

Review

Legume Biofortification and the Role of Plant Growth-Promoting Bacteria in a Sustainable Agricultural Era

Mariana Roriz ¹, Susana M. P. Carvalho ^{1,2}, Paula M. L. Castro ¹ and Marta W. Vasconcelos ^{1,*}

¹ CBQF—Centro de Biotecnologia e Química Fina—Laboratório Associado, Universidade Católica Portuguesa, Escola Superior de Biotecnologia, Rua Diogo Botelho 1327, 4169-005 Porto, Portugal; mroriz@porto.ucp.pt (M.R.); susana.carvalho@fc.up.pt (S.M.P.C.); plcastro@porto.ucp.pt (P.M.L.C.)

² GreenUPorto—Research Centre on Sustainable Agrifood Production & DGAOT, Faculty of Sciences, University of Porto, Campus de Vairão, Rua da Agrária 747, 4485-646 Vairão, Portugal

* Correspondence: mvasconcelos@porto.ucp.pt

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Abstract: World population growth, together with climate changes and increased hidden hunger, bring an urgent need for finding sustainable and eco-friendly agricultural approaches to improve crop yield and nutritional value. The existing methodologies for enhancing the concentration of bioavailable micronutrients in edible crop tissues (i.e., biofortification), including some agronomic strategies, conventional plant breeding, and genetic engineering, have not always been successful. In recent years, the use of plant growth-promoting bacteria (PGPB) has been suggested as a promising approach for the biofortification of important crops, including legumes. Legumes have many beneficial health effects, namely, improved immunological, metabolic and hormonal regulation, anticarcinogenic and anti-inflammatory effects, and decreased risk of cardiovascular and obesity-related diseases. These crops also play a key role in the environment through symbiotic nitrogen (N) fixation, reducing the need for N fertilizers, reducing CO₂ emissions, improving soil composition, and increasing plant resistance to pests and diseases. PGPB act by a series of direct and indirect mechanisms to potentially improve crop yields and nutrition. This review will focus on the: (i) importance of legumes in the accomplishment of United Nations Sustainable Development Goals for production systems; (ii) understanding the role of PGPB in plant nutrition; (iii) iron biofortification of legumes with PGPB, which is an interesting case study of a green technology for sustainable plant-food production improving nutrition and promoting sustainable agriculture.

Keywords: Biofortification; iron; legumes; malnutrition; plant growth-promoting bacteria; sustainable agriculture

1. Introduction

The world population has considerably increased in the past 10 years and is expected to reach around 9.5 billion by 2050 [1], with developing countries accounting for much of this increase [2], and this represents a huge challenge for agricultural sustainability [3]. The population growth is increasing the pressure on arable land and natural resources, which together with the environmental stresses associated with climate change, is severely affecting plant growth, productivity, and nutritional value. Furthermore, the excessive use of fertilizers and pesticides has a great impact on the environment, causing soil and water deterioration [4–7]. All these issues are reflected in human health, with increased malnutrition problems, not only in developing economies but also in developed countries where, although food is available, its nutritional value is poor [8]. Nowadays, consumers in developed countries

are increasingly concerned with the chemical residues in products, demanding more sustainable agricultural practices focusing on safer products, free of chemical residues. It is urgent to act in a sustainable manner to face the current societal challenges to guarantee the production of foods with high nutritional content combined with low environmental footprint.

Biofortification appears to be a promising strategy to fulfill the constraints previously described. It is defined, according to the World Health Organization (WHO) as, “the process by which the nutritional quality of food crops is improved through agronomic practices, conventional plant breeding, or modern biotechnology” [9]. Within this context, the agronomical practices aim to improve mineral uptake, either through fertilizer application or increased nutrient solubilization and mobilization in the soil [10]. The other two methodologies focus on the improvement of micronutrient contents of edible plant tissues and their bioavailability for humans [11].

The first steps in biofortification programs were made when rice genetically modified with beta-carotene, golden rice, appeared [12]. However, golden rice is not yet commercialized as genetically modified crops are not very well accepted by several societies [13]. The HarvestPlus program is one of the most significant, systematic, and symbolic breeding programs. It is a large biofortification platform launched in 2004 to reduce micronutrient malnutrition in Asia and Africa. The program has focused on seven staple food crops (rice, beans, cassava, maize, sweet potatoes, pearl millet, and wheat) and targeted three major nutrients (Fe, Zn, and vitamin A) [11].

Carvalho and Vasconcelos [11] and Garg et al. [14] have reviewed these three biofortification methodologies and performed an analysis of their strengths, weaknesses, opportunities, and threats. They concluded that the success of the biofortification programs is strongly dependent on the farmers and public acceptance as well as on political support, which will dictate their cost/benefit. Regarding future scientific challenges, one of the major issues in this field is the incomplete understanding of the rate-limiting steps that are involved in translocating minerals to seeds, and further studies in this area are required. Also, the assurance that careful and systematic safety analyses of these products will be conducted before they become readily available to consumers is of extreme importance. Metabolomic studies will provide added value for food safety assessment programs, allied with currently used analytical methods.

There is still a long way to go before biofortification is strongly implemented and sustained. Some efforts have already been made in this direction to integrate biofortification into global standards and guidelines by the Codex Alimentarius, the food standards-setting agency, together with WHO, the Food and Agriculture Organization of the United Nations (FAO), and the Sanitary and Phytosanitary Agreement (SPS) of the World Trade Organization (WTO) [15].

The utilization of biofertilizers—“products that contain living microorganisms, which exert direct and indirect beneficial effects on plant growth and crop yield through different mechanisms”—[16] is an important environmentally friendly alternative to the strategies described above. Many studies show the possible roles of rhizospheric and endophytic microbes in crop biofortification [17]. More recently, several studies have shown that plant growth-promoting bacteria (PGPB), directly or indirectly, enhance plant growth, crop nutrition, and tolerance to abiotic stress [18–26] through several mechanisms. The utilization of these bacteria has been suggested as a promising green technology for increasing the nutrient content of crops from a biofortification perspective.

Legumes are a good target for increasing the nutritional value of foods, particularly in developing countries where cereals and legumes are the major food source. The association of legumes with their natural colonizing microorganisms appears to be a powerful combination for a sustainable and eco-friendly approach to cope with climate change effects on crops and to improve plant nutrition. Apart from their rich nutritional value, legumes also play an important ecological role [27].

In this review, we will focus on the: (i) importance of legumes in the accomplishment of United Nations Sustainable Goals for production systems; (ii) understanding the role of PGPB in plant nutrition; (iii) iron biofortification of legumes with PGPB, which is an interesting case study of a green technology for sustainable plant-food production improving nutrition and promoting sustainable agriculture.

2. The Importance of Legumes in the Accomplishment of the Sustainable Development Goals

The world is facing a time of important agricultural losses in terms of productivity and nutritional crop value due to the well-known climate change phenomenon, which includes global warming and more frequent occurrence of severe weather events (heavy rains and drought). As a consequence, more than two billion people suffer from malnutrition problems due to food shortage (acute hunger) or insufficient intake of essential micronutrients (hidden hunger) [28]. Deficiency in the main micronutrients, zinc (Zn), iron (Fe), and selenium (Se), has a great impact on human health. Zn deficiency reflects in inappropriate physical growth, wound healing, and skeletal development, and is associated with augmented risk of infection. Fe deficiency is associated with cases of anemia and fatigue, also affecting the immune system. Se deficiency can affect male fertility, impair the immune system, increase infection vulnerability, cause mental slowing, and result in cases of hypothyroidism [29].

There has been a growing demand for sustainable agricultural practices to achieve food security in this milieu, and so-called “climate-smart agriculture”, which aims at using agricultural approaches that are “resistant” to climate change effects and are environment-friendly, has emerged [28]. In 2015, the United Nations (UN) outlined 17 goals in a “Sustainable Development Goals Project”, with the second being to “end hunger, achieve food security and improve nutrition, and promote sustainable agriculture” [30]. This problem is not only affecting human health and the environment but also has a great impact on the economy, representing the most important socio-economic challenge of the century [31]. Amongst the strategies proposed by the UN to improve food nutrition and fight malnutrition are increases in dietary diversity, food supplementation, food fortification, and biofortification [32]. Fortification of foods during processing appears to be a promising way to improve the nutrient composition of meals; however, this strategy is not accessible to all populations [32].

Biofortification appears to be a feasible approach to improve the nutritional value of foods, with a special significance for the most deprived populations [11,33]. Plants are an important source of essential minerals and vitamins, and in developing countries grains and legumes are the primary, and often the only, source of food [34]. In particular, legumes are excellent sources of amino acids, nutrients, and vitamins, being similar to or even better than cereals [32]. Their inclusion in the human diet has been reported as having many potential health benefits (Table 1). The presence of some particular compounds in legumes, such as soluble fibers, antioxidants, flavonoids, etc., seems to be associated with reduced cases of diabetes, cardiovascular diseases, and some types of cancers, among others [35,36]. However, these types of studies are still not conclusive as the effect of legume consumption on human health seems to be dependent on the type, amount, and frequency of legume consumption, and they also do not consider the effects of processing [35]. In the environment, legumes are part of the symbiotic N fixation process, reducing the need for N fertilizer, decreasing agricultural CO₂ emissions, and improving soil composition [37]. The inclusion of legumes in crop rotation systems, besides conferring pest and disease resistance to the succeeding crops [38], can reduce greenhouse gas emissions by up to 25% [39].

Table 1. Summary of the potential beneficial effects of legume consumption on human health.

Potential Beneficial Health Effects	References
Increased immunological, metabolic, and hormonal regulation	[40,41]
Anticarcinogenic (breast, colorectal, endometrium, and prostate cancers) and anti-inflammatory effects	[42–46]
Reduced risk of cardiovascular and obesity-related diseases, and metabolic syndrome	[47–50]
Reduced cholesterol levels	[51,52]
Reduced risk of type 2 diabetes mellitus	[53–55]
Reduced risk of osteoporosis and depression	[56–59]

In 2014, the UN highlighted the importance of legume biofortification programs, making them a good target in the fight against hidden hunger. However, little has been done since then, and the biofortification of legumes remains little explored [32]. Also, 2016 was considered the International Year of the Pulses by the UN. Pulses are legume crops harvested for dry grain production and are the cheapest source of vitamins, micronutrients, and proteins, making them available for everyone and the perfect target for biofortification [60]. Although legume consumption and cultivation have clear benefits, their cultivation has decreased considerably in the last 50 years compared to cereals [38]. One of the reasons for this decrease might be related to their high susceptibility to climate stresses, making them less attractive to farmers. Research working towards improved legume cultivars less susceptible to environmental stresses and with increased yield is therefore essential in a climate change era [32,61].

3. The Role of PGPB in Legume Nutrition

Relationships between plants and microorganisms occur, generally, in the rhizosphere and exert beneficial effects on plant nutrition and growth, providing plant resistance and/or protection against biotic and abiotic stresses [62]. Bacteria are the most predominant microorganisms in the soil (95%) and the greater concentration is found in the rhizosphere [63].

There is a special type of bacteria, the PGPB, which includes either free-living bacteria or those that establish symbiotic relationships with plants in the rhizosphere or via endophytic colonization [64], that are very promising to be used in plant-based biofortification programs for the nutritional improvement of food crops. Plant growth promotion can be achieved by a series of mechanisms that can be direct: N fixation [65], nutrient (Fe, K, P, and Zn) solubilization [66,67], production of several phytohormones (auxins, cytokinins, gibberellins, ethylene, and abscisic acid) [68–70], and production of siderophores and organic acids [19,71,72], or indirect: biocontrol activity through Fe chelation, induced resistance, production of antibiotic, extracellular enzymes and cyanide, and competition for niches in the rhizosphere [73,74]. This promotion involves a series of bacterial components that act in very specific ways. Molecules produced by PGPB are involved in several overlapping mechanisms, influencing plant growth and nutrition and resistance simultaneously. This subject has been reviewed by Premachandra et al. [75] and Rosier et al. [76]. Figure 1 illustrates the main mechanisms underlying plant growth promotion by bacteria, regarding important molecules involved in the different mechanisms.

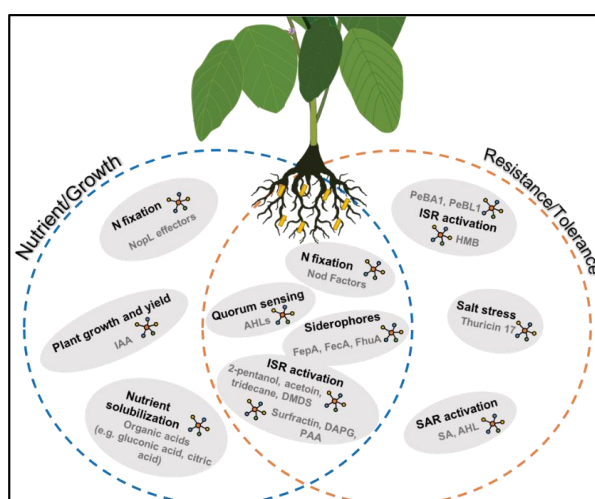


Figure 1. Schematic representation of the main processes and relevant molecules underlying plant growth promotion by bacteria. Abbreviations: AHL = N-acyl homoserine lactone; DAPG = 2,4-diacetylphloroglucinol; DMDS = dimethyl disulfide; HMB = 3-hydroxy-5-methoxy benzene methanol; IAA = indole-3-acetic acid; ISR = induced systemic resistance; N = nitrogen; Nod = nodulation; PAA = phenylacetic acid; SA = salicylic acid.

Apart from all these mechanisms, PGPB have an important impact on the control of several abiotic stresses and in the bioremediation of polluted soils [77–79].

Focusing on nutrient uptake, in particular, PGPB can act in three different ways: replacing soil nutrients, increasing nutrient availability, and/or improving plant access to nutrients [80].

Several studies have shown the importance of PGPB in the uptake of B, Cu, Fe, Mn, and Zn, through the release of organic acids or the production of siderophores [22]. Furthermore, these microorganisms excrete chelating agents and potentiate redox changes and acidification of the rhizosphere, improving the mobility and availability of plant nutrients [18,20,81]. Inoculation with PGPB has had notable success in several crops such as cereals, oil crops, vegetables, and legumes [23–26].

The utilization of PGPB in the improvement of nutrient content in plants is an example of a biofortification strategy that seems to be very promising. Regarding legume biofortification with PGPB, some studies are showing their potential, most of them in chickpeas, mung beans, and soybeans (Table 2). Co-inoculation with *Rhizobium galegae* bv. *orientalis* HAMBI 540 and *Pseudomonas trivialis* 3Re27 increased the nodule numbers and N content of fodder galega plants [82]. Two similar studies in lentils and peas proved that co-inoculation with *Rhizobium leguminosarum*-PR1 and *Pseudomonas* sp. NARs1 or *Pseudomonas* sp. PGERs17 improved nodulation, leghemoglobin, Fe and chlorophyll contents, and N and P uptake [83,84]. A study in common beans showed that co-inoculation with *Pseudomonas* sp. LG and *Rhizobium phaseoli* strain 123 potentiated plant growth and contents of N and phosphorus (P) [85]. Also, inoculation with two *Bacillus aryabhattai* strains (MDSR7 and MDSR14) improved the Zn uptake of soybeans and wheat in Zn-deficient soils [86]. Gopalakrishnan et al. [87] tested seven PGPB in a study with chickpeas and pigeon peas and found *Enterobacter ludwigii* SRI-229 to be the strain better promoting root and shoot development, nodule formation, crop productivity, and soil nutritional factors, followed by *Brevibacterium antiquum* SRI-158 and *Acinetobacter tandoii* SRI-305. In that study, *E. ludwigii* and *A. tandoii* strains significantly increased Fe, Zn, copper (Cu), manganese (Mn), and calcium (Ca) uptake in chickpeas and pigeon peas, respectively. *Pantoea dispersa* MPJ9 and *Pseudomonas putida* MPJ6 isolates have been tested for their ability to produce siderophores, showing a great Fe chelating potential under Fe deficient conditions; in this study, the Fe content of mung beans was increased 3.4-fold, protein content 2-fold, and carbohydrate content 1.5-fold after inoculation with the strain of *P. dispersa* [88]. Co-inoculation with *Bradyrhizobium japonicum* SAY3-7 and *Streptomyces griseoflavus* P4 improved N, P, K, Ca, and magnesium (Mg) uptake in soybean plants [89]. A recent study showed that seed coating with Zn solution in combination with a Zn solubilizer PGPB, *Enterobacter* sp. MN17, improved plant and grain yield and bioavailable Zn, rather than Zn application alone, in chickpeas [90]. Co-inoculation of mung beans with *Bacillus aryabhattai* S10 and *B. subtilis* ZM63 proved to be effective in the improvement of plant growth and nutritional composition; N, P, and potassium (K) concentrations were significantly increased in shoots [91]. Also, inoculation of two varieties of chickpeas with five different PGPB (*Symbion-K* (*Frauteria aurantia*), *Pseudomonas* sp. RA6, *P. citronellis* (PC), *Serratia* sp. S2, and *Serratia marcescens* CDP-13) increased macro- and micronutrient concentrations in plants [92].

Table 2. Summary of studies showing the potential of some bacterial genera for legume biofortification.

Bacterial Genera	Crops	Contribution to Biofortification	References
<i>Rhizobium galegae</i> bv. <i>orientalis</i> HAMI 540 + <i>Pseudomonas trivialis</i> 3Re27	Fodder galega	Increase N content	[82]
<i>Rhizobium leguminosarum</i> -PR1 + <i>Pseudomonas</i> sp. NARs1/ <i>Pseudomonas</i> sp. PGERs17	Lentil, Pea	Increase Fe, N, and P uptake	[83,84]
<i>Pseudomonas</i> sp. LG + <i>Rhizobium phaseoli</i> strain 123	Common bean	Increase P and N uptake	[85]
<i>Bacillus aryabhatai</i> MDSR7 and MDSR14, <i>Enterobacter</i> sp. MN17.	Chickpea, Soybean, Wheat	Increase Zn uptake	[86,90]
<i>Acinetobacter tandoii</i> SRI-305, <i>Enterobacter ludwigii</i> SRI-229	Chickpea, Pigeonpea	Increase Fe, Zn, Cu, Mn, and Ca uptake	[87]
<i>Bradyrhizobium japonicum</i> SAY3-7 and <i>Streptomyces griseoflavus</i> P4	Soybean	Increase N, P, K, Ca, and Mg uptake	[89]
<i>Pantoea dispersa</i> MPJ9, <i>Pseudomonas putida</i> MPJ6	Mung bean	Increase Fe uptake	[88]
<i>Bacillus aryabhatai</i> S10 + <i>B. subtilis</i> ZM63	Mung bean	Increase N, P, and K uptake	[91]
Symbion-K (<i>Frauteria aurantia</i>), <i>Pseudomonas</i> sp. RA6, <i>P. citronellis</i> (PC), <i>Serratia</i> sp. S2, <i>Serratia marcescens</i> CDP-13	Chickpea	Increase macro- and micronutrient uptake	[92]

In recent years, the investigation into the role of PGPB as biofertilizers (BF) for biofortification programs has intensified, although it is still rare. BF, also termed biostimulants, are considered “any substance (of biological origin) or microorganism or their combination applied to plants, seeds, or soil to enhance nutrient uptake efficiency, stress tolerance activation, and crop quality improvement” [93]. Their ability to improve crop quality, productivity, and nutrient uptake is of particular interest at present. BF act in the recycling of nutrients between plant roots, microorganisms, and soils and are key components of integrated nutrient management [94].

Commercial rhizobia-based bioinoculants have existed for more than 100 years, and it is estimated that only 5% of the total fertilizer market includes BF, with about 150 microbe-based registered products available for use in agriculture [95,96]. There are several types of BF including N fixers and solubilizers of boron, P, potash, sulfur, Zn, among others [79]. N fixer BF are the most predominant in the market (78%), followed by P solubilizer BF (15%) [97]. Phytohormone-based BF are also used in agriculture as plant growth regulators [70]. Some examples of commercially available BF are Bio-N, Azonik, Green Earth Reap N4, Get-Phos, BioPotash, Siron, MicroZ-109, and BioSilica, which include strains of *Azospirillum*, *Azotobacter*, *Rhizobium*, *Bacillus*, and *Thiobacillus* and contribute to increased crop yields and soil fertility, showing their potential to be used in sustainable agriculture practices [98,99].

Crop yield can be improved up to 10%–40% with the inclusion of BF, mainly through increases in nutrient uptake [100].

The contribution of PGPB as BF is still very limited at a global level, and it is expected that in the near future the BF market will increase substantially to cope with population growth, the requirements of sustainable agricultural, consumer awareness of product residues, and the environmental impact of crop production. Furthermore, most of the research in this area is focused on rhizobacteria, and the role of endophytic bacteria is still little explored or understood.

4. Iron Biofortification of Legumes with PGPB: A Case Study

In the human diet, Fe is one of the most important micronutrients, being involved in the proper functioning of hemoglobin [31]. Human Fe deficiency is associated with cases of anemia, especially

prevalent in pregnant women and preschool children. This micronutrient deficiency is the only one common to developing and developed economies [101].

In plants, Fe is an essential micronutrient required for multiple biological events, being the fourth most abundant element in the soil. It is required for photosynthesis, respiration, chlorophyll synthesis, and N fixation [102]. Ferric Fe (Fe^{3+}), the form present in the soil, cannot be absorbed by plants, especially in calcareous soils with pH ranging from 7.5 to 8.5 [103,104]. Fe deficiency compromises the production of crops growing on alkaline soils around the world [102,105], and to mitigate this problem plants have evolved two strategies for Fe uptake. Strategy I, found in non-graminaceous monocots and dicots, is characterized by the release of protons, which results in the acidification of the rhizosphere, followed by the reduction of Fe^{3+} to Fe^{2+} through the activity of the ferric chelate reductase (FC-R) FRO2, and transportation to the root epidermal cells by the iron-regulated transporter 1 (IRT1) [102]. Strategy II, found in graminaceous monocots, is characterized by the production of phytosiderophores, which are responsible for Fe chelation, being the Fe-chelating complexes transported to the root epidermic cells [106].

In the Fe uptake process, there are specific low-molecular-weight organic compounds (1–2 kDa) produced by PGPB, under Fe-limiting conditions, called microbial siderophores [107]. They can bind Fe^{3+} at high specificity, increasing Fe solubility, and when this complex connects to specific bacterial receptors, Fe is more easily absorbed and converted to Fe^{2+} [108]. They are classified into three groups: hydroxamates, catecholates (phenolates), and carboxylates, according to the ligands that bind to Fe^{3+} [109]. It has been proposed that bacterial siderophores are involved in the promotion of Fe uptake by Strategy I plants (where legumes are included) through three different approaches: (1) sharing of ferric ions between microbial siderophores and plant FC-R, thus promoting Fe reduction and transport into the plant, (2) influence on the plant's perception of Fe deficiency conditions through the production of indole-acetic acid and ethylene, or (3) sequestration of the Fe required for the growth of phytopathogens [3,110–112]. Gram-positive and Gram-negative bacteria can produce siderophores under Fe deficiency [113,114]. These iron-chelating compounds are produced by several bacterial genera such as *Agrobacterium*, *Bacillus*, *Burkholderia*, *Citrobacter*, *Enterobacter*, *Escherichia*, *Klebsiella*, *Pseudomonas*, *Rhizobium*, and *Stenotrophomonas* [115].

As previously discussed, PGPB help in the uptake of several macro- and micronutrients, particularly of Fe. Few studies have shown the potential of legume biofortification regarding Fe uptake. Inoculation of chickpeas with siderophore-producer PGPB increased the Fe concentration by 81% and 75% in grains and shoots, respectively [116]. Also, in chickpeas, a study proved that inoculation with 19 *Acinetobacter* species increased overall seed nutrient content, with an increase of 10%–38% in Fe composition [117]. Also, pigeon peas and chickpeas treated with *Enterobacter ludwigii* SRI-229 and *Pseudomonas monteilii* SRI-360 had augmented nutrient composition and plant biomass; Fe content was increased up to 18% [87].

Both studies warn of the effects of postharvest processing and cooking on Fe concentration. Patel et al. [88] showed that the Fe content of mung beans could be improved 3.4-fold when inoculated with a *Pantoea dispersa* MPJ9 isolate. Biofortification of Fe using PGPB is a potential reality. Further studies are needed to assess the feasibility of using such types of bacteria at large scale and in field conditions. Efforts for Fe biofortification should also combine strategies to reduce the loss of Fe content during postharvest and processing.

5. Conclusions

Legumes are undoubtedly highly important targets to improve human nutrition while promoting sustainable agriculture. Biofortification of legumes with PGPB is potentially a cost-effective and environmentally safe approach to reduce dependency on chemical fertilizers and on costly biofortification techniques. We face an era where climate changes and increasing population are prevailing, and the combination of PGPB and legumes will most probably be a powerful tool to cope with hidden hunger and a trend for sustainable modern agriculture. Nonetheless, further investigation

on which legumes, bacteria, and specific traits are needed and how they work under different soil compositions and environmental conditions is still essential. There are several studies regarding plant–microbe interactions and their important role in the environment; however, their transposition to agroecosystems and all their implications are still little explored. Furthermore, although the importance of legumes in providing essential nutrients is obvious, the lack of investigation limits the extent of their application in comparison with cereals.

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