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The Role of Plant Growth-Promoting Bacteria in the Growth of Cereals under Abiotic Stresses

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Abstract

Plant growth-promoting rhizobacteria (PGPR) are known to improve plant performance by multiple mechanisms, such as the production of beneficial hormones, the enhancement of plant nutritional status, and the reduction of the stress-related damage. The interaction between plants and PGPR becomes of particular interest in environments that are characterized by suboptimal growing conditions, e.g., high or low temperatures, drought, soil salinity, and nutrient scarcity. The positive role of PGPR will become even more appealing in the future, as world agriculture is facing issues as climate change and soil degradation. This chapter aims to discuss the main mechanisms of the interaction between PGPR and plants and will focus on how PGPR can decrease abiotic stress damage in cereals, which are critical crops for human diet.

Keywords: PGPR bacteria, global warming, abiotic stresses, cereals, growth-promoting mechanisms

1. Introduction

Global agriculture is facing the difficult challenge of increasing the productivity and output required to feed a growing population. Additionally, fertile land areas available for agriculture are gradually decreasing due to climate change, soil degradation, and pressure from urban developments. These concerns are particularly relevant as they negatively affect yields of cereal crops, which are a fundamental diet component in global society [1].

To help overcome this problem, researchers have turned their attention to understanding interactions between plants and soil microorganisms. Plant roots interact with the soil microbiota, which have various effects on plant growth and development, ranging from beneficial to pathogenic [2]. Plant growth-promoting rhizobacteria (PGPR) play important, but still poorly understood, roles in plant growth promotion, especially under environmental stress such as drought, temperature, and salinity [2–4].

There are various mechanisms through which PGPR improve plant performance, often in a synergic manner; some examples include the production of plant growth-promoting hormones, improvement of plant nutritional status, and decreased stress damage [2]. Interactions between plants and PGPR can result in

improvement of plant performance and enhanced resistance to biotic and abiotic stresses which are important traits for cultivated crops [5].

2. Importance of cereals in global nutrition

Cereals are annual plants belonging to the monocotyledonous Poaceae family and are a vital food source for humans as they provide almost one half of the calories that are consumed daily in the world [6]. Furthermore, cereals are also extensively used as animal feed, mainly for livestock and poultry, and as raw materials for many industrial processes, primarily the production of alcoholic beverages [1].

In the last 50 years, the increase of cereal production (+240% in the time window 1961–2017 shown in **Figure 1**) is the result of increased yields per hectare (+201%) rather than the expansion of land allocated to cereal production (+12%) (**Figure 1**). However, this trend has recently decreased. The average production rate of cereals was 3.6% per year between 1961 and 2007, and it decreased to an average of 2.7% between 2007 and 2017 [7]. This is likely to be linked to multiple factors, including climate change, soil degradation, use of soil for non-alimentary purposes, restrictions on water, nutrients and land for agriculture, and limitations of traditional breeding.

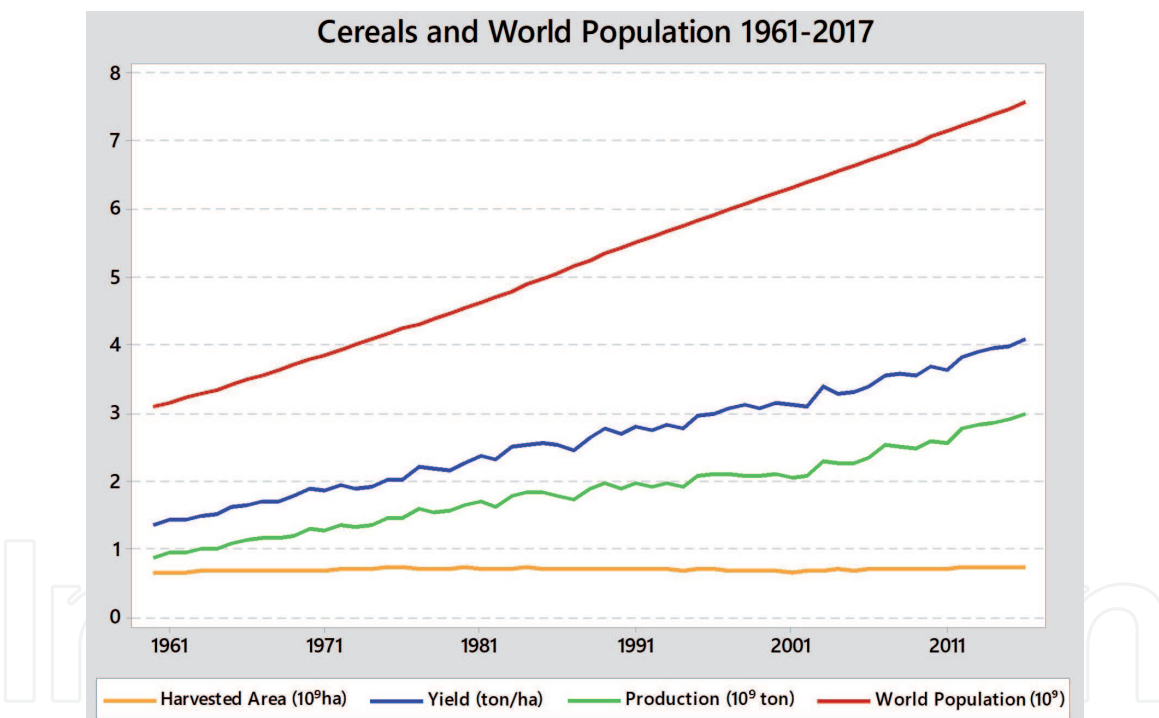


Figure 1. Cereal cultivation records and world population data since 1961. Cereals cultivated land, soil productivity as yield, world grain production, and world population are displayed [7].

3. Abiotic stress effects on agriculture

Most cultivated soils in the world are characterized as being suboptimal. Any deviation from optimal growth conditions causes several interconnected reactions in plants that can be described as an attempt to adapt to new environmental conditions in an effort to maintain homeostasis. If the stress endures too long or is too severe, it can permanently damage plant physiology or result in death. While many plants are able to adapt to stress, the process requires energy that is diverted from active growth, resulting in smaller acclimated plants [8]. Abiotic stresses, that is,

stresses caused by nonliving factors, are thought to be the main cause of global crop loss with decreased productivity of more than 50% annually [9]. Drought and salinity stress are potent environmental hazards for agriculture, particularly in arid and semiarid regions which are already approaching the limits of crop productivity, and due to global warming and degradation of agricultural soils, these regions may no longer support crop plants in the future [10, 11].

3.1 Climate change

Food security is positively correlated with social and economic stability; given climate change is threatening food production, there are extended and complex implications. Since the mid-nineteenth century, average temperatures have increased by 0.8°C, and by the end of this century, temperatures are predicted to increase between 1.8 and 4°C compared to the end of the last century [12]. This change is causally related with human activities by the production of greenhouse gases such as carbon dioxide, the concentration of which rose from ~284 ppm in 1832 to 397 ppm in 2013 [13].

While CO₂ is generally accepted as a greenhouse gas, there is now increased interest in the role of nitrous oxide (N₂O). This compound can originate from the denitrification of N fertilizers, which are commonly used in modern agriculture. In 2014–2015, more than half of all N fertilizer was applied to cereal crops alone [14]. The reintroduction of N in N-depleted soil is an essential agricultural practice that has led to increased yields over the last few decades. However, the application of N fertilizer is inefficient, and it is estimated that only one third of the applied N is absorbed by plants, with the excess being lost in surface runoff, leaching in groundwater, or volatilization into the atmosphere [15]. Atmospheric N₂O, while less abundant than CO₂, is 300 times more potent as a greenhouse gas [16].

Climate change caused by greenhouse gas emissions is predicted to directly impact the productivity of agricultural systems in almost every part of the planet. While many agricultural sites in cold-continental areas will benefit from the increased temperatures, regions characterized by temperate, tropical arid, or subarid climates are likely to face decreasing yields [17]. By modeling the effects of climate change on the yields of various cereals in different areas of the world, it was predicted that by the end of the century, heat stress events will increase in areas of Central and Eastern Asia, Southern Australia, Central North America, and Southeast Brazil (rice); Northern India, the Sahel region, Southeast Africa, and Central South America (maize); and Central Asia (wheat) [18]. Kompas et al. [10] estimated that if no measures are taken to reduce greenhouse gas emissions, the average world temperature increase of 4°C by 2100 will severely decrease food production in almost all countries in the world. This will result in economic loss of approximately 23 thousand billion US\$ on average, with Southeast Asia and developing countries of Africa predicted to face the largest losses (21 and 26% of GDP, respectively).

3.2 Agricultural soil degradation

Soil degradation is one of the main concerns impacting agricultural productivity, especially in tropical and subtropical areas [19]. Globally, one third of land is affected by some form of deterioration [20]. Unsuitable agricultural techniques, together with excessive crop residue removal and unbalanced use of chemical fertilizers, can decrease soil quality, deplete organic matter stocks, and increase erosion. Crop removal from the production site causes the loss of elements that are essential for plant growth, and these elements must be constantly reintroduced to avoid productivity decreases [21].

Using soils for agricultural purposes can cause degradation of water sources, due to leaching of degraded fertilizers into groundwater. Many rivers in developing countries have severe water pollution and eutrophication issues. Irrigation is an essential management strategy to obtain sufficient productivity to meet food demands in many arid and semiarid areas, but it can lead to undesirable effects. Improper irrigation techniques have increased saline-sodic soils that now occur in more than 20% of irrigated lands [22].

4. Plant growth-promoting bacteria

A common misconception during the nineteenth century was that healthy plants should be sterile, not interacting with any microorganisms. This assumption was initially questioned by Victor Galippe [23], who proved that healthy plants could host various microbes in their tissues. Today, we know that almost all terrestrial plants from various environments interact with the surrounding microbiota during all stages of plant development. The relationship between host plant and microbe can range from parasitism, commensalism or mutualism, or neutral or beneficial for plant growth and can vary greatly due to a multitude of factors, both biotic and abiotic. PGPR are attracted to plants by organic exudates released through roots and colonize the root surface and the soil directly in contact with the root. The soil matrix directly in contact with plant roots is called the rhizosphere [24], and the extracellular surface of roots is termed the rhizoplane [25]. Here, colonizing microorganisms can establish the exchange of nutrients and various compounds with the plant, summarized in **Figure 2**.

Nutrients and organic compounds released into the rhizosphere from roots are derived from photosynthesis, and plants release up to 30% of their photosynthates through the roots [26]. These include a variety of compound classes such as carbohydrates, amino acids, organic acids, flavonoids, and lipids that can be used as energy sources for microbes [27]. The sensing and active migration of bulk soil bacteria toward these compounds is called chemotaxis, leading bacteria to colonize the rhizosphere and rhizoplane [28]. By producing exudates, plants can select bacterial species that are attracted to specific compounds, thereby directing the abundance and diversity of microbes in the rhizosphere [29, 30]. Wild oat has been reported to modify the bacterial population of its rhizosphere enriching mainly the Firmicutes, Actinobacteria, and Proteobacteria [31]. The latter group in particular is commonly believed to be the main microbial component in PGPR interactions, due to their capacity for fast growth and diverse metabolic pathways capable of utilizing a great variety of exudate compounds as an energy source [29]. In the model cereal plant *Brachypodium*, the rhizosphere microbiome changes not only within the loosely bound rhizosphere soil and tightly bound rhizosphere soil but also within seminal and nodal roots [32]. It is noteworthy that plants can indirectly influence the colonization of the rhizosphere, by changing the environment conditions. Some examples are changes in pH levels by ion uptake, the reduction of O₂ and H₂O levels caused by root respiration, and water absorption [29].

Different types of root exudates can attract different PGPR. For example, various strains of *Azospirillum brasilense*, a gram-negative Alphaproteobacteria, showed different degree of attractions to various compounds released by different host plants [33]. The composition of root exudates can vary greatly among different plant species. Two different studies [34, 35] reported how even different genotypes of the same plant species can host different bacterial populations in their rhizosphere. Exudates vary between different parts of the roots, different developmental stages of the plant, or as a response to different growth conditions [36]. This means that the same plant can interact with a multitude of different soil bacterial strains over time and space [37].

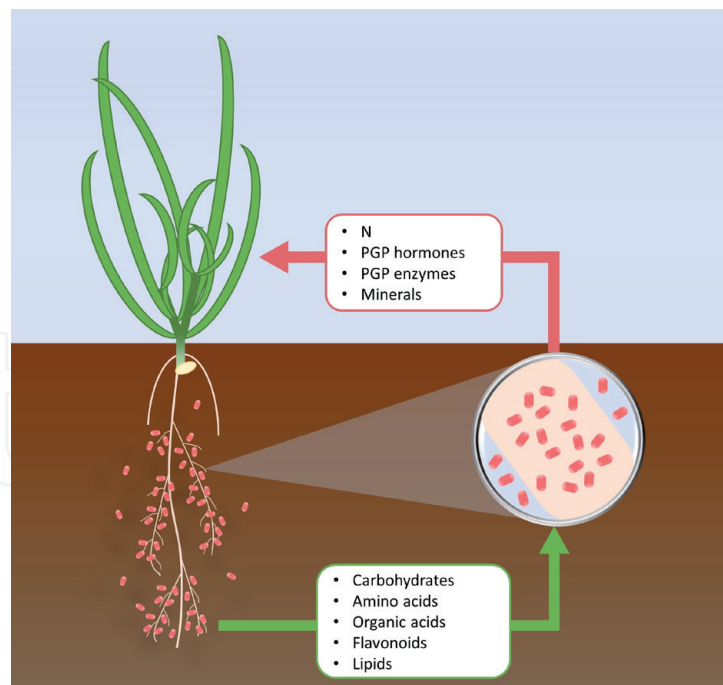


Figure 2.

A model of interactions between plants and PGPR. Exudates released by plant roots attract soil bacteria that can colonize rhizosphere and/or plant tissues. Here, they provide various beneficial compounds to the plant in exchange of nutrients, mainly photosynthates.

Nehl et al [38] use the term “rhizobacteria” to describe rhizoplane/rhizosphere bacteria, but there are also endophytic bacteria that can reside inside plant tissues. To date, numerous interactions between plants and rhizosphere-/rhizoplane-colonizing bacteria have been described, but some microbes are even more specialized. Once they have colonized the rhizoplane, they are able to penetrate root tissues and directly access apoplastic organic compounds, thereby avoiding competition with other microbes in the rhizosphere [39]. Root penetration can be both active, by the production of cell wall-degrading enzymes such as cellulase, and passive, for example, entering via the cracks that form on the root surface during lateral root development [40]. Colonization beyond the rhizosphere into the apoplast requires specialized microbial morphology. Czaban et al. [41] described how the occurrence of flagellar motility in bacterial strains isolated from the internal root tissue of wheat was five times higher than what was observed in bacteria isolated from the rhizosphere.

Bacillus, *Pseudomonas*, *Enterobacter*, *Klebsiella*, *Serratia*, and *Streptomyces* are some of the most commonly found genera of endophytic bacteria in plant tissues [42]. By passing the endodermis, many bacterial species are able to spread from the roots, reaching and colonizing other organs of the stems [43]. Endophytic bacteria can also spread from plant tissue to seeds becoming the starting inoculum for the colonization of subsequent generations of plants. The transmission of bacteria through generations of plants is a process known as vertical transmission. Johnston-Monje and Raizada [44] described how modern varieties of maize and their wild ancestors share common endophytic bacteria communities hosted in their seeds, and a following study conducted on wheat demonstrated how these communities play a positive role in plant growth [45].

4.1 Plant growth promotion driven by rhizobacteria

Galippe’s intuition that plants interact with microbes throughout their life led to a significant increase in the comprehension of the beneficial role that bacteria can have on plant growth. PGPR interactions can result in higher plant biomass, higher

nutritional value, better survival rates, and generally require lower agricultural inputs. Focusing on cereals, PGPR can significantly improve plant performance in several environments, particularly those characterized by suboptimal growth conditions. Some of the main benefits that plants obtain are increased root development which imparts improved resistance to temperature and osmotic stress, soil pollutants, pests, and pathogens [46].

It is well established that plant responses to biotic and abiotic stresses require complex adaptations to structure and metabolism. When biotic and abiotic stresses are applied simultaneously, plants respond much differently compared to stresses applied separately [9]. It is therefore reasonable to assume if a plant is exposed to both biotic and abiotic stresses that PGPR may directly mitigate the effect of biotic stresses by improving plant resistance to abiotic stresses.

4.1.1 Hormone-related mechanisms

The most well-described mechanism by which PGPR can improve cereal productivity is the production of various plant growth-promoting hormones that usually co-affect the performance of the plant in a highly integrated manner [47]. Auxins are a class of hormones typically synthesized by apical buds, and from there they are transported to other parts of the plant. In this class of hormones, the most characterized is indole-3-acetic acid (IAA), which enhances cell elongation and differentiation and, in roots, stimulates lateral root development [42, 48]. Various reports have shown how the production of auxins from PGPR is one of the most important mechanisms for plant growth promotion. Barbieri and Galli [49] inoculated wheat with two strains of *Azospirillum brasilense*, of which one was a mutant with impaired IAA production. They observed how only the wild-type strain promoted lateral root development, a result that suggests a primary role of IAA in improving plant root development. IAA can indirectly improve the nutritional status of the plant by increasing root development (specifically lateral roots), hence allowing the plant to explore a higher portion of soil substrate, an important trait particular for the acquisition of low-mobility nutrients such as phosphorus [50].

Gibberellins (GAs) can be produced by PGPR [51] and are believed to play an important role in promoting plant growth. These diterpene hormones are naturally present in plants, regulating key processes such as seed germination, stem elongation, leaf expansion, root growth, and root hair abundance [52, 53]. One of the best known GAs is GA₃, commonly known as gibberellic acid, which plays a key role in determining plant source-sink relations. The role of gibberellins in the response of cereals to stresses varies depending on the stress type [54], but in general, plants tend to reduce GAs levels when growing in suboptimal conditions. The exogenous application of gibberellins has been reported to improve wheat and rice performance undergoing saline stress [55, 56] and to reduce heavy metal stress symptoms in rice [57].

Many PGPR are able to degrade 1-aminocyclopropane-1-carboxylic acid (ACC) through the enzyme ACC deaminase and use the degradation products as a nitrogen source [42]. ACC is the biosynthetic precursor of ethylene, a hormone naturally present in plants, and its abundance is often increased in response to stresses. While at optimal levels, ethylene is involved in essential processes such as tissue differentiation, root development, flowering, grain development, and natural tissue senescence and abscission; when overproduced it can decrease plant performance [58]. In abiotically stressed plants, the increase of ethylene can trigger chlorosis and early maturation and senescence of organs, seeds in particular [59, 60], and have an inhibitory effect on root growth [42]. By impairing the ethylene signaling pathway, the interaction with PGPR can decrease the stress-related damage in the plant [2].

Similar to ethylene, abscisic acid (ABA) is a hormone commonly produced by plants in response to various types of stress, particularly osmotic stress [61]. Naturally involved in seeds and buds dormancy, ABA shares the first biosynthetic steps with cytokinins, a phytohormone class that often plays an antagonistic role to ABA. In dry or saline soils, reactive oxygen species (ROS) increase the biosynthesis of ABA, which is then transported to leaves, where it causes stomatal closure to reduce transpiration and water loss [62]. As a consequence, the diffusion of CO₂ into leaves is decreased, lowering photosynthetic rates [63, 64]. PGPR have been reported to increase the resistance of plants to salinity, hence decreasing the stress-related ABA accumulation in plants and preserving photosynthetic efficiency [65, 66].

5. Plant-bacterial interactions enhance abiotic stress responses

Bacteria can have various effects on their host plant. PGPR can affect plant growth both directly, such as by fixing atmospheric N₂ into biologically available N compounds or by producing growth-promoting hormones [52], and indirectly, by preventing the growth of plant pathogens or increasing plant resistance to them [43]. A necessary condition for bacteria to be beneficial to a plant is rhizosphere competence as the competition and conditions in the rhizosphere are vastly different to that of bulk soil. The rhizosphere contains a higher abundance of bacteria than bulk soil, but the diversity is much lower. The colonization of the root system of plants is not homogenous; the density of specific bacteria varies in different parts of the root system and is likely to be related to different root exudates released by different parts of the roots [37]. Another mechanism likely to regulate the colonization of the rhizosphere is bacterial quorum sensing, which is the regulation of gene expression driven by bacterial population density and can occur both within bacteria of the same species and among different species [67]. Quorum sensing can influence the bacterial competitiveness, therefore affecting the roots colonization patterns [37].

5.1 Thermic stress adaptation

Temperature stress causes a shift in hormone production, particularly ethylene, which can often impair plant growth [58]. High-temperature stress causes denaturation and aggregation of cellular proteins that, if left unchecked, leads to cell necrosis. Imbalance between ABA and cytokinins derived from prolonged heat stress during the reproductive stage can lead to grain abortion [68]. Heat responses include inhibition of normal transcription and translation and increased expression of genes coding for heat shock proteins and thermotolerance induction [69]. Low-temperature stress, conversely, damages metabolic processes, changes membrane properties, causes structural changes in proteins, and inhibits enzymatic reactions [70]. If it occurs during spore formation, cold can cause sterility of flowers by interfering with meiosis [71].

The literature on PGPR interactions with cereals at suboptimal temperatures is relatively scarce, and the mechanisms by which cereals adapt are not well defined. It is suggested that the geographical origin of the bacteria determines the optimal growth range at which they interact beneficially with plants. In a study on wheat, bacteria isolated from cold climates have been reported to efficiently colonize the plant rhizosphere and improve their resistance to low-temperature stress, and the same trend was observed when wheat plants were inoculated with bacteria isolated from warm environments and subjected to high-temperature stress [72]. It is possible that the bacteria isolated from different temperatures can outcompete

the indigenous microbial population by tolerating either cold or warm conditions giving rise to a higher abundance and colonization of the rhizosphere.

Inoculation with a *Pseudomonas aeruginosa* strain isolated from a hot semiarid environment improved survival rate, development, and biochemical parameters of sorghum seedlings when the plants were exposed to heat treatment, while the biomass production was not affected at optimal temperatures [73]. In another study, various cold-tolerating *Pseudomonas* spp. were inoculated onto wheat grown at low temperatures, giving analogous results. The authors suggest the beneficial effect was linked to a better root development in inoculated strains that improved nutrient uptake and, in general, caused a better adaptation to cold [74].

As global warming threatens to change significantly the temperature of most cultivated lands [17], the development of cereals with enhanced adaptation capacity to heat or cold stress is an essential task in order to sustain profitability and production at suboptimal temperature conditions. While further research is necessary to better understand the mechanisms that regulate PGPR-plant interactions in such conditions, the studies done so far suggest how PGPR can be a valuable source of temperature-stress resistance, especially when they evolved in areas characterized by warm or cold climates, depending on the case.

5.2 Osmotic stress adaptation

Both dry and saline soils can cause osmotic stress in plants, which results in cell dehydration due to lack of water (drought) or unavailability of water (salinity). These two stresses are often agronomically significant, as high salinity in soil is mainly caused by irrigation, a necessary practice for increasing yields in many areas of the world characterized by insufficient rainfalls. When water supply is insufficient to remove ions from superficial soil layer, they accumulate causing an increase of salinity [75].

Salinity is also the result of land clearing, as deep subsurface roots no longer are able to keep the water table below ground level. As the water table rises, it brings with it saline water that can render hundreds of square kilometers of agricultural land uncultivable [76]. Plants growing on such soils often suffer from osmotic stress that reduces water absorption and increases ionic concentration in tissues to toxic levels [77]. PGPR can decrease these stress symptoms through various mechanisms, such as production of Na⁺-binding exopolysaccharides [78], improvement of ion homeostasis [79], decrease of ethylene levels in plants through ACC deaminase [80], and synthesis of IAA [81]. Wheat seeds inoculated with a species from the genus *Pseudomonas* showed increased germination rates in a saline environment; Egamberdiyeva [82] ascribed this to the production of plant growth regulators by the bacteria.

Drought is considered as the major cause of yield loss [83], negatively affecting most physiological processes in plants. Plant cells respond to water loss by increasing the production of abscisic acid (ABA) in roots that increases water uptake and causes leaf stomatal closure and reduces leaf expansion to reduce dehydration [84]. Smaller leaves cause impaired photosynthesis, consequently decreasing dry matter accumulation and grain yield [85]. Under water deficiency, both cell division and enlargement are lowered due to damaged enzyme activities, leading to overall smaller plant organs. Grain production is also reduced in cereals due to flower abortion [86, 87].

Plants often react to drought by increasing the amount of osmolytes in their tissues and consequently increase their osmotic potential [88]. Drought can also cause an increase of ROS in plant tissues. Proline, an amino acid whose abundance is increased under water deficiency, can both work as an osmolyte and scavenger

for ROS under stress [89]. In general, PGPR can improve the performance of plants in dry environments by exuding osmolytes that increase the osmotic potential of plants [42, 90, 91].

Another mechanism for improving resistance to drought is the synthesis of beneficial hormones (IAA) and enzymes (ACC deaminases) and the decrease of stress-related hormones such as ethylene and ABA in the plant. Naveed et al. [92] reported that two maize cultivars exposed to drought showed reduced damage when inoculated with two different PGPR, probably due to hormones produced by the bacteria and stress-reducing enzymes synthesized by both the plants and the bacteria during the interaction. Wheat plants inoculated with various PGPR showed an improved resistance to salt and drought treatments, linked to decreased ABA and ACC levels in plant tissues [65]. In a similar study [66], rice plants showed decreased endogenous ABA levels and increased biomass when inoculated with *Bacillus amyloliquefaciens*; the authors hypothesize that inoculation increased salt tolerance in plants through an ABA-independent pathway, and this prevented the stress-dependent ABA accumulation and the resulting growth impairment [63].

Sarig et al. [93] report that sorghum plants subjected to osmotic stress after their emergence showed decreased damage when colonized by *Azospirillum brasilense*. It is unclear, however, if the observations were a drought-specific response or an indirect effect of inoculated plants showing a better root development and higher hydraulic conductivity at the time of the stress. In two successive studies [94, 95] conducted on various *Azospirillum* spp., inoculated wheat plants subjected to drought had decreased grain loss, better water status, and higher K and Ca content, with the latter in particular suggested to be involved in the adaptation of the plants to environmental stress. Bacterial nitrate reductase was also suggested to play an important role in nitrate assimilation of plants under drought [95].

As previously mentioned, drought and saline stress are related, since salinity is often the result of irrigation practices to avoid plant desiccation from drought stress. This concern may become more relevant in future years, as higher temperatures caused by global warming will result in higher evapotranspiration, hence requiring increased irrigation. By the year 2050, 50% of all arable lands might be affected by serious salinization [96]. Improving the resistance of plants to dry environments would decrease the necessity of irrigation, indirectly decreasing the ongoing salinization process in agricultural land.

5.3 Improvement of the plant nutritional status

In natural environments, plants die and decompose where they grew, and the subsequent detritus reintroduces soils with most of the nutrients they absorbed during their growth. In cultivated lands, those nutrients are removed at harvest and must be constantly replaced to avoid productivity decrease. Among the macronutrients, nitrogen, phosphorus, and potassium are the most important for plant growth, and they are typically reintroduced using synthetic fertilizers. Unbalanced use of fertilizers can decrease soil quality, consume organic matter stocks, and increase erosion risk. Soil bacteria can improve the nutritional status of plants directly by increasing nutrient bioavailability and/or indirectly by improving plant root development, hence allowing them to explore higher areas of soil [97].

5.3.1 N₂ fixation and absorption

Several bacterial species are classified as diazotrophs, which are microorganisms that are able to utilize the nitrogenase enzyme to fix atmospheric N₂. Diazotrophic bacteria can fix N₂ in either a free-living form or in association with a host as an

endosymbiont. The most well-described interaction between plants and diazotrophic bacteria is the rhizobia-legume symbiosis. Rhizobia are a group of various Proteobacteria that can colonize plant roots and fix atmospheric nitrogen, which is then partly provided to the plant in exchange of photosynthates [98]. While this association has been observed mainly in legumes, some species of rhizobia can also colonize cereals. Gutierrez-Zamora and Martinez-Romero [99] showed how maize and bean plants cultivated in association shared the same *Rhizobium etli* strains, with the bean plants probably constituting the source of inoculum for maize. The interaction with the rhizobia increased the biomass of both crops, but in maize this outcome might have been linked to mechanisms other than N₂ fixation, such as hormone production. Rice inoculated with an *Azoarcus* sp. showed improved growth regardless of colonization by the wild-type strain or with a mutant strain deficient in the nitrogenase genes [3]. When spring wheat and maize were inoculated with two different rhizobia and grown at various soil N levels, the two strains were effective in enhancing plant growth only at low and intermediate levels of soil N. The authors suggest that plant growth-promoting hormones released by the bacteria caused a better root development in inoculated plants that were able to absorb more nutrients from the soil [100].

In general, diazotrophic bacteria associated with cereal roots often carry the nitrogenase genes necessary for the fixation of atmospheric nitrogen, but the relative enzymes are not always synthesized inside plant tissues. Furthermore, the amount of fixed N provided to the plant is often negligible, due to low presence of diazotrophic bacteria or because bacteria use fixed nitrogen for their own growth [101]. The nitrogenase enzyme cannot function in the presence of O₂, so it may be desirable to engineer free-living diazotrophic bacteria that are able to colonize plant tissues. Other possible ways might be to increase the fixing bacteria population by engineering plants capable of exuding diazotroph favorable compounds or engineering bacteria capable of providing the plant with higher levels of nitrogen [102].

Fox et al. [103] modified a *Pseudomonas* sp. genome by adding a gene cluster with nitrogenase activity that improved the performance of wheat and maize by fixing N₂. This is an example of some of the approaches toward nitrogen-fixing cereals, that is, plants capable of sourcing the N necessary for their growth from the atmosphere via endosymbionts [104].

Farmers have benefited from the rhizobia-legume symbiosis for centuries, and extending this characteristic to cereals would be a decisive benefit for modern agriculture, providing a continuous, ecologically, and economically sustainable source of N to the most important crops.

5.3.2 Improvement of soil nutrient uptake

Despite the benefits PGPR impart on plant nutrient content, it is often unclear if this improvement is related to an enhanced mineral uptake or if it is the result of improved root system development in inoculated plants due to bacterial hormones and/or enzymes [48].

Various bacterial strains are known to increase bioavailability of phosphorus in soil, due to the mineralization of organic phosphate and solubilization of inorganic phosphate. Some of the bacterial compounds linked to these two processes are acid phosphatases and organic acids, respectively [105]. Phosphate-solubilizing bacteria have been reported to improve the growth of maize [106], rice [107], and wheat [108].

PGPR can also synthesize siderophores that are low-molecular-weight compounds with high iron-binding affinity [109] that can complex with Fe (predominantly Fe³⁺) in soil. The iron-siderophore complex is then assimilated by the

bacterium using a complex-specific receptor [110]. This has various effects, it depletes the soil iron supply, thereby preventing the growth of other potentially pathogenic microbes, and, if the iron is then provided to the plant, it can directly improve plant growth [48]. Furthermore, the bacterial nitrogenase activity and *nif* gene expression are iron dependent [111, 112]; hence, the absorption of iron from the soil enables diazotroph bacteria to convert atmospheric N₂ to a form that is bioavailable for the plant.

PGPR can indirectly improve plant performance neutralizing the stress-related hormones produced by the plant in poor soils. Wheat plants grown at various levels of N, P, and K, showed increased grain yield and biomass production when colonized by *Pseudomonas* spp., with the bacterial growth promotion being negatively correlated with the amount of provided nutrients [97]. The authors ascribe this outcome to bacterial production of ACC deaminase that decreased ethylene levels produced by plants as a response to low nutrients levels, which impaired root development in uninoculated plants.

Overall, plant growth promotion is ascribed to a combination of multiple mechanisms. Egamberdiyeva [113] inoculated maize seeds with PGPR with nitrogenase and/or IAA activity and grew them on two soil types with different nutrient availabilities. Inoculated plants generally developed a higher root and shoot biomass and had higher N, P, and K contents, the improvement being more pronounced in plants grown on nutrient-poor soils. However, this study did not consider the possible interactions of inoculated strains with the native microbial populations that may have affected the results.

In 2014–2015, out of 182 million metric tons (Mt) of consumed fertilizer, one half was applied to cereals [14]. Cereals consumed more than one half of N fertilizers and more than one third of P and K fertilizers. As previously mentioned, these amendments have both a high economical and environmental cost, as they can cause soil degradation, pollution of water, and eutrophication. While developing N-fixing PGPR is a task yet to be achieved in cereal agriculture, it is well documented how PGPR can improve the efficiency of nutrient uptake in crops. This can occur by either increasing the bioavailability of nutrients in the soil or as a consequence of better root development, resulting in better soil exploration.

6. Issues and perspectives

Cereal-PGPR interactions have been widely studied over the last few decades, and the positive influence that they can have on plant growth is still being established. However, the lack of consistency among different studies is still a concern, highlighting that when multiple biological actors are involved, no generalizations can be made. The same bacterial strain can be beneficial to a plant species and damage another [114] or have no effects or even be detrimental for plant performance when the growing conditions are optimal but become beneficial when growing conditions worsen [2–4]. In two studies on maize and rice subjected to water deficiency [90, 115], the beneficial effects of various bacterial isolates on plant growth increased with the severity of the stress. Studying the interaction between PGPR and gum rockrose (*Cistus ladanifer*), Solano et al. [116] hypothesized that a possible explanation for this is that poor environments may impair the growth of indigenous microbial communities, this way decreasing the competition for those microbes that establish advantageous relationships with plants. Another possible explanation is that when the main bacterial mechanism of plant growth promotion is providing them with nutrients, the benefit might be limited in nutrient-rich soil, while it can be significant in the case of limiting nutrients [117].

The observed outcomes change particularly from laboratory and climate chamber trials to more open setups such as greenhouses and field, in which bacteria often fail to improve plant growth [37]. Most of the studies conducted so far on the interaction between cereals and PGPR were performed in controlled environments, usually applying only one single stress at a time. While this is a necessary compromise when starting to study this interplay, it often entails a significant bias from realistic field environment [2], in which plants frequently face more variable growing conditions and face multiple stresses at the same time, triggering unique responses in plants that are different from the sum of plant response to stress applied individually [118]. So far, very few experiments have studied the interaction between bacteria and crops under multiple stresses, but replicating as accurately as possible real field conditions is an essential step for understanding and exploiting the role of PGPR in agriculture. In addition to the more unstable growing environment, another important variable added in field experiments is the interaction with the native microbiota. Often inoculated bacteria in the field show lower rhizosphere or root colonization than laboratory, climate chamber, and greenhouse trials [119], in which the growth medium is usually sterilized at the beginning of the experiment.

One of the hypotheses that can be drawn from the current literature is that the origin of the inoculated bacteria is often a decisive factor for the interaction to improve plant growth. Bacteria isolated from the same plant species used in trials are more likely to play a beneficial role, probably due to the plant-specific exudates that have a key role in the early phases of the interaction [100]. Similarly, bacteria isolated from environments characterized as suboptimal (temperature in particular) that are similar to the conditions and stress applied in plant trials may be more beneficial than bacteria isolated from optimal conditions, delivering more benefits to the plant, due to adaptations that allow the bacteria to be more competitive than the native microbiota [72]. Unfortunately, inoculum used in trials may become less effective due to continual cultivation in laboratory environments, and when planning a plant trial, this should be taken into consideration.

One of the problems facing commercialization of PGPR on markets is the inoculation delivery method on plants. In the laboratory, a common method is dip inoculation where seedling roots are immersed in bacterial culture and then transplanted into the growth substrate, but this approach is not feasible for annual cereals on the field scale. The on-field application of bacterial solutions after seedling germination, while less laborious, still requires considerable equipment and technical knowledge. The most feasible way to apply PGPR on field is probably the use of pre-inoculated seeds (this is already used for rhizobia-legume inoculation) allowing farmers to bulk sow, relieving them from the inoculation step. When the seed bacterial treatment is done immediately before germination, the required strength of bacterial inoculum is typically smaller than in seedling treatments, but ideally inoculants should survive long enough on seed coats to be present during germination; however, prolonged survival of microbial treatment on seeds is still a challenge [120]. Moreover, inconsistencies between performances of seed inoculants are often observed in different trials, and further research is required to address this issue [121]. Utilizing vertical transfer of microbial endosymbionts in seeds may also present a possible inoculation technology that has not been explored extensively and may provide economic benefits to farmers [120] and could potentially mitigate the problem of inoculum viability in seed coats. Recently, studies on bacterial strains vertically transmitted in cereal seeds have shown promising plant growth-promoting effects, likely linked to their ability to solubilize phosphorus, produce hormones, siderophores, and ACC deaminase [122]. By exploiting the existing interactions between plants and known seed endophytic bacteria or isolating new

bacterial strains capable of inhabiting seeds for vertical transmission by crops, new technologies may emerge that have large-scale economical applications.

During the last decades, selection of crops has been driven by increased productivity in nutrient-rich environments, with scarce focus on the positive effects of PGPR, and this trend might have led to the loss of plant traits associated with the microbial interaction [5]. The identification and reintroduction of the genes associated with those traits might enhance the positive effects of PGPR, especially in poor environments, and selecting plants that have superior interaction with rhizosphere microbiota should be considered in plant breeding programs. Additionally, a more immediate way to alleviate temperature stress could be to inoculate plants with bacteria originated from hot-climate regions that as a consequence are more likely to help their host to perform better in a warming environment [29, 72].

The interaction with microbes will gain more attention in the future, considering the effects of climate change, due to the microbial genetic plasticity compared to plants. PGPR may evolve rapidly, developing efficient adaptation strategies to the benefit of the plant host as well.

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