

The Recent Use of Plant-Growth-Promoting Bacteria to Promote the Growth of Agricultural Food Crops

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Abstract: In the past 15–20 years, the employment of Plant-Growth-Promoting Bacteria (PGPB) to facilitate the growth of agricultural food crops has increased dramatically. These beneficial soil bacteria, whose use and demonstrations of efficacy have previously been largely limited to the laboratory, have now been shown to be effective under field conditions. In addition, the mechanisms that these bacteria utilize to facilitate plant growth are now mostly well characterized. Moreover, several companies across the globe have commercialized a number of PGPB and there is every indication that this trend will continue to grow. As a consequence of these developments, in this review article, a large number of recent reports on the successful testing of many different types of PGPB and their effects on various food crops is discussed.

Keywords: plant-growth-promoting bacteria; PGPB; commercialized PGPB; organic agriculture; plant growth; plant stress

1. Introduction

The human population is currently ~8 billion people and, according to some estimates, the world will contain ~10 billion inhabitants by 2050 [1]. In addition, the existing level of global food productivity must intensify to be sufficient to meet this increase in the world population. Moreover, the income growth that is expected to occur in lower- and middleincome countries by 2050 will put an additional demand on global agriculture [2]. Several potential solutions to this conundrum have been suggested [3] and it is essential that global agricultural productivity be significantly increased. Some of the major ways of increasing food availability to sustain the world's future needs include: (i) decreasing food wastage, (ii) increasing the use of agricultural chemicals, including both fertilizers and pesticides, (iii) developing and employing more transgenic plants in worldwide agricultural practice, and (iv) dramatically increasing the use of plant-growth-promoting microorganisms (both bacteria and fungi) [3]. None of these approaches by themselves are likely to be sufficient to provide the increased level of global agricultural productivity that will be needed to feed the growing global population by 2050, and it is expected that different countries in the world will employ a combination of these approaches. For a start, many obvious benefits can occur through the increased use of transgenic plants. For example, genetically modifying plants to obtain increased crop yields can lower the amount of agricultural land that is needed for plant production [4]. While not necessarily always tested in the field, over the past twenty years, scientists have developed a number of approaches to increasing the yields of some agricultural plants [5-12]. In contrast to the very active pursuit of higher-yield transgenic plants, the agricultural potential of naturally occurring plant-growth-promoting bacteria (PGPB) has barely been explored. However, we believe that, in the future, PGPB will likely provide a highly effective means of promoting plant growth throughout the many different agricultural environments that exist globally [13,14].



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2. Plant-Growth-Promoting Bacteria (PGPB)

Soil contains a very large number of bacteria, with the highest concentrations of these bacteria typically being found around the roots of plants, i.e., in the plant rhizosphere [3,15,16]. These bacteria may be beneficial for plant growth (i.e., PGPB), inhibitory to plant growth (i.e., phytopathogenic bacteria), or not have any discernible effect on plant growth (i.e., commensal bacteria). This typical bacterial localization reflects the fact that most plant roots commonly exude a significant fraction, i.e., from 5–30%, of all of the carbon that is fixed by the plant through the process of photosynthesis, and provide this fixed carbon to soil microbes that use it as a food source [17–19]. Considerable evidence suggests that different plants attract different types of soil bacteria [16,20–25]. This occurs as a consequence of the fact that each plant's root exudes contain a unique mixture of small molecules (mostly sugars, amino acids, and organic acids) that attract a specific portion of the soil bacterial population.

The interest in PGPB is a consequence of their ability to positively affect plant growth and development as follows: (i) increasing the plant biomass, (ii) increasing the plant nutrient content (including nitrogen, phosphorus, potassium, and iron) [3], (iii) increasing the root and/or shoot length, (iv) increasing the rate of the seed germination, (v) protecting plants against various disease-causing pathogens (including phytopathogenic bacteria and fungi, as well as nematodes and insects) [26–29], and (vi) increasing the plant tolerance to various abiotic stresses (such as temperature extremes, high salt levels, root oxygen concentration, flooding, and drought) [3,30–35].

Some PGPB bind to and colonize the root outer surface (i.e., the rhizoplane), while others enter the plant root and permanently colonize the spaces between the root cells (i.e., they are endophytic), and other bacteria form nodules on the plant roots (i.e., they are said to symbiotic). Notwithstanding the fact that different PGPB preferentially interact with different plants and occupy different niches within those plants (i.e., root surface, root or shoot interior, or within a root nodule), all PGPB appear to use the same mechanisms to promote plant growth. Conceptually, the mechanisms that PGPB use to facilitate plant growth are considered to be either direct or indirect. Direct mechanisms include anything performed or produced by the PGPB that directly affects the growth of the plant (Figure 1). The direct mechanisms that are employed by PGPB include: facilitating the solubilization and uptake of minerals such as iron, potassium, and phosphorus; nitrogen fixation; the synthesis of phytohormones such as cytokinin, gibberellin, and auxin; and the modulation of plant ethylene and 1-aminocyclopropane-1-carboxylate (ACC) levels via the enzyme ACC deaminase [3,36–38]. On the other hand, indirect mechanisms include the PGPB preventing or lowering the damage or growth inhibition to the target plant using a phytopathogen (Figure 1). The indirect mechanisms that are employed by PGPB include: antibiotic and hydrogen cyanide synthesis; the solubilization and sequestration of iron that might otherwise be used by phytopathogens; the synthesis of fungal cell-wall-degrading enzymes; outcompeting pathogens; the synthesis of volatile organic compounds; auxin synthesis; the modulation of plant ethylene levels; inducing systemic resistance; and quorum quenching [3,36–38]. To date, all the PGPB that have been studied possess a few, but not all, of these mechanisms. This is because having too many non-essential genes functioning simultaneously will put a metabolic load on a bacterium, thereby decreasing its overall environmental fitness [39].

One way in which PGPB can provide plants with an extensive range of plant-growthpromoting mechanisms, without creating a metabolic load for the PGPB, is by having these organisms act in concert with other PGPB in the soil as part of a bacterial consortium [11,25,40] or microbiome containing both PGPB and plant-growth-promoting fungi [16,41–43].

In addition to bacteria, rhizospheric soils contain a large number of mycorrhizae, plant-beneficial fungi that have been estimated to form a relationship with more than 90% of all land plants [44–47]. Mycorrhizae colonize plant roots, either intracellularly or extracellularly, with ectomycorrhizae extracellularly colonizing the outside of plant roots (commonly in gymnosperms and other woody plants) and the more common endomycor-

rhizae (also referred to as arbuscular mycorrhiza; AM) colonizing roots intracellularly. This 400–460-million-year-old relationship between plants and mycorrhizae has been suggested to have co-evolved with land plants and is, in fact, argued to be responsible for the development of all land plants [44]. In the relationship between mycorrhizae and plants, energy sources and carbon compounds move from the plant to the fungus, thereby enabling its growth and development, while inorganic resources (i.e., minerals) and water concomitantly move from the fungus to the plant, thereby aiding its development [47]. Mycorrhizae act as effective extensions of plant roots in their uptake of minerals and water. Some soil bacteria bind to both plant roots and mycorrhizal hyphae and actively contribute to the mycorrhizal symbiosis [46,48–50]. The interaction of PGPB with mycorrhizae and plants facilitates the growth of plants under a wide range of stressful conditions [51].



Figure 1. Schematic representation of the plant-growth-promoting effects used by PGPB. Abbreviations: HCN, hydrogen cyanide; VOC, volatile organic compounds; ISR, induced systemic resistance; P, phosphorus; K, potassium; Fe, iron; and N, nitrogen.

3. Recent Research in PGPB and Agricultural Food Crops

The greatest utility of plant-growth-promoting bacteria (PGPB) has been for agricultural and horticultural practices, including their use as inoculants for food crops. This area has been extensively researched [52] and is work that continues presently. Early investigations of PGPB occurred in the mid-20th century in India and the former Soviet Union. This research was extensive and sometimes indicated mixed results; however, more recent studies have elaborated on the mechanisms used by these bacteria and demonstrated a plethora of positive results under a wide range of conditions [37,38,53,54]. The elucidation of the plant-growth-promoting mechanisms of PGPB, significant advances in microbe identification and characterization, and an increased interest in alternative fertilizers have allowed for work to continue in this area.

Selected examples of the published research over the last decade examining the effects of plant-growth-promoting bacteria on various major food crop types are summarized in Table 1. Overall, there are many examples of the successful inoculation of PGPB with major crops such as maize, rice, soybeans canola, and wheat in greenhouse and field-scale experiments. A diversity of other crops is present in the literature, albeit to a lesser extent, with crops such as pulses (e.g., peas, lentils, fava beans, lima beans, Adzuki beans, kidney beans, pinto beans, mung beans, black-eyed peas, lupins, and cowpea, etc.), vegetables, fruit crops, and trees. Table 1 summarizes the results of many studies and indicates that PGPB provide a large number of benefits to treated plants, including facilitating root growth, germination rates, yield, leaf area, chlorophyll content, nitrogen content, root and shoot (dry and fresh) weights, and delayed leaf senescence. There has been some debate in the past about the transferability of the positive impacts of inoculation from in vivo

results to in-field results [52,55]. However, Table 1 shows a number of field and greenhouse studies that emphasize that the efficacy of inoculation is being explored in practical settings and that there is now considerable work that correlates the increased benefits of PGPB inoculation at the in vivo level to field results [56].

Table 1. Some examples of agricultural food crop responses to PGPB inoculation. AMF are arbuscularmycorrhizal fungi.

Plant	Bacteria	Experimental Conditions	Results	References
Apple	Alcaligenes sp. Agrobacterium sp. Staphylococcus spp. Bacillus sp. Pantoea sp.	Outdoor pots	 Increased citric, malic, malonic, butyric, and lactic acid content in the leaf by 25.1%, 21.8%, 29.6%, 18.0%, and 18.2%, respectively 	[57]
Banana	Bacillus amyloliquefaciens Pseudomonas fluorescens	Greenhouse	 Increased leaf area (69% to 80%) Increased growth similar to or slightly greater than with 100% chemical fertilization Increased root length by 40% to 49.5% 	[58]
Barley Oats	Pseudomonas sp. Pseudomonas corrugate	Growth pouchGreen- houseField	 Salt stress In the greenhouse, <i>Pseudomonas corrugate</i> increased root biomass of barley and oats by 200% and 50%, respectively In field tests, shoot biomass of oats tripled when treated with <i>Pseudomonas</i> sp. and doubled with <i>Pseudomonas corrugate</i> 	[59]
Barley Wheat	Bacillus megaterium Bacillus subtilis Bacillus megaterium Azospirillum brasilense	Field	 Increased grain yield (27.5% to 31.9%), straw (1.1% to 5.3%), and total yield (15.1% to 27.8%) in wheat with individual strains Mixtures of strains increased grain yield (54.7%), straw (2.1%), and total yield (6.7%) in wheat Increased grain yield (15.1% to 27.8%), straw (10.8% to 15.5%), and total yield (14.5% to 18.5%) in barley with individual strains Mixtures of strains increased yield (57.8%), straw (14.6%), and yield (17.5%) in barley 	[60]
Bean, common (Phaseolus vulgaris)	Rhizobium tropici	Greenhouse	 Co-inoculation with AMF <i>Glomus intraradices</i> Increased soil P (30% to 40%) and N (29% to 42%) Increased nodule number (63% to 70%), nodule mass (40% to 43%), shoot dry weight (23% to 24%), and root growth (39% to 48%) 	[61]
Bean, common (Phaseolus vulgaris)	Bacillus subtilis	Greenhouse	 Biocontrol of bacterial wilt caused by Curtobacterium flaccumfaciens pv. flaccumfaciens (Cff) Disease control of 42% to 76% 	[62]
Bean, common (Phaseolus vulgaris)	Bacillus subtilis Burkholderia sp.	Greenhouse Field	 Co-inoculation with AMF, <i>Rhizobium tropici</i>, and <i>Trichoderma asperellum</i> Increased shoot and root accumulation, number of nodules, and yield components (24.63%) 	[63]

Plant	Bacteria	Experimental Conditions	Results	References
Bean, faba Wheat	Acinetobacter sp. Rahnella sp.Ensifer meliloti	Field	 Co-inoculation with rhizobia Single and mixture increased fava bean pod weight (up to 123.78%) Increased wheat spike dry weight up to 63.05% Highest values when plants were inoculated with mixture 	[64]
Bean, mung (Vigna radiata L.)	Pseudomonas syringae Pseudomonas fluorescens	Outdoor pots	 Salt stress conditions Co-inoculation with <i>Rhizobium phaseoli</i> Increased shoot fresh weight (145%), root fresh weight (173%), number of pods per plant (150%), pod fresh weight (182%), and total dry matter (269%) 	[65]
Bean, mung (Vigna radiata L.)	Rhizobium sp. Pseudomonas putida	Pot experiment	 Co-inoculation with fungi Aspergillus niger, Rhizopus sp., and Trichoderma viride Dual inoculation of Pseudomonas putida with Trichoderma viride increased root length (up to 86.57%), shoot length (up to 56.91%), root dry weight (up to 94.42%), and shoot dry weight (up to 56.09%) 	[66]
Bean, runner	Bacillus pummilus Bacillus mycoides	Field	- Increased grain yield (41.40%) and soluble protein content (16.24%)	[67]
Canola	Azotobacter chroococcum Azospirillum brasilense Paenibacillus polymyxa	Field	 Azospirillum brasilense + 30 kg N/fed produced the highest increases in both seed yield/plant and seed yield/hectare Seed yield increased by 40% over two growing seasons 	[68]
Canola	Bacillus megaterium	Greenhouse	 Highest seed yield with combined bacterial and chemical fertilizer treatment 	[69]
Canola	Azotobacter chroococcum Pseudomonas putida	Field	- Azotobacter and Pseudomonas increased yield components by 15.8% and 13.7%	[70]
Canola	Azospirillum sp. Azotobacter chroococcum	Field	- Increased seed oil content	[71]
Canola	Paenibacillus polymyxa	Growth chamber	 Increased seedling length, biomass, and fixed N by 70%, 200%, and 27%, respectively Increased pod mass (greater than 50%) 	[72]
Canola	Bacillus spp. Serratia spp. Arthrobacter spp. Pantoea spp.	Field	- Increased seed yield from 21% to 44%	[73]
Canola	Pseudomonas fluorescens Azotobacter chroococcum Azospirillum brasilense (combined commercial product)	Greenhouse	- Inoculation increased stress tolerance to cabbage aphid (<i>Brevicoryne brassicae</i>)	[74]
Canola	Pseudomonas sp. Azospirillum brasilense	Greenhouse	 Pseudomonas, together with salicylic acid, alleviated salt stress effects 	[75]
Canola	Pseudomonas brassicacearum	In vitro Greenhouse Field	- Inoculation in field tests increased pod number, pod dry weight, and shoot dry weight by 216.0%, 174.3%, and 197.8%, respectively	[56]
Canola	Azotobacter chroococcum Azospirillum brasilense Bacillus megaterium	Field	- Under reduced nitrogen fertilization conditions, mixture of species increased seed yield (7.7% to 9.8%) and fat yield (9.2% to 11.4%)	[76]
Canola	Streptomyces sp.	Growth chamber	- Increased root length (53.14%), shoot length (65.6%), and plant fresh weight (60%)	[77]

Plant	Bacteria	Experimental Conditions	Results	References
Canola	Pseudomonas sp. Frigoribacterium sp. Sphingomonas sp. Sphingobacterium sp. Microbacterium sp. Bacillus sp. Rhodococcus sp.	Greenhouse	- <i>Pseudomonas</i> sp. had the greatest effect on increased seedling growth and germination	[78]
Canola	Azomonas sp. Azospirillum brasiliense Methylobacterium komagatae Rhizobium sp.	Greenhouse	 <i>M. komagacae</i> increased root area by 44% <i>M. komagacae</i> and <i>A. brasiliense</i> increased grain yield up to 55% 	[79]
Canola	Acinetobacter radioresistens Enterobacter cloacae	In vitro Field	 Salt stress conditions Increased fresh weight, dry weight, total seed weight, and oil yield (187.53%, 112.32%, 368.14%, and 90.24%, respectively, for <i>A. radioresistens</i>) and 162.67%, 109%, 306.8%, and 84.39%, respectively, for <i>E. cloacae</i>) 	[80]
Canola, wheat	Pseudomonas sp. Bacillus sp.	Greenhouse	 Silicon co-inoculation with <i>Pseudomonas</i> strain reduced stress indicators the most for both crops Salt stress conditions 	[81]
Cassava	Azospirillum amazonense Herbaspirillum seropedicae Gluconacetobacter diazotrophicus	Greenhouse	 Co-inoculation with AMF Glomus clarum Inoculated plants assimilated N in equal proportion to those that received mineral nitrogen Herbaspirillum seropedicae was the most efficient to fix N 	[82]
Cassava Okra	Herbaspirillum seropedicae Burkholderia silvatlantica Burkholderia sp.	Outdoor pots Field	 Combined PGPB and humic acid mixture Pot trials showed increased root weight of 200% Plant treatment in the field increased yields of cassava and okra by 70% and 50%, respectively 	[83]
Chickpea	Pseudomonas pseudoalcaligens Pseudomonas putida	Pot experiments	 In salt stress conditions Both PGPB increased leaf size, lateral roots, number of leaves, and number of fruits 	[84]
Chickpea	Pantoea dispersa Chryseobacterium indologenes Pseudomonas geniculata Stenotrophomonas pavanii Stenotrophomonas maltophilia Chryseobacterium sp. Chryseobacterium indologenes Stenotrophomonas acidaminiphila	Field	 Increased nodule number (46%), nodule mass (50%), shoot mass (42%), and grain yield (25%) Increased organic carbon (24%), total nitrogen (19%), and available phosphorous (29%) 	[85]
Finger Millet Pigeon Pea	Pseudomonas spp.	Field	 Co-inoculation with AMF Intercropping yield increase due to inoculation was 126% to 128% 	[86]
Lettuce	Bacillus amyloliquefaciens Bacillus pumilus Bacillus subtilis	Field	- Increased plant vigor and head weight by 49%	[87]
Maize	Azospirillum lipoferum Azospirillum brasilense Azotobacter chroococcum	Field	- Coinoculation with <i>Azotobacter</i> and <i>Azospirillum</i> increased dry weight up to 115%	[88]

Plant	Bacteria	Experimental Conditions	Results	References
Maize	Pseudomonas sp Bacillus sp. Azotobacter chroococcum	Greenhouse Field	 Increased height (up to 17.15%) and dry weight (up to 35.48%) Highest dry weight and yield were with coinoculation with all three strains 	[89]
Maize	Azotobacter chroococcum	Growth chamber	 Salt-tolerant strains partially ameliorated yield decrease in salt stress conditions 	[90]
Maize	Pseudomonas fluorescens Pseudomonas putida Azospirillum lipoferum	Field	- <i>A. lipoferum</i> increased plant height by 37% and below ground mass by 56%	[91]
Maize	Herbaspirillum seropedicae	Field	 Application of inoculant at the V8 growth stage as foliar spray resulted in an increased grain yield of 38% Co-inoculation with humic acid 	[92]
Maize	Bacillus spp. Pseudomonas spp.	Greenhouse	 Significantly increased root and shoot yield and nitrogen and phosphorus uptake by plant tissue 	[93]
Maize	Azospirillum brasilense Azospirillum sp. Enhydrobacter sp. Rhizobium sp.	Field	- <i>Rhizobium</i> sp. 8121 and <i>Azospirillum</i> sp. L26 increased yield equivalent to nitrogen inoculation of 160 kg/ha	[94]
Maize	Klebsiella sp. Klebsiella pneumoniae Bacillus pumilus Acinetobacter sp.	Greenhouse	- Nitrogen-fixing <i>Bacillus pumilus</i> S1r1 increased ear yield up to 30.9%	[95]
Maize	Pseudomonas sp. Bacillus amyloliquefaciens	Greenhouse Field	 Pseudomonas sp. DSMZ 13134 improved biomass yield, but mixed reproducibility across experiments 	[96]
Maize	Lysinibacillus sphaericus Paenibacillus alvei Bacillus safensis Bacillus pumilus Brevundimonas vesicularis	Field	- Yield increased from 24% to 34% over two growing seasons	[97]
Maize	Kosakonia radicincitans	Field	 Grain and silage yields increased by 18.7% to 32.8% and 14.9% to 29.3%, respectively Differences observed on inoculant formulation–solid formulation produced 9.7% to 18.7% grain yield increases, while liquid formulation produced 20% to 32.8% 	[98]
Maize	Azospirillum brasilense Pseudomonas fluorescens	Field	 Combined strain inoculant significantly increased grain yield Differential effects observed depending on existing microbial biota in soil Paired with N fertilization, grain yield and root length increased 	[99]
Maize	Pseudomonas fluorescens	Field	- Co-inoculation with AMF <i>Funneliformis</i> <i>mosseae</i> in water-stressed conditions increased grain yield by 31%	[100]
Maize	Bacillus spp. Pseudomonas moraviensis sp.	Greenhouse	 Inoculation effect not apparent at later growth stages with multiple fertilization treatments The fertilizers, at optimal N rate, may mask the influence of PGPB on growth parameters 	[101]
Maize	Bacillus amyloliquefaciens	Greenhouse Field	 61.38% decrease in <i>Bipolaris maydis</i> blight disease index Marketable yield increased by 7.28% to 10.89% 	[102]
Maize	Pseudomonas fluorescens Azospirillum brasilense	Field	 <i>P. fluorescens</i> increased plant biomass from 20% to 24% Grain yield increased from 29% to 31% 	[103]

Plant	Bacteria	Experimental Conditions	Results	References
Maize	Bacillus megaterium Azotobacter chroococcum Bacillus subtilis	Field	 <i>B. subtilis</i> increased total solids content in seeds (92%), as well as crude fiber content (46%) Increased grain yield from 5.5% to 13.4% 	[104]
Maize	Pseudomonasreactans Pantoea alli	Growth chamber	 Coinoculation with AMF (<i>Rhizoglomus</i> <i>irregulare</i>) ameliorated salt stress effects by promoting biomass increase of 35% and significantly increased nitrogen content in shoots 	[105]
Maize	Azospirillum brasilense Bacillus subtilis Pseudomonas fluorescens	Field	 <i>B. subtilis</i> and <i>A. brasilense</i> inoculation resulted in respective increases of 100.5% and 54.6% on phosphorus use efficiency Differential response in yield depending on inoculation strain and phosphorus rate 	[106]
Maize	Aeromonas encheleia Pseudomonas azotoformans	In vitro and greenhouse	 <i>A. encheleia</i> increased germination by 78% Increased root elongation and biomass 	[107]
Maize	Bacillus mojavensis Bacilllus subtilis Bacillus pumilus Bacillus pseudomycoides	Field	- B. mojavensis increased yield by 16%, B. subtilis by 13.8%, B. pumilus by 11.8%, and B. pseudomycoides by 9.8%	[108]
Maize Soybean	Azospirillum sp.	Field	 Dry shoot yield not enhanced for either maize or soybean Significant differences in yield between different soil types 	[109]
Maize Soybean	Bacillus sp. Burkholderia ambifaria	Greenhouse	 Dry weight shoot increased by at least 47% for both strains and crops Increase in maize root dry weight from 136.9% to 247.8% Soybean root dry weight did not increase after inoculation with either strain 	[110]
Maize Wheat	Azospirillum brasilense	Field Outdoor pots	 Co-inoculation with <i>Trichoderma harzianum</i> Single and double inoculation with <i>A. brasilense</i> and <i>T. harzianum</i> increased wheat yield growth Treatment with <i>A. brasilense</i> doubled plant fresh and dry weight Increased wheat spike length (40%), dry grain weight of 100 grains (50% to 180%), and number of grains per spike (65%) 	[111]
Millet	Bacillus spp.	Greenhouse	 Biological control of <i>Rhizoctonia solani</i>, Sclerotium rolfsii, and <i>Fusarium solani</i> by 35.68% to 71.96% Increased plant biomass 	[112]
Mustard (Brassica juncea)	Pseudomonas argentinensis Pseudomonas azotoformans	Greenhouse	 Salt stress conditions Increased root and shoot dry weight by 139% to 291% 	[113]
Onion	Bacillus subtilisPseudomonas fluorescens Azotobacter chroococcum	Field	 Highest bulb size and onion yield with Bacillus subtilis and Azotobacter chroococcum All inocula increased plant height 60 days post-sowing 	[114]
Palm	Bacillus cereus	Greenhouse	 Co-inoculation with Trichoderma asperellum increased root dry mass Individual inoculation increased plant top and root dry weights 	[115]
Pepper	Pseudomonas fluorescens	Field	- With AMF and <i>Trichoderma</i> , triple inoculation significantly increased fruit yield	[116]

Plant	Bacteria	Experimental Conditions	Results	References
Pepper	Bacillus spp. Pseudomonas spp. Stenotrophomonas spp. Enterobacter spp. Achromobacter spp. Comamonas spp. Acinetobacter spp. Burkholderia spp. Serratia spp. Ocrobactrum spp. Pantoea spp. Rhizobium spp. Aeromonas spp. Klebsiella spp.	Greenhouse	- Drought-tolerant isolates increased root and shoot length by 23.6% to 52.8% and 41% to 79.6%, respectively	[117]
Potato	Pseudomonas koreensis Pseudomonas corrugata Enterobacter sp. Pseudomonas koreensis Psuedomonas fluorescens Bacillus spp.	Growth chamber	- Three isolates significantly increased plant growth in healthy plantlets and seven isolates increased plant growth in <i>R.</i> <i>solani</i> -diseased plantlets compared to commercial <i>Bacillus</i> spp. strain	[118]
Potato	Bacillus subtilis	Greenhouse Field	 Biocontrol of <i>Rhizoctonia solani</i> Increased tuber biomass, tuber number per plant, and plant biomass in greenhouse and the field 	[119]
Potato	Bacillus subtilis	Greenhouse	 Increased root and shoot length by 20.89% and 19.18%, respectively Increased root and shoot dry weight by 95.94% and 60.83%, respectively 	[120]
Potato	Azospirillum brasilense	Greenhouse to Field	 Tuber yield per square meter increased by more than 45% for all cultivars Overall tuber weight increased by 30% 	[121]
Potato	Azospirillum sp. Agrobacterium sp. Pseudomonas sp. Enterobacter sp. Rhizobium sp.	Growth chamber	- <i>Azospirillum</i> sp. yielded greatest increases for plant growth and N uptake	[122]
Potato	Pseudomonas fluorescens Azospirillum brasilense	Field	- Yield increase of 17% to 31%	[123]
Potato	Bacillus megaterium Bacillus subtilis	Field	 With humic acid, increased total potato tuber yield by ~140% compared to NPK fertilization tuber yield of 111% 	[124]
Potato	Bacillus sphaericus Erwinia sp., Klebsiella sp., Azospirillum brasilense	Field	- <i>Klebsiella</i> and application of 33 kg N/ha demonstrated the highest N, P, K, Ca, and Mg contents of storage roots	[125]
Potato	Azospirillum brasilense	Growth chamber	 Increased shoot height (16%) and in-leaf blade number (14%) Yield per square meter increased by an average of 17% in two cultivars 	[126]
Potato	Bacillus licheniformis	Greenhouse	 Inoculation with biochar No increase in plant growth and water use efficiency Increased leaf gas exchange rates, including photosynthesis rate, stomatal conductance, and transpiration rate at early seedling stage 	[127]
Rice	<i>Azospirillum</i> sp. <i>Trichoderma</i> sp. Unidentified rhizobacteria	Field	- Azospirillum-based biofertilizer increased seasonal yields from 5% to 18%	[128]

Plant	Bacteria	Experimental Conditions	Results	References
Rice	Azospirillum brasilense Azospirillum lipoferum Pseudomonas sp.	Laboratory Field	 Azospirillum brasilense increased grain weight by 39.5% Azospirillum lipoferum increased grain weight by 18.5% Pseudomonas increased grain weight by 13.8% 	[129]
Rice	Azospirillum brasilense Pseudomonas fluorescens	Field	 Biomass increased from 1.9% to 8.7% Yield increased from 7.3% to 20.2% Differential responses depending on rice cultivar, increases for both semi-dwarf and tall varieties with inoculation 	[130]
Rice	Pseudomonas putidaPseudomonas fluorescens Azospirillum lipoferum	Field	- <i>P. putida</i> nearly doubled the grain iron content	[131]
Rice	Bacillus pumilus	Field	 Combination of inoculation and 100% fertilization on 21-day-old seedling increased biomass Growth and yield similar to 50% fertilization 	[132]
Rice	Pseudomonas koreensis Bacillus coagulans	Field	 When PGPB were combined with biochar, the salt stress effect was eliminated for 1000 grain weight yield 	[133]
Rice	Bacillus tequilensis Bacillus aryabhattai	Greenhouse	- Increased grain yield under saline conditions	[134]
Rice	Acidovorax delafieldii	Greenhouse	- Inoculation, in combination with 50% recommended rate of fertilization, as effective for yield enhancement as full-rate fertilization	[135]
Rice	Kosakonia sp. Staphylococcus sp.	Greenhouse	 Increased survival rates in cold stress conditions, 69% and 85%, respectively No yield (1000 grain weight) loss with cold stress 	[136]
Rice	Bacillus pumilus	Outdoor pots	 Increased plant height by 12.90% to 26.48%, root length by 9.55% to 23.09%, chlorophyll content by 10.13% to 27.24%, carotenoids by 8.38% to 25.44%, plant fresh weight by 12.33% to 25.59%, and dry weight by 8.66% to 30.89% 	[137]
Rice	Bradyrhizobium japonicum Bradyrhizobium elkanii	Field	- <i>B. elkanii</i> increased rice growth to the greatest extent by approximately 1000 kg/ha	[138]
Rice	Bacillus cereus Staphylococcus coagulans Psuedomonas aeruginosa Bacillus paramycoides Psuedomonas aeruginosa Psuedomonas aeruginosa Bacillus tequilensis Bacillus wiedmannii	Field trials	 Iron content of grain increased from 37.46% to 54.97% 1000 grain weight increased from 11.88% to 38.11% for all bacterial treatments 	[139]
Rice	Rhodopseudomonas palustris	Field	- Increased root length (25%), root dry weight (57%), productive tillers per plants (26%), average grains per plant (38%), grain yield (33%), and 1000 grain weight (1.6%)	[140]
Rice Wheat	Ochrobactrum anthropic Pseudomonas fluorescens Pseudomonas palleroniana	Field	 Increased grain yield by 65.6% in rice and 74.4% in wheat Increased straw yield by 26.8% in rice and 36.9% in wheat 	[141]
Soybean	Rhizobium japonicum Azotobacter chroococcum Azospirillum brasilense	Field	 Drought stress conditions Inoculation increased membrane stability, chlorophyll content, nitrogen content, and relative water content 	[142]

Plant	Bacteria	Experimental Conditions	Results	References
Soybean	Bradyrhizobium japonicum Azospirillum sp.	Outdoor pots Field	 Increased seed yield by three to six times Increased nodule dry weight by 26.51% and 18.83% 	[143]
Soybean	Bacillus amyloliquefaciens Bradyrhizobium japonicum	Growth chamber	- Co-inoculation with two strains increased nodulation	[144]
Soybean	Pseudomonas chlororaphis Enterobacter asburiae Cellulosimicrobium cellulans Pseudomonas putida Stenotrophomonas maltophilia Stenotrophomonas sp.	Greenhouse	- Increased root and shoot dry weight from 28% to 63%	[145]
Soybean	Bacillus subtilis Bacillus licheniformis	Field	 Water deficit stress Inoculation increased grain yield (22.9%), followed by protein content (18.8%) and radiation use efficiency (15.2%) 	[146]
Soybean	Bradyrhizobium japonicum Pseudomonas fluorescens	Field	 Inoculation with <i>P. fluorescens</i> more effective than <i>R. japonicum</i> in improving grain yield and quality 	[147]
Soybean	Bacillus cereus Bacillus megaterium	In vitro Outdoor pots	 In salt and drought conditions, bacterial co-inoculants combined with single fungal strain produced the greatest increases in germination properties and seedling biomass 	[148]
Soybean	Bradyrhizobium japonicum Bradyrhizobium diazoefficiens Bacillus subtilis Azospirillum brasilense Bradyrhizobium diazoefficiens Rhizobium tropici	Greenhouse Field	 Increased root diameter (1.6%), root length (28.5%), root volume (19.7%), root surface area (17.8%), number of nodules (29%), nodule dry weight (27.2%), root dry weight (13.5%), and shoot dry weight (3.8%) Field yield increase of 485 kg/ha 	[149]
Soybean	Pseudomonas fluorescens Pseudomonas putida Bacillus subtilis	In vitro Greenhouse	Salt stress conditionsIncreased stem length and shoot fresh weight	[150]
Soybean	Enterobacter spp. Pseudomonas spp. Xanthomonas spp.	Greenhouse	 Selection of a consortium of native microbes as inoculants Increased seedling radicle length, hypocotyl length, and total dry weight by 44%, 30%, and 29%, respectively 	[151]
Soybean	Enterobacter spp.	Outdoor pots Field	- Some strains increased seed weight per plant by up to 65%, pod number per plant (79.82%), and seed oil content (5.23%)	[152]
Soybean	Azospirillum brasilense Bradyrhizobium japonicum	Field	 25 field studies conducted across soybean-growing regions in U.S. Seed yield response with co-inoculation was significant in 2 of 25 sites 	[153]
Soybean	Arthobacter sp. Bacillus sp. Lysinibacillus sp. Paenibacillus sp. Sinomonas sp. Kosakosania radicincitans	Field	 Co-inoculation with AMF Mixture of PGPB and AMF increased the number of root nodules by 67.2% and 57%, respectively Co-application of PGPB and AMF increased the number of root nodules by 68.4% Increased grain yield ranged between 0.50 and 1.16 tons/ha in all applied treatments 	[154]
Soybean	Azotobacter chroococcum Piriformospora indica	Field	 In drought stress conditions, increased oil content by 9.37% to 12.87% Co-inoculation more effective than single-strain inoculation 	[155]

Plant	Bacteria	Experimental Conditions	Results	References
Soybean Wheat	Enterobacter cloacae subsp. dissolvens	Field	 Increased soybean shoot and seed weight up to 13.77% and 16.09%, respectively Increased wheat shoot and seed weight by 39.13% and 49.14%, respectively 	[156]
Stevia	Bacillus safensis	Greenhouse	 Increased fresh and dry weight Increased concentration of stevioside by 153.12% 	[157]
Strawberry	Alcaligenes sp. Staphylococcus spp. Agrobacterium sp. Pantoea sp. Bacillus sp.	Greenhouse	 Calcareous soil conditions increased growth measurements with all bacterial treatments <i>Alcaligenes</i> sp. increased fruit yield, number, and weight by 47.5%, 34.7%, and 9.4%, respectively 	[158]
Sugar beet	Azotobacter chroococcum Azospirillum brasilense Bacillus megaterium	Field	 Reduction in N fertilization requirements with no yield cost increased sugar yield 	[159]
Sunflower	Achromobacter sp. Chryseobacterium sp. Azospirillum sp. Burkholderia sp.	Growth chamber	 Increased dry shoot weight by 58% to 77% Enhanced N uptake by 62% to 140% 	[160]
Sweet potato	Bacillus cereus Achromobacter xylosoxidans	Greenhouse	- Increased plant growth and N, P, K, Ca, and Mg uptake in 60-day-old plants	[161]
Sweet Potato	Bacillus cereus Bacillus subtilis Serratia sp.	Field	 Increased potato yield by 26.44% over two trial years Reduction in <i>Erwinia</i> and <i>Ralstonia</i> detected in soil 	[162]
Tomato	Herbaspirillum seropedicae	Greenhouse Field	 Inoculation with vermicompost Increased root, fruit biomass (87.1%), and brix (a measure of sweetness) 	[163]
Tomato	Pseudomonas fluorescens Pseudomonas sp.	Field	 AMF combination inoculation Mixture of bacteria and fungi increased fruit weight (35%) 	[50]
Tomato	Bacillus subtilis Bacillus amyloliquefaciens Pseudomonas fluorescens	Greenhouse	 Biocontrol of tomato wilt caused by <i>Clavibacter michiganensis</i> subsp. Michiganensis <i>B. amyloliquefaciens</i> reduced disease severity by 74.4%, <i>P. fluorescens</i> by 40%, and <i>B. subtilis</i> by 53.3% 	[164]
Tomato	Pseudomonas sp.	Greenhouse	 Salt stress conditions Wild-type and trehalose-over-producing mutant strains significantly increased root and shoot length, total dry weight, and chlorophyll content 	[165]
Wheat	Providencia sp. Anabaena sp.	Field	 Increased protein content up to 18.6% Increased Fe, Mn, and Cu contents by 105.3%, 36.7%, and 150.0%, respectively 	[166]
Wheat	Bacillus subtilis Bacillus megaterium Azospirillum brasilense	Field	- Increased grain yield by 19% to 24%	[167]
Wheat	Bacillus amyloliquefaciens Azospirillum brasilense	Growth chamber	Drought stress conditionsReduced drought stress on wheat	[168]
Wheat	Pseudomonas putida Enterobacter cloacae Serratia ficaria Pseudomonas fluorescens	Field	Salt stress conditionsIncreased grain yield by 20% to 31%	[169]

Plant	Bacteria	Experimental Conditions	Results	References
Wheat	Burkholderia phytofirmans	Field	 Increased grain yield (by 18 to 21%) Decreased adverse effects of drought on relative water contents and CO₂ assimilation rate Increased photosynthetic rate, water use efficiency, and chlorophyll content 	[170]
Wheat	Bacillus pumilus Bacillus aquimaris Bacillus arsinicus Arthrobacter sp. Bacillus cereus Bacillus mendocina Bacillus subtilis	Field	 Salt stress conditions <i>B. subtilis</i> SU 47 reduced Na content in wheat leaves by 23% and increased yield by 17.8% 	[171]
Wheat	Bacillus amyloliquefaciens Bacillus brevis Bacillus circulans Bacillus coagulans Bacillus firmus Bacillus halodenitrificans Bacillus laterosporus Bacillus licheniformis Bacillus megaterium Bacillus mycoides Bacillus pasteurii Bacillus polymyxa Bacillus subtilis	Field	 Co-inoculation with commercial AMF Inoculation with microorganisms (AMF or PGPB, or both) increased the above-ground biomass yield in both the fertilized and unfertilized treatments 	[172]
Wheat	Pseudomonas moraviensis Bacillus cereus	Field	 <i>P. moraviensis</i> increased seeds/spike (15%) and seed weight (22%) <i>B. cereus</i> increased seeds/spike (18%) and seed weight (21%) 	[173]
Wheat	Bacillus sp. Pseudomonas sp.	Field	 Increased grain yield for two varieties by 35.5% to 38.9% 	[174]
Wheat	Pseudomonas jessenii Pseudomonas synxantha	Field	 Co-inoculation with AMF spp. Increased grain yield by 16.7% with 25% less N, P fertilizer 	[175]
Wheat	Bacillus sp. Azospirillum lipoferum Azospirillum brasilense	Greenhouse	 Combination of nanoparticles of silicon and PGPB Drought conditions Increased biomass (fresh and dry weight) and chlorophyll-a and -b content by 138.78%, 65.70%, 128.57%, and 283.33%, respectively 	[176]
Wheat	Agrobacterium sp. Azotobacter chroococcum	Greenhouse	 Enhanced N, Zn, and P content with inoculation Increased total dry weight (shoot, root, spike, and leaves) by 35%, 32.4%, and 28.5%, respectively 	[177]
Wheat	Bacillus amyloliquefaciens	Greenhouse	 Co-inoculation with AMF Drought stress conditions PGPB increased water use efficiency by 27.9% to 34.3% and AMF increased by 20% to 22.1% Grain yield increased by 12.13% to 34.34% with PGPB and 20.03% to 30.77% with AMF Co-inoculation of AMF and PGPB promoted water use efficiency increase of 11.12% to 27.77% and grain yield of 18.26% to 21.68% AMF-PGPB co-inoculation increased chlorophyll and carotenoid contents during anthesis 	[178]

A notable trend in the work that has been reported recently is towards microbial mixing, either with multiple bacterial species, a bacterial consortia of numerous species, or in combination with mycorrhizal (plant-beneficial fungi) species. For example, mixtures of

microbial strains have enhanced plant growth over single-strain inoculation in a number of studies on canola [76,79], rice [88], maize [89,99,104], fava bean [64], wheat [60,64], and barley [64]. The co-inoculation of PGPB with arbuscular mycorrhizal fungi (AMF) performed better than single-microorganism inoculation in maize under salt stress conditions [100,105], wheat [172,175] in drought stress [178], and also increased the N-fixation in beans [61].

Several studies have examined soybean co-inoculation. The inoculation of soybean with PGPB plus other bacterial or fungal microorganisms showed substantial soybean grain yield increases [149], oil yield increases [155], and increased levels of nodulation [144]. A notable exception was a large-scale multi-field experiment, where an increased soybean yield was lacking in all but two of the locations, with an *Azospirillum* sp. and *Bradyrhizobium* sp. co-inoculation. However, the authors noted that a consideration of the strain type and adaption to local environments may be a constraint on the system [153]. A meta-analysis of 42 co-inoculation studies (1987–2018) of *Bradyrhizobium* sp. and rhizobacteria in soybean did not show significant increases in yield in the field, but did indicate that co-inoculation increases nodulation, which may aid the crop to overcome various stresses [179].

In addition to mixing with other microbia, research has explored mixing PGPB with some plant components in combined inoculants. A humic acid co-inoculation with PGPB species showed benefits for maize, cassava, and okra [83,92]. A combination of PGPB with silicon was beneficial to the growth of wheat [176]. Potatoes co-inoculated with biochar, a prospective PGPB carrier, did not yield any benefits [127]. A combination of the plant hormone salicylic acid and PGPB showed positive results for relieving plant stress in canola [76]. Some combined ingredient inoculants may have prospects for use in agriculture if there are synergies to be realized for the end user.

A reduction in fertilizer application, such as a reduction in nitrogen application, has continued to be a point of study for PGPB, including the use of nitrogen-fixing PGPB. Numerous studies have shown improvements in nitrogen use efficiency in wheat and maize with inoculation, where nitrogen requirements could be significantly reduced [87,99,103,175]. It has also been demonstrated that PGPB growth promotion could provide results that are equivalent to increased rates of N fertilization in maize [94,95] and canola [68,76]. Measuring the yield of rice and potato also showed that PGPB, in combination with a reduced rate of fertilizer application, was effective for plant growth promotion [124,128,132,135]. PGPB combined with AMF also demonstrated the possibility of an increased nitrogen assimilation in cassava [82], which speaks to the diversity of crop types explored in this area and the possible enhancements with an AMF co-inoculation. In the area of phosphorus fertilization, the phosphorus use efficiency was increased in maize with PGPB [106] and in canola [73]. An inoculation with phosphate-solubilizing bacteria showed a higher canola seed yield [69]. Masking of the effects of PGPB via the use of optimal levels of fertilization was demonstrated in a greenhouse study; in this case, the authors surmised that the results may have been influenced by the soil conditions [101] and are consistent with the notion that PGPB are most effective in poor soil or suboptimal growing conditions [180].

As food cropping on farms worldwide is ubiquitously exposed to abiotic stressors, PGPB continue to be studied for their benefits for plants subject to drought, salt, and cold. Regarding studies in drought conditions, PGPB have been shown to yield positive results when used to inoculate peppers [117] and cereal crops [168,170]. Saline soils are also a challenge for cereal crop production and PGPB use was able to both promote the growth of cereals and remediate soils [59,81,169,171]. The bacteria were selected for their salt-resistant characteristics and used in field experiments with canola, where many yield components were enhanced by the PGPB inoculation [80]. Other recent experiments in saline conditions include work with rice [133,137] and maize [90]. Additionally, the rice tolerance to cold conditions was enhanced by an inoculation using rhizospheric bacterial isolates [136].

The plant defense benefits of PGPB have also been explored with biotic challenges. An investigation into insect feeding and PGPB inoculation was tested with aphid feeding in canola [74] and wheat, where it was hypothesized that multiple factors of growth promotion were at play, including siderophores and increased plant defense mechanisms [174]. Addi-

tionally, a potato–PGPB inoculation study was conducted with Colorado potato beetles, with observed yield increases [123]. The production of ground tubers is especially susceptible to fungal (as well as bacterial) disease and PGPB inoculants have shown protective effects in experiments with *Rhizoctonia solani* in potato [118,137] and *Erwinia* and *Ralstonia* in sweet potato [162]. Tomato fungal disease resistance [164], as well as blight in maize, has also been demonstrated [102]. For both abiotic and biotic stressors, the mechanisms of plant growth promotion are generally well understood [37].

The majority of recent studies have shown overall benefits for plant and grain yield, but other yield components are also of interest. For example, oil yield increases in canola [71,80] and soybean [152,155] are important outcomes of PGPB crop inoculation. Other studies have looked at the yield of human nutritional components, such as the amplified bioavailability of iron in rice [131,139] and the enhancement of nutrients in beans [67], apples [57], and wheat [166].

Concerning plant health, other nutrient enhancements have been observed with PGPB inoculations. Inoculated strawberry plants have been shown to overcome calcium deficiencies in soil [158]. An increased nutrient efficiency has been seen in wheat [177], including an increased phosphorus mobilization and uptake [167]. Inoculation with PGPB has also led to increased nutritional benefits for potato, through the enhancement of nitrogen, potassium, and phosphorus solubility [125].

As for the sourcing of PGPB organisms for research, novel bioprospecting is a possibility. Interestingly, a PGPB that promoted maize growth was isolated from the gut of an earthworm in a study by Houida et al. [107]. PGPB, from soils in the part of the world where potato is the origin species, were efficacious in enhancing potato growth [118]. Bacterial isolates from nodules of chickpea plants have also proved to be effective PGPB [85].

When optimizing the utility of PGPB in practice, the experimental work provides clues to be considered. For example, the cultivar response of a plant species may vary with different PGPB inocula, as seen with rice [130]. The plant growth stage of the PGPB application is important, as seen in maize [91], as well as the inoculant formulation [92]. Additionally, differences have been seen with inoculant substrates, where a liquid formulation was more effective at increasing the maize yield than a solid formulation [98]. The existing microbiota in the soil also need to be considered, as differences in native populations can cause variances in the plant yield responses with a PGPB inoculation, even with nitrogen fertilization [99]. There is a possibility of significant variability in terms of promoting plant growth in the field, but in general terms, if the mechanistic basis of plant growth promotion in a particular scenario is understood on a fundamental level, there is a high probability that PGPB will behave as expected in the field.

The number and diversity of plant-growth-promoting bacteria products that are commercially available for agriculture have increased significantly over the last 20 years. These products are available for a variety of plant types, including major crops, and are available to growers in most regions of the world. Table 2 summarizes a selection of these commercial PGPB products. The majority of the commercial products available are nitrogen-fixing microbes, with some inoculants that are phosphate, potassium, and zinc solubilizers, as well as phytostimulators, biocontrol organisms [181], and sulfur solubilizers. Biocontrol agents tend to contribute indirectly to plant growth, while the other commercial PGPB stimulate this growth directly. It should be noted that confidence in the efficacy of these products should be apparent with the presence of prominent and diverse organizations in this commercial niche and the existence of open collaboration models to develop innovative and efficacious products for growers. Practical considerations for the delivery of these commercial inoculants should include their efficacy, the availability of ingredients, product safety, the method of delivery, shelf life, and the regulatory requirements in various jurisdictions.

PGPB Ingredient	Product	Company	Intended Crop
Azoarcus sp. Azorhizobium sp. Azospirillum sp.	TwinN	Mapleton Agri Biotec, Mapleton, Australia	Agricultural and horticultural crops
Azospirillum brasilense	AzoFer	Biofabrica, Mexico City, Mexico	Maize and field crops
Azotobacter chroococcum	Dimargon	Biocultivos, Ibague, Columbia	Soybean and coffee
Azotobacter chroococcum Azospirillum brasilense Bacillus megaterium	Azoter	Azoter, Gyor, Hungary	Agricultural and horticultural crops
Azospirillum brasilense Azotobacter chroococcum Pseudomonas fluorescens	RoshdAfza	Biorun company, Karaj, Iran	Maize, rice, cereals, sugarcane, and fruit trees
Azotobacter chroococcum Bacillus megaterium	Phylazonit M	Phylazonit, Nyiregyhaza, Hungary	Maize, soybean, cereal, canola, and sunflower
Azotobacter chroococcum Pseudomonas fluorescensin	Bio Gold	Bio Power Lanka, Columbo, Sri Lanka	Agricultural and horticultural crops
Azotobacter vinelandii (with Rhizophagus irregularis)	Rhizosum N	Syngenta, Basel, Switzerland	Maize, rice, soybean, canola, sunflower, sugar beet, and sorghum
<i>Bacillus</i> spp. (with <i>Glomus intraradices</i>)	CataPult	Bio-Tech Organics, Virginia, Australia	Winter cereals
Bacillus amyloliquefaciens (with Trichoderma virens)	QuickRoots	Novozymes BioAg Ltd., Bagsvaerd, Denmark	Maize, soybean, canola, pulse, sunflower, and sugar beet
Bacillus mucilaginosus	K Sol-B	AgriLife, Hyderabad, India	Pulse crops
Bacillus subtilis	Serenade ASO	Bayer CropScience, Monheim, Germany	Fruit and vegetable crops
Bacillus subtilis Bradyrhizobium japonicum	Nodulator N/T	BASF, Ludwigshafen, Germany	Soybean
Bacillus subtilis Bacillus licheniformis Bacillus amyloliquefaciens Bacillus megaterium Bacillus pumilus Pseudomonas putida Paenibacillus ploymyxa	BioLevel-PhosN	Biolevel Ltd., Chipping Norton, UK	Maize, small grains, potato, vegetables, and specialty crops
Bradyrhizobium spp.	NoduMax	UPL OpenAg, Lagos, Nigeria	Soybean
Bradyrhizobium japonicum	Biagro10	Biagro, Cambe, Brazil	Maize, soybean, wheat, pulse crops, sugarcane, and coffee
Bradyrhizobium japonicum	Liquifix	Legume Technology Ltd., East Bridgford, UK	Soybean
Bradyrhizobium japonicum	Optimize LV	Novozymes BioAg Ltd., Bagsvaerd, Denmark	Soybean
Bradyrhizobium japonicum	Rizoliq Top	Rizobacter, Buenos Aires, Argentina	Soybean
Bradyrhizobium japonicum Rhizobium sp.	LegumeFix	Legume Technology, Nottingham, UK	Soybean and pulse crops
Bradyrhizobium japonicum Delftia acidovorans	Bioboost+	Lallemand, Montreal, Canada	Canola

 Table 2. Examples of commercial products using plant-growth-promoting bacteria.

PGPB Ingredient	Product	Company	Intended Crop
Methylobacterium symbioticum	Utrisha N	Corteva Agriscience, Indianapolis, IN, USA	Maize, rice, soybeans, canola, sunflower, sugar beet, and sorghum
Paenibacillus polymyxa	Custom N2	Custom Biologicals, Deerfield Beach, FL, USA.	Agricultural and horticultural crops
Pseudomonas chlororaphis	Cedomon	Lantmännen BioAgri, Uppsala, Sweden	Barley and oats
Thiobacillus thiooxidans	Symbion-S	Stanes, Coimbatore, India	Agricultural and horticultural crops
Thiobacillus thiooxidans	ZN Sol-B	AgriLife, Hyderabad, India	Rice, sugarcane, orchard crops, and vegetables

4. Summary and Conclusions

In a world where the population continues to increase and agricultural land is limited, safely increasing the food supply with biological approaches may be addressed by the increased use of either transgenic plants or plant-growth-promoting bacteria and fungi. These biological advances complement innovative means for growing plants, e.g., using hydroponics [182]. Fortunately, over the past 15–20 years, and since our first review of this topic [52], there has been a dramatic increase in the development, testing, and use of PGPB worldwide to facilitate the growth of a wide range of plants under a large variety of conditions. While many reports of the successful use of PGPB do not include a detailed characterization of the mechanisms used by these bacteria, it has become abundantly clear that under nearly every imaginable condition, when PGPB are tested, they are remarkably efficacious. Interestingly, and in contrast to 20 years ago, PGPB have been shown to be effective not only under laboratory conditions, but also in the field. Moreover, many PGPB have now been commercialized and are available in many countries across the globe. Unfortunately, PGPB still comprise only a very small fraction of the global market of products used for promoting plant growth. To increase the use of PGPB, it is necessary to educate the global agricultural industry and public to understand that naturally occurring PGPB, which have been interacting with plants for millions of years, can provide a safe and effective means for facilitating plant growth.

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