleviation Various studies have reported the ability of PGPB to alleviate drought stress. To alleviate drought stress, PGPB adopt the following mechanisms: phytohormone production, ACC deaminase enzyme production, induced systemic resistance, and production of exopolysaccharides (Ojuederie *et al.* 2019). PGPB induces the production of abscisic acid (ABA) which is an important hormone in plant drought tolerance. Inoculation with beneficial microbes reduces the effects of antioxidants produced during drought stress (Hakim *et al.* 2021). *Azospirillum brasilense* has been found to mitigate the negative effect of drought stress on *Arabidopsis thaliana* by increasing ABA production (Cohen *et al.* 2015). *Bacillus* spp. HYD-B17, HYTAPB18, HYDGRFB19, BKB30, and RMPB44 increase the biomass, relative water content, leaf water potential, root adhering soil/root tissue ratio, aggregate stability, and proline, sugar and free amino acid concentrations and decrease water loss and electrolyte leakage of maize plants (Vardharajula *et al.* 2011).

Salinity stress alleviation Salinity leads to osmotic stress, poor nutrient availability, generation of reactive oxygen species, ion toxicity, cell damage, and an increase in ethylene level (Alexander *et al.* 2019). Arid and semiarid regions of the world are more affected because of inadequate rain (Glick *et al.* 2007). Among the methods employed in tackling the effect of salinity on crops, the use of halotolerant plants and PGPB are the most environmentally friendly (Fazeli-Nasab and Sayyed 2019). Studies with *Bacillus megaterium* NRCB001, *Bacillus subtilis* subsp. *subtilis* NRCB002, and *Bacillus subtilis* NRCB003 have shown improved plant growth of *Medicago sativa* under salinity stress (Zhu *et al.* 2020). Detailed information on salinity stress and amelioration by plant growth promoting rhizobacteria is provided in the study of Abbas *et al.* (2019).

7. Unravelling the rhizobiome complex: past and future

A search into the studies on the plant rhizosphere microbiome on Google Scholar and PubMed using the search word “rhizobiome” returned a result of

18 591 and 1 230 reports, respectively. These reports contained both review and research studies but for the sake of the present review, we were only interested in research studies undertaken to determine how research on the plant rhizosphere has evolved. We also removed those studies that did not exclusively deal with the plant rhizosphere and plant health. Some of the studies were selected (from 1981 to 2020 using the keyword “rhizobiome”) and are presented in Table 1, progressing from the most recent to the oldest.

As indicated by the number of publications, it was after 2010 that interest in rhizosphere studies developed strongly (Table 1). The majority of the studies focused on the structure and variability of the microbiome as affected by plant genotype, plant age, nutrient availability, soil type, and water availability (Simonin *et al.* 2020). Fewer studies focused on biocontrol, bio-fertilization, and bioremediation (Srivastava and Singh 2014; Babalola *et al.* 2019).

Very recently, research focus has shifted to an in-depth analysis of individual organisms due to the advancement in technology and reduction in the cost of genome sequencing. This is necessary to fully identify the characteristics of rhizosphere microbes to understand the interactions between them (and between the microbes and host plants). Techniques such as genomics, transcriptomics, metagenomics, proteomics, and metabolomics are at the forefront of microbiome research to unravel the complex interactions in the rhizobiome.

Co-colonization is one key factor to the success of the rhizobiome in improving plant health, and a few studies have identified this trait as an indicator of a sustainable rhizobiome. Fewer studies have gone further to explain the mechanisms involved in successful co-colonization, which forms the basis for complex interactions in the rhizosphere. In the study of Molina-Santiago *et al.* (2019), the extracellular matrix of *Bacillus subtilis* was reported to prevent *Pseudomonas* invasion as well as improve/modulate co-colonization of plant growth-promoting bacteria genera on melon. The rhizosphere is the microbial hot zone in the soil and several genera of bacteria, fungi, and other beneficial organisms are drawn to this zone along with non-beneficial organisms. Competition, and production of antibiotics, toxins and other compounds are all part of the mechanism used by a single microbe to survive (Ahemad and Kibret 2014; Babalola *et al.* 2019). Co-colonization can also add more insight into the resistance mechanisms adopted by some pathogens, as shown in the clinical trial of Marchaim *et al.* (2012). In their study, they reported an increase in antibiotic resistance and mortality rate in co-colonization of patients with carbapenem-resistant *Enterobacteriaceae* and *Acinetobacter baumannii* or *Pseudomonas aeruginosa*. Although this study was

Table 1 Results of a search of studies on the rhizosphere focusing on the rhizobiome and plant health from Google scholar and PubMed

Study details			
Search engine			
Year	PubMed	Google scholar	
Title of article			
Inferences from the study			
Reference			
2011–2020	1 204	16 300	Korenblum et al. (2020)
Rhizobiome mediates systemic root metabolite exudation by root-to-root signaling			
Soil indigenous microbiome and plant genotypes cooperatively modify Soybean rhizobiome assembly			
The structure and function of the global Citrus rhizobiome			
Rhizobiome metagenomics of gray mangroves (<i>Avicennia marina</i>) in the red sea			
Deciphering the rhizobiome for disease-suppressive bacteria			
Diversity and heritability of the maize rhizobiome under field conditions			
Comparative metatranscriptomics reveals kingdom level changes in the rhizobiome of plants			
Deciphering the rhizobiome for disease-suppressive bacteria			
2001–2010	22	1910	Mendes et al. (2011)
Effects of <i>Azospirillum brasilense</i> with genetically modified auxin biosynthesis gene ipdC upon the diversity of the indigenous microbiota of the wheat rhizosphere			
Spatial variation of active microbiota in the rice rhizosphere revealed by in situ stable isotope probing of phospholipid fatty acids			
Structure and activity of bacterial community inhabiting rice roots and the rhizosphere			
Linking microbial community dynamics to rhizosphere carbon flow in a wetland rice soil			
1991–2000	3	322	Lu et al. (2006)
Stability in natural bacterial communities: II. Plant resource allocation effects on rhizosphere diazotroph assemblage composition			
Increased killing of <i>Bacillus subtilis</i> on the hair roots of transgenic T4 lysozyme-producing potatoes			
Effect of root exudates and bacterial metabolic activity on conjugal gene transfer in the rhizosphere of a marsh plant			
Movement of <i>Pseudomonas aureofaciens</i> from the rhizosphere to aerial plant tissue			
1981–1990	1	29	Lu et al. (2004)
Chemotaxis of fluorescent <i>Pseudomonas</i> spp. to soybean seed exudates in vitro and in soil			
Induction of root exudation through a systemic root–root signaling mechanism by the rhizobiome			
This study shows the relationship between genotypes and the rhizobiome with the focus on soybean			
Using both amplicon and shotgun deep sequencing technologies, this study reports a comprehensive coverage of the structural and functional composition of the <i>Citrus</i> rhizobiome			
This study was the first to look at the function of the microbiome and the microbial diversity in the rhizosphere and soil of gray mangrove using unbiased 454-pyrosequencing			
This study infers that plants can use microbial consortia from the rhizosphere for protection against pathogens.			
This study infers that intra-genotype variations have an impact on the rhizosphere microbial composition			
There are differences in plant rhizobiome especially at the kingdom level			
This study infers that plants can use microbial consortia from the rhizosphere for protection against pathogens.			
Inference was made on the responses of both fungal and bacterial communities upon inoculation with modified <i>Azospirillum brasilense</i>			
Microbial population differ between the upper and lower layers of the soil as well as the distance from the roots			
Dominant bacteria inhabiting rice rhizosphere were identified to belong to <i>Alphaproteobacteria</i> , <i>Betaproteobacteria</i> , and <i>Firmicutes</i> . The authors also suggested that cycling of iron and sulfur is active in the rhizosphere.			
Microbial populations in Rice soil differ in their response to plant photosynthate input			
Composition of diazotrophs is impacted by the duration of carbon source available in the rhizosphere			
The bactericidal effect of transgenic potato plants expressing the phage T4 lysozyme was reported			
Root exudates and metabolism are not responsible for the stimulation of conjugal transfer in the rhizosphere			
Using <i>Pseudomonas aureofaciens</i> Ps3732RNL11, this study was able to suggest direct vascular transport of rhizobacteria from plant roots			
Movement of <i>Pseudomonas</i> to colonize roots in the soil was credited to the presence of exudates			

in humans, the results can also serve as a clue to what might happen in the rhizosphere. Co-colonization of some genera can lead to increased antibiotic resistance in the rhizosphere.

Only a few of the microorganisms present in the rhizobiome and the soil can be cultured in the laboratory. The majority remain unculturable, therefore research to explain the traits and functions of these microorganisms has until recently been difficult. Nuccio *et al.* (2020) were able to use metagenomics to predict the interaction and fate of the microbial community based on the guild dynamics of carbohydrate depolymerization. Hayden *et al.* (2018) used metatranscriptomics to identify expressed microbial functional genes that play active roles in disease suppression. Therefore, the use of omics studies can help to decipher these complex communities and their multipartite interactions for successful microbiome engineering.

8. Conclusion and future research directions

This paper reviewed the plant responses to pathogen attack and the use of root exudates to recruit beneficial microorganisms. Moreover, we reviewed the interactions between beneficial, pathogenic, and mutually beneficial microbes in the inter-root biota, increasing and assisting plant resistance to disease infestation. However, more fundamental research is needed to decipher the evolutionary and biological properties of these microorganisms, which would greatly assist in their improvement and evaluation for use in crop production. In addition, the development of sequencing and 'omics' technologies will improve the ability to fully elucidate the inter- and intra-kingdom species interactions, rhizobacterial composition, function, and even genetic aspects of microorganisms in different environments.

Acknowledgements

The research was funded by the National Research Foundation (NRF) of South Africa (UID123634 and UID132595) which was granted to Olubukola O. Babalola.

Declaration of competing interest

The authors declare that they have no conflict of interest.

References

Abbas R, Rasul S, Aslam K, Baber M, Shahid M, Mubeen F,

- Naqqash T. 2019. Halotolerant pgpr: A hope for cultivation of saline soils. *Journal of King Saud University (Science)*, **31**, 1195–1201.
- Argov T, Azulay G, Pasechnek A, Stadnyuk O, Ran-Sapir S, Borovok I, Sigal N, Herskovits A A. 2017. Temperate bacteriophages as regulators of host behavior. *Current Opinion in Microbiology*, **38**, 81–87.
- Ahemad M, Kibret M. 2014. Mechanisms and applications of plant growth promoting rhizobacteria: Current perspective. *Journal of King Saud University (Science)*, **26**, 1–20.
- Ahrenholtz I, Harms K, de Vries J, Wackernagel W. 2000. Increased killing of *Bacillus subtilis* on the hair roots of transgenic T4 lysozyme-producing potatoes. *Applied and Environmental Microbiology*, **66**, 1862–1865.
- Alexander A, Mishra A, Jha B. 2019. Halotolerant rhizobacteria: A promising probiotic for saline soil-based agriculture. In: Kumar M, Etesami H, Kumar V, eds., *Saline Soil-based Agriculture by Halotolerant Microorganisms*. Springer, Singapore. pp. 53–73.
- Alori E T, Glick B R, Babalola O O. 2017. Microbial phosphorus solubilization and its potential for use in sustainable agriculture. *Frontiers in Microbiology*, **8**, 971.
- Alzubaidy H, Essack M, Malas T B, Bokhari A, Motwalli O, Kamanu F K, Jamhor S A, Mokhtar N A, Antunes A, Simões M F, Alam I, Bougouffa S, Lafi F F, Bajic V B, Archer J A. 2016. Rhizosphere microbiome metagenomics of gray mangroves (*Avicennia marina*) in the Red Sea. *Gene*, **576**, 626–636.
- Babalola O O, Ayangbenro A S, Olanrewaju O S. 2019. Draft genome sequences of three rhizospheric plant growth-promoting bacteria. *Microbiology Resource Announcements*, **8**, e00455–00419.
- Babalola O O, Olanrewaju O S, Dias T, Ajillogba C F, Kutu F R, Cruz C. 2017. Biological nitrogen fixation: The role of underutilized leguminous plants. In: Panpatte D, Jhala Y, Vyas R, Shelat H, eds., *Microorganisms for Green Revolution*. Springer, Singapore. pp. 431–443.
- Backer R, Rokem J S, Ilangumaran G, Lamont J, Praslickova D, Ricci E, Subramanian S, 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*, **9**, 1473.
- Bais H P, Weir T L, Perry L G, Gilroy S, Vivanco J M. 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. *Annual Review in Plant Biology*, **57**, 233–266.
- Bakhshandeh E, Pirdashti H, Shahsavarpour Lendeh K, Gilani Z, Yaghoubi Khanghahi M, Crecchio C. 2020. Effects of plant growth promoting microorganisms inoculums on mineral nutrition, growth and productivity of rice (*Oryza sativa* L.). *Journal of Plant Nutrition*, **43**, 1643–1660.
- Baudoin E, Lerner A, Mirza M S, El Zemrany H, Prigent-Combaret C, Jurkevich E, Spaepen S, Vanderleyden J, Nazaret S, Okon Y, Moënné-Loccoz Y. 2010. Effects of *Azospirillum brasilense* with genetically modified auxin biosynthesis gene *ipdC* upon the diversity of the

- indigenous microbiota of the wheat rhizosphere. *Research in Microbiology*, **161**, 219–226.
- Beneduzi A, Ambrosini A, Passaglia L M. 2012. Plant growth-promoting rhizobacteria (PGPR): Their potential as antagonists and biocontrol agents. *Genetics and Molecular Biology*, **35**, 1044–1051.
- Berendsen R L, Pieterse C M, Bakker P A. 2012. The rhizosphere microbiome and plant health. *Trends in Plant Science*, **17**, 478–486.
- Billah M, Khan M, Bano A, Hassan T U, Munir A, Gurmani A R. 2019. Phosphorus and phosphate solubilizing bacteria: Keys for sustainable agriculture. *Geomicrobiology Journal*, **36**, 904–916.
- Castaldi S, Petrillo C, Donadio G, Piaz F D, Cimmino A, Masi M, Evidente A, Istatico 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**, 3324.
- Cohen A C, Bottini R, Pontin M, Berli F J, Moreno D, Boccanlandro H, Travaglia C N, Piccoli P N. 2015. *Azospirillum brasilense* ameliorates the response of *Arabidopsis thaliana* to drought mainly via enhancement of ABA levels. *Physiologia Plantarum*, **153**, 79–90.
- David L, Harmon A C, Chen S. 2019. Plant immune responses—from guard cells and local responses to systemic defense against bacterial pathogens. *Plant Signaling & Behavior*, **14**, e1588667.
- Dey R, Pal K, Bhatt D, Chauhan S. 2004. Growth promotion and yield enhancement of peanut (*Arachis hypogaea* L.) by application of plant growth-promoting rhizobacteria. *Microbiological Research*, **159**, 371–394.
- Di D W, Zhang C, Luo P, An C W, Guo G Q. 2016. The biosynthesis of auxin: How many paths truly lead to IAA? *Plant Growth Regulation*, **78**, 275–285.
- Dion M B, Oechslin F, Moineau S. 2020. Phage diversity, genomics and phylogeny. *Nature Review Microbiology*, **18**, 125–138.
- Doughari J. 2015. An overview of plant immunity. *Journal of Plant Pathology and Microbiology*, **6**, 322.
- Dukare A, Paul S. 2021. Biological control of *Fusarium* wilt and growth promotion in pigeon pea (*Cajanus cajan*) by antagonistic rhizobacteria, displaying multiple modes of pathogen inhibition. *Rhizosphere*, **17**, 100278.
- Dunlap C, Bowman M, Rooney A P. 2019. Iturinic lipopeptide diversity in the *Bacillus subtilis* species group — Important antifungals for plant disease biocontrol applications. *Frontiers in Microbiology*, **10**, 1794.
- Egamberdiyeva D. 2007. The effect of plant growth promoting bacteria on growth and nutrient uptake of maize in two different soils. *Applied Soil Ecology*, **36**, 184–189.
- Eitas T K, Dangl J L. 2010. NB-LRR proteins: Pairs, pieces, perception, partners, and pathways. *Current Opinion in Plant Biology*, **13**, 472–477.
- Esitken A, Yildiz H E, Ercisli S, Donmez M F, Turan M, Gunes A. 2010. Effects of plant growth promoting bacteria (PGPB) on yield, growth and nutrient contents of organically grown strawberry. *Scientia Horticulturae*, **124**, 62–66.
- Fazeli-Nasab B, Sayyed R. 2019. Plant growth-promoting rhizobacteria and salinity stress: A journey into the soil. In: Sayyed R, Arora N, Reddy M, eds., *Plant Growth Promoting Rhizobacteria For Sustainable Stress Management*. Springer, Singapore. pp. 21–34.
- Ferreira M J, Silva H, Cunha A. 2019. Siderophore-producing rhizobacteria as a promising tool for empowering plants to cope with iron limitation in saline soils: A review. *Pedosphere*, **29**, 409–420.
- Figueiredo M V, Burity H A, Martinez C R, Chanway C P. 2008. Alleviation of drought stress in the common bean (*Phaseolus vulgaris* L.) by co-inoculation with *Paenibacillus polymyxa* and *Rhizobium tropici*. *Applied Soil Ecology*, **40**, 182–188.
- Fredeen A L, Raab T K, Rao I M, Terry N. 1990. Effects of phosphorus nutrition on photosynthesis in *Glycine max* (L.) Merr. *Planta*, **181**, 399–405.
- Gaba V P. 2005. Plant growth regulators in plant tissue culture and development. In: Robert N Trigiano, Dennis J G, eds., *Plant Development and Biotechnology*. CRC Press, Boca Raton, FL. pp. 87–99.
- Gamalero E, Marzachi C, Galetto L, Veratti F, Massa N, Bona E, Novello G, Glick B, Ali S, Cantamessa S. 2017. An 1-aminocyclopropane-1-carboxylate (ACC) deaminase-expressing endophyte increases plant resistance to *Flavescence dorée* phytoplasma infection. *Plant Biosystems — An International Journal Dealing with all Aspects of Plant Biology*, **151**, 331–340.
- Gao Z, Karlsson I, Geisen S, Kowalchuk G, Jousset A. 2019. Protists: Puppet masters of the rhizosphere microbiome. *Trends in Plant Science*, **24**, 165–176.
- Ghavami N, Alikhani H A, Pourbabaei A A, Besharati H. 2017. Effects of two new siderophore-producing rhizobacteria on growth and iron content of maize and canola plants. *Journal of Plant Nutrition*, **40**, 736–746.
- Glick B R. 2014. Bacteria with ACC deaminase can promote plant growth and help to feed the world. *Microbiological Research*, **169**, 30–39.
- Glick B R, Todorovic B, Czarny J, Cheng Z, Duan J, McConkey B. 2007. Promotion of plant growth by bacterial ACC deaminase. *Critical Reviews in Plant Sciences*, **26**, 227–242.
- Guo Q, Sun Y, Shi M, Han X, Jing Y, Li Y, Li H, Lai H. 2021. *Pseudomonas koreensis* promotes tomato growth and shows potential to induce stress tolerance via auxin and polyphenol-related pathways. *Plant and Soil*, **462**, 141–158.
- Gupta P, Roy S, Nandi A K. 2020. Medea-interacting protein long-chain base kinase 1 promotes pattern-triggered immunity in *Arabidopsis thaliana*. *Plant Molecular Biology*, **103**, 173–184.
- Gupta S, Pandey S. 2019. Unravelling the biochemistry and genetics of ACC deaminase — An enzyme alleviating the biotic and abiotic stress in plants. *Plant Gene*, **18**, 100175.
- Hakim S, Naqqash T, Nawaz M S, Laraib I, Siddique M J, Zia R, Mirza M S, Imran A. 2021. Rhizosphere engineering

- with plant growth-promoting microorganisms for agriculture and ecological sustainability. *Frontiers in Sustainable Food Systems*, **5**, 16.
- Hassani M A, Özkurt E, Seybold H, Dagan T, Stukenbrock E H. 2019. Interactions and coadaptation in plant metaorganisms. *Annual Review of Phytopathology*, **57**, 483–503.
- Hayden H L, Savin K W, Wadeson J, Gupta V V, Mele P M. 2018. Comparative metatranscriptomics of wheat rhizosphere microbiomes in disease suppressive and non-suppressive soils for *Rhizoctonia solani* Ag8. *Frontiers in Microbiology*, **9**, 859.
- Honma M, Shimomura T. 1978. Metabolism of 1-aminocyclopropane-1-carboxylic acid. *Agricultural and Biological Chemistry*, **42**, 1825–1831.
- Ilangumaran G, Smith D L. 2017. Plant growth promoting rhizobacteria in amelioration of salinity stress: A systems biology perspective. *Frontiers in Plant Science*, **8**, 1768.
- Jeon J S, Lee S S, Kim H Y, Ahn T S, Song H G. 2003. Plant growth promotion in soil by some inoculated microorganisms. *Journal of Microbiology*, **41**, 271–276.
- Jones J D, Dangl J L. 2006. The plant immune system. *Nature*, **444**, 323–329.
- Kaushal M, Wani S P. 2016. Plant-growth-promoting rhizobacteria: Drought stress alleviators to ameliorate crop production in drylands. *Annals of Microbiology*, **66**, 35–42.
- Ke X, Feng S, Wang J, Lu W, Zhang W, Chen M, Lin M. 2019. Effect of inoculation with nitrogen-fixing bacterium *Pseudomonas stutzeri* A1501 on maize plant growth and the microbiome indigenous to the rhizosphere. *Systematic and Applied Microbiology*, **42**, 248–260.
- Kechid M, Desbrosses G, Rokhsi W, Varoquaux F, Djekoun A, Touraine B. 2013. The *NRT 2.5* and *NRT 2.6* genes are involved in growth promotion of *Arabidopsis* by the plant growth-promoting rhizobacterium (PGPR) strain *Phyllobacterium brassicacearum* Strm 196. *New Phytologist*, **198**, 514–524.
- Khan M S, Ullah M, Ahmad W, Shah S U A. 2020a. The use of modern technologies to combat stripe rust in wheat. *Romanian Biotechnological Letters*, **25**, 1281–1288.
- Khan N, Bano A, Ali S, Babar M A. 2020b. Crosstalk amongst phytohormones from planta and pgpr under biotic and abiotic stresses. *Plant Growth Regulation*, **90**, 189–203.
- Knox J, Hess T, Daccache A, Wheeler T. 2012. Climate change impacts on crop productivity in Africa and South Asia. *Environmental Research Letters*, **7**, 034032.
- Korenblum E, Dong Y, Szymanski J, Panda S, Jozwiak A, Massalha H, Meir S, Rogachev I, Aharoni A. 2020. Rhizosphere microbiome mediates systemic root metabolite exudation by root-to-root signaling. *Proceedings of the National Academy of Sciences of the United States of America*, **117**, 3874–3883.
- Kroer N, Barkay T, Sørensen S, Weber D. 1998. Effect of root exudates and bacterial metabolic activity on conjugal gene transfer in the rhizosphere of a marsh plant. *FEMS Microbiology Ecology*, **25**, 375–384.
- Kumar P, Thakur S, Dhingra G, Singh A, Pal M K, Harshvardhan K, Dubey R, Maheshwari D. 2018. Inoculation of siderophore producing rhizobacteria and their consortium for growth enhancement of wheat plant. *Biocatalysis and Agricultural Biotechnology*, **15**, 264–269.
- Kumari S, Bharat N K. 2018. *In vitro* screening and efficacy of plant growth promoting rhizobacteria and biocontrol agents in bell pepper (*Capsicum annuum* L.). *Journal of Pharmacognosy and Phytochemistry*, **7**, 1472–1475.
- Lamb T G, Tonkyn D W, Kluepfel D A. 1996. Movement of *Pseudomonas aureofaciens* from the rhizosphere to aerial plant tissue. *Canadian Journal of Microbiology*, **42**, 1112–1120.
- Lee C G, Iida T, Uwagaki Y, Otani Y, Nakaho K, Ohkuma M. 2017. Comparison of prokaryotic and eukaryotic communities in soil samples with and without tomato bacterial wilt collected from different fields. *Microbes and Environments*, **32**, 376–385.
- Lee S, Trinh C S, Lee W J, Jeong C Y, Truong H A, Chung N, Kang C S, Lee H. 2020. *Bacillus subtilis* strain I1 promotes nitrate reductase activity in *Arabidopsis* and elicits enhanced growth performance in *Arabidopsis*, lettuce, and wheat. *Journal of Plant Research*, **133**, 231–244.
- Liu F, Hewezi T, Lebeis S L, Pantalone V, Grewal P S, Staton M E. 2019. Soil indigenous microbiome and plant genotypes cooperatively modify soybean rhizosphere microbiome assembly. *BMC Microbiology*, **19**, 201.
- Liu Y, Chen L, Zhang N, Li Z, Zhang G, Xu Y, Shen Q, Zhang R. 2016. Plant-microbe communication enhances auxin biosynthesis by a root-associated bacterium, *Bacillus amyloliquefaciens* SQR9. *Molecular Plant-Microbe Interactions*, **29**, 324–330.
- Liu Y, Teng K, Wang T, Dong E, Zhang M, Tao Y, Zhong J. 2020. Antimicrobial *Bacillus velezensis* HC6: Production of three kinds of lipopeptides and biocontrol potential in maize. *Journal of Applied Microbiology*, **128**, 242–254.
- Lu Y, Abraham W R, Conrad R. 2007. Spatial variation of active microbiota in the rice rhizosphere revealed by *in situ* stable isotope probing of phospholipid fatty acids. *Environmental Microbiology*, **9**, 474–481.
- Lu Y, Murase J, Watanabe A, Sugimoto A, Kimura M. 2004. Linking microbial community dynamics to rhizosphere carbon flow in a wetland rice soil. *FEMS Microbiology Ecology*, **48**, 179–186.
- Lu Y, Rosencrantz D, Liesack W, Conrad R. 2006. Structure and activity of bacterial community inhabiting rice roots and the rhizosphere. *Environmental Microbiology*, **8**, 1351–1360.
- Mahmud K, Makaju S, Ibrahim R, Missaoui A. 2020. Current progress in nitrogen fixing plants and microbiome research. *Plants*, **9**, 97.
- Marchaim D, Perez F, Lee J, Bheemreddy S, Hujer A M, Rudin S, Hayakawa K, Lephart P R, Blunden C, Shango M, Campbell M L, Varkey J, Manickam P, Patel D, Pogue J M, Chopra T, Martin E T, Dhar S, Bonomo R A, Kaye K S. 2012. “Swimming in resistance”: Co-colonization with carbapenem-resistant *Enterobacteriaceae* and *Acinetobacter baumannii* or *Pseudomonas aeruginosa*.

- American Journal of Infection Control*, **40**, 830–835.
- Mejri S, Siah A, Coutte F, Magnin-Robert M, Randoux B, Tisserant B, Krier F, Jacques P, Reignault P, Halama P. 2018. Biocontrol of the wheat pathogen *Zymoseptoria tritici* using cyclic lipopeptides from *Bacillus subtilis*. *Environmental Science and Pollution Research*, **25**, 29822–29833.
- Mendes R, Kruijt M, de Bruijn I, Dekkers E, van der Voort M, Schneider J H, Piceno Y M, DeSantis T Z, Andersen G L, Bakker P A. 2011. Deciphering the rhizosphere microbiome for disease-suppressive bacteria. *Science*, **332**, 1097–1100.
- Mercier J, Lindow S. 2000. Role of leaf surface sugars in colonization of plants by bacterial epiphytes. *Applied and Environmental Microbiology*, **66**, 369–374.
- Minden V, Deloy A, Volkert A M, Leonhardt S D, Pufal G. 2017. Antibiotics impact plant traits, even at small concentrations. *AOB Plants*, **9**, 1–19.
- Molina-Santiago C, Pearson J R, Navarro Y, Berlanga-Clavero M V, Caraballo-Rodriguez A M, Petras D, García-Martín M L, Lamon G, Habenstein B, Cazorla F M. 2019. The extracellular matrix protects *Bacillus subtilis* colonies from *Pseudomonas* invasion and modulates plant co-colonization. *Nature Communications*, **10**, 1–15.
- Morffy N, Strader L C. 2020. Old town roads: Routes of auxin biosynthesis across kingdoms. *Current Opinion in Plant Biology*, **55**, 21–27.
- Morris A, Meyer K, Bohannon B. 2020. Linking microbial communities to ecosystem functions: What we can learn from genotype–phenotype mapping in organisms. *Philosophical Transactions of the Royal Society*, **375**, 20190244.
- Müller M. 2021. Foes or friends: ABA and ethylene interaction under abiotic stress. *Plants*, **10**, 448.
- Nascimento F X, Vicente C S, Barbosa P, Espada M, Glick B R, Mota M, Oliveira S. 2013. Evidence for the involvement of acc deaminase from *Pseudomonas putida* UW4 in the biocontrol of pine wilt disease caused by *Bursaphelenchus xylophilus*. *BioControl*, **58**, 427–433.
- Naseem M, Kunz M, Dandekar T. 2017. Plant–pathogen maneuvering over apoplastic sugars. *Trends in Plant Science*, **22**, 740–743.
- Newman M A, Sundelin T, Nielsen J T, Erbs G. 2013. MAMP (microbe-associated molecular pattern) triggered immunity in plants. *Frontiers in Plant Science*, **4**, 139.
- Nguyen Q-M, Iswanto A B B, Son G H, Kim S H. 2021. Recent advances in effector-triggered immunity in plants: New pieces in the puzzle create a different paradigm. *International Journal of Molecular Sciences*, **22**, 4709.
- Nimchuk Z, Eulgem T, Holt Iii B F, Dangl J L. 2003. Recognition and response in the plant immune system. *Annual Review of Genetics*, **37**, 579–609.
- Nuccio E E, Starr E, Karaoz U, Brodie E L, Zhou J, Tringe S G, Malmstrom R R, Woyke T, Banfield J F, Firestone M K, Pett-Ridge J. 2020. Niche differentiation is spatially and temporally regulated in the rhizosphere. *The ISME Journal*, **14**, 999–1014.
- Ojuederie O B, Olanrewaju O S, Babalola O O. 2019. Plant growth promoting rhizobacterial mitigation of drought stress in crop plants: Implications for sustainable agriculture. *Agronomy*, **9**, 712.
- Olanrewaju O S. 2016. *Isolation of Bacterial Strains for Improved Maize Production*. North-West University, South Africa.
- Olanrewaju O S, Ayangbenro A S, Glick B R, Babalola O O. 2018. Plant health: Feedback effect of root exudates-rhizobiome interactions. *Applied Microbiology and Biotechnology*, **103**, 1155–1166.
- Olanrewaju O S, Babalola O O. 2019a. Bacterial consortium for improved maize (*Zea mays* L.) production. *Microorganisms*, **7**, 519.
- Olanrewaju O S, Babalola O O. 2019b. *Streptomyces*: Implications and interactions in plant growth promotion. *Applied Microbiology and Biotechnology*, **103**, 1179–1188.
- Olanrewaju O S, Glick B R, Babalola O O. 2017. Mechanisms of action of plant growth promoting bacteria. *World Journal of Microbiology and Biotechnology*, **33**, 197.
- Olorunleke F E, Kieu N P, De Waele E, Timmerman M, Ongena M, Höfte M. 2017. Coregulation of the cyclic lipopeptides orfamide and sessilin in the biocontrol strain *Pseudomonas* sp. Cmr 12a. *Microbiologyopen*, **6**, e00499.
- Ortiz N, Armada E, Duque E, Roldán A, Azcón R. 2015. Contribution of arbuscular mycorrhizal fungi and/or bacteria to enhancing plant drought tolerance under natural soil conditions: Effectiveness of autochthonous or allochthonous strains. *Journal of Plant Physiology*, **174**, 87–96.
- Osugi A, Sakakibara H. 2015. How do plants respond to cytokinins and what is their importance? *BMC Biology*, **13**, 1–10.
- Pal K K, Gardener B M. 2006. Biological control of plant pathogens. *The Plant Health Instructor*, **2**, 1117–1142.
- Paramanandham P, Rajkumari J, Pattnaik S, Busi S. 2017. Biocontrol potential against *Fusarium oxysporum* f. sp. *Lycopersici* and *Alternaria solani* and tomato plant growth due to plant growth-promoting rhizobacteria. *International Journal of Vegetable Science*, **23**, 294–303.
- Peiffer J A, Spor A, Koren O, Jin Z, Tringe S G, Dangl J L, Buckler E S, Ley R E. 2013. Diversity and heritability of the maize rhizosphere microbiome under field conditions. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 6548–6553.
- Peng H, Borg R E, Dow L P, Pruitt B L, Chen I A. 2020. Controlled phage therapy by photothermal ablation of specific bacterial species using gold nanorods targeted by chimeric phages. *Proceedings of the National Academy of Sciences of the United States of America*, **117**, 1951–1961.
- Piceno Y M, Lovell C R. 2000. Stability in natural bacterial communities: II. Plant resource allocation effects on rhizosphere diazotroph assemblage composition. *Microbial Ecology*, **39**, 41–48.
- Prashanth S, Mathivanan N. 2010. Growth promotion of groundnut by IAA producing rhizobacteria *Bacillus licheniformis* MML2501. *Archives of Phytopathology and Plant Protection*, **43**, 191–208.

- Pratama A A, Terpstra J, de Oliveria A L M, Salles J F. 2020. The role of rhizosphere bacteriophages in plant health. *Trends in Microbiology*, **28**, 709–718.
- Rana S, Bhawal S, Kumari A, Kapila S, Kapila R. 2020. pH-dependent inhibition of ahl-mediated quorum sensing by cell-free supernatant of lactic acid bacteria in *Pseudomonas aeruginosa* PAO1. *Microbial Pathogenesis*, **142**, 104105.
- Richardson A E, Barea J M, McNeill A M, Prigent-Combaret C. 2009. Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. *Plant and Soil*, **321**, 305–339.
- Rodríguez H, Fraga R. 1999. Phosphate solubilizing bacteria and their role in plant growth promotion. *Biotechnology Advances*, **17**, 319–339.
- Rolfe S A, Griffiths J, Ton J. 2019. Crying out for help with root exudates: Adaptive mechanisms by which stressed plants assemble health-promoting soil microbiomes. *Current Opinion in Microbiology*, **49**, 73–82.
- Saharan B, Nehra V. 2011. Plant growth promoting rhizobacteria: A critical review. *Life Science and Medical Research*, **21**, 30.
- Salguero-Linares J, Coll N S. 2019. Plant proteases in the control of the hypersensitive response. *Journal of Experimental Botany*, **70**, 2087–2095.
- Scher F M, Kloepper J W, Singleton C A. 1985. Chemotaxis of fluorescent *Pseudomonas* spp. to soybean seed exudates *in vitro* and in soil. *Canadian Journal of Microbiology*, **31**, 570–574.
- Schuhegger R, Ihring A, Gantner S, Bahnweg G, Knappe C, Vogg G, Hutzler P, Schmid M, Van Breusegem F, Eberl L. 2006. Induction of systemic resistance in tomato by N-acyl-L-homoserine lactone-producing rhizosphere bacteria. *Plant, Cell and Environment*, **29**, 909–918.
- Sharma R S, Nayak S, Malhotra S, Karmakar S, Sharma M, Raiping S, Mishra V. 2019. Rhizosphere provides a new paradigm on the prevalence of lysogeny in the environment. *Soil and Tillage Research*, **195**, 104368.
- Shilev S, Babrikova I, Babrikov T. 2020. Consortium of plant growth-promoting bacteria improves spinach (*Spinacea oleracea* L.) growth under heavy metal stress conditions. *Journal of Chemical Technology and Biotechnology*, **95**, 932–939.
- da Silva E C, Nogueira R, da Silva M A, de Albuquerque M B. 2011. Drought stress and plant nutrition. *Plant Stress*, **5**, 32–41.
- Simonin M, Dasilva C, Terzi V, Ngonkeu E L M, Diouf D, Kane A, Béna G, Moulin L. 2020. Influence of plant genotype and soil on the wheat rhizosphere microbiome: Evidences for a core microbiome across eight African and European soils. *FEMS Microbiology Ecology*, **96**, fiae067.
- Srivastava S, Singh N. 2014. Mitigation approach of arsenic toxicity in chickpea grown in arsenic amended soil with arsenic tolerant plant growth promoting *Acinetobacter* sp. *Ecological Engineering*, **70**, 146–153.
- Suttle C A. 2007. Marine viruses — major players in the global ecosystem. *Nature Reviews Microbiology*, **5**, 801–812.
- Swamy M K, Akhtar M S, Sinniah U R. 2016. Root exudates and their molecular interactions with rhizospheric microbes. In: Hakeem K, Akhtar M, eds., *Plant, Soil and Microbes*. Springer, Cham. pp. 59–77.
- Teklić T, Parađiković N, Špoljarević M, Zeljković S, Lončarić Z, Lisjak M. 2021. Linking abiotic stress, plant metabolites, biostimulants and functional food. *Annals of Applied Biology*, **178**, 169–191.
- Tiwari S, Vaish B, Singh P. 2016. Population and global food security: Issues related to climate change. In: *Environmental Issues Surrounding Human Overpopulation*. IGI Global, Hershey, USA. pp. 40–63.
- Turan M, Kıtır N, Alkaya Ü, Günes A, Tüfenkçi Ş, Yıldırım E, Nikerel E. 2016. Making soil more accessible to plants: The case of plant growth promoting rhizobacteria. *InTech Open*, **5**, 61–69.
- Turner T R, Ramakrishnan K, Walshaw J, Heavens D, Alston M, Swarbrick D, Osbourn A, Grant A, Poole P S. 2013. Comparative metatranscriptomics reveals kingdom level changes in the rhizosphere microbiome of plants. *The ISME Journal*, **7**, 2248–2258.
- Valetti L, Iriarte L, Fabra A. 2018. Growth promotion of rapeseed (*Brassica napus*) associated with the inoculation of phosphate solubilizing bacteria. *Applied Soil Ecology*, **132**, 1–10.
- Vandeputte O M, Kiendrebeogo M, Rajaonson S, Diallo B, Mol A, El Jaziri M, Baucher M. 2010. Identification of catechin as one of the flavonoids from *Combretum albiflorum* bark extract that reduces the production of quorum-sensing-controlled virulence factors in *Pseudomonas aeruginosa* PAO1. *Applied and Environmental Microbiology*, **76**, 243–253.
- Vardharajula S, Zulfikar Ali S, Grover M, Reddy G, Bandi V. 2011. Drought-tolerant plant growth promoting *Bacillus* spp.: Effect on growth, osmolytes, and antioxidant status of maize under drought stress. *Journal of Plant Interactions*, **6**, 1–14.
- Verma S K, Sahu P K, Kumar K, Pal G, Gond S K, Kharwar R N, White J F. 2021. Endophyte roles in nutrient acquisition, root system architecture development and oxidative stress tolerance. *Journal of Applied Microbiology*, **131**, 2161–2177.
- Wahyudi A T, Astuti R P, Widyawati A, Mery A, Nawangsih A A. 2011. Characterization of *Bacillus* sp. strains isolated from rhizosphere of soybean plants for their use as potential plant growth for promoting rhizobacteria. *Journal of Microbiology and Antimicrobials*, **3**, 34–40.
- Wan W L, Fröhlich K, Pruitt R N, Nürnberger T, Zhang L. 2019. Plant cell surface immune receptor complex signaling. *Current Opinion in Plant Biology*, **50**, 18–28.
- Wang C J, Yang W, Wang C, Gu C, Niu D D, Liu H X, Wang Y P, Guo J H. 2012. Induction of drought tolerance in cucumber plants by a consortium of three plant growth-promoting rhizobacterium strains. *PLoS ONE*, **7**, e52565.
- Wonglom P, Suwannarach N, Lumyong S, Ito S I, Matsui K, Sunpapao A. 2019. *Streptomyces angustmyceticus* NR8-2 as a potential microorganism for the biological control of leaf spots of *Brassica rapa* subsp. *pekinensis* caused by *Colletotrichum* sp. and *Curvularia lunata*. *Biological Control*,

- 138, 104046.
- Worst E G, Exner M P, De Simone A, Schenkelberger M, Noireaux V, Budisa N, Ott A. 2015. Cell-free expression with the toxic amino acid canavanine. *Bioorganic and Medicinal Chemistry Letters*, **25**, 3658–3660.
- Xiong W, Song Y, Yang K, Gu Y, Wei Z, Kowalchuk G A, Xu Y, Jousset A, Shen Q, Geisen S. 2020. Rhizosphere protists are key determinants of plant health. *Microbiome*, **8**, 27.
- Xu J, Kloepper J W, Huang P, McInroy J A, Hu C H. 2018a. Isolation and characterization of N²-fixing bacteria from giant reed and switchgrass for plant growth promotion and nutrient uptake. *Journal of Basic Microbiology*, **58**, 459–471.
- Xu J, Zhang Y, Zhang P, Trivedi P, Riera N, Wang Y, Liu X, Fan G, Tang J, Coletta-Filho H D, Cubero J, Deng X, Ancona V, Lu Z, Zhong B, Roper M C, Capote N, Catara V, Pietersen G, Vernière C, et al. 2018b. The structure and function of the global *Citrus* rhizosphere microbiome. *Nature Communications*, **9**, 4894.
- Xu Q, Tang C, Wang L, Zhao C, Kang Z, Wang X. 2020. Haustoria — arsenals during the interaction between wheat and *Puccinia striiformis* f. sp. *tritici*. *Molecular Plant Pathology*, **21**, 83–94.
- Yuan Y, Gao M. 2017. Jumbo bacteriophages: An overview. *Frontiers in Microbiology*, **8**, 1–9.
- Zaidi A, Khan M, Ahemad M, Oves M. 2009. Plant growth promotion by phosphate solubilizing bacteria. *Acta Microbiologica et Immunologica Hungarica*, **56**, 263–284.
- Zhao Y J, Li J H, Wang Z F, Yan C, Wang S B, Zhang J B. 2012. Influence of the plant development on microbial diversity of vertical-flow constructed wetlands. *Biochemical Systematics and Ecology*, **44**, 4–12.
- Zhu Z, Zhang H, Leng J, Niu H, Chen X, Liu D, Chen Y, Gao N, Ying H. 2020. Isolation and characterization of plant growth-promoting rhizobacteria and their effects on the growth of *Medicago sativa* L. under salinity conditions. *Antonie van Leeuwenhoek*, **113**, 1263–1278.

Exeutive Editor-in-Chief ZHANG Wei-li

Managing Editor SUN Lu-juan