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REVIEW

From Research to Revolution: Two Decades Rewriting Maize Production in Brazil with Bacterial Bio-Inputs (2005–2025)

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Abstract

Over the past two decades (2005–2025), Brazil has been at the forefront of research and commercialization of bacterial bio-inputs for maize (*Zea mays* L.), transforming plant growth-promoting bacteria (PGPB) from a research subject into consolidated agricultural technologies. This review synthesizes the principal microorganisms investigated, the mechanisms of action elucidated, the agronomic outcomes reported, the knowledge gaps identified, and the prospects for the next technological frontier. Brazil, that nowadays carries the global leadership in the use of bio-inputs based on PGPB is given as the main example. Two commercial successes stand out: *Azospirillum brasilense* strains Ab-V5 and Ab-V6, with 10 million ha treated in 2025/26, an average increase of 5.4% in grain productivity and a possible 25% reduction in N fertilization; and the BiomaPhos® formulation (*Priestia megaterium* B119 + *Bacillus subtilis* B2084), yielding average increases of 8.6% across eight Brazilian states. Building on these results, a new generation of multifunctional strains is emerging: Some strains of the genus *Bacillus* may contain clusters of biosynthetic genes that encode antifungal lipopeptides; *Pseudomonas* spp. may combine phosphate solubilization, ACC-deaminase activity, and biocontrol within a single strain; and *Stenotrophomonas* spp. show remarkable growth-promoting potential. Molecular mechanisms, non-ribosomal peptides, siderophores, induction of systemic resistance, and benzoxazinoid-mediated chemotaxis toward maize roots, have been characterized through genomic mining and validated metabolomics. It is concluded that Brazil leads a transition from single-strain inoculation towards integrated microbial systems capable of redefining the foundations of nutrition and plant protection in maize, with key remaining challenges in response variability, formulation stability, and compatibility of inoculants with foliar, in-furrow, and chemical seed treatments.

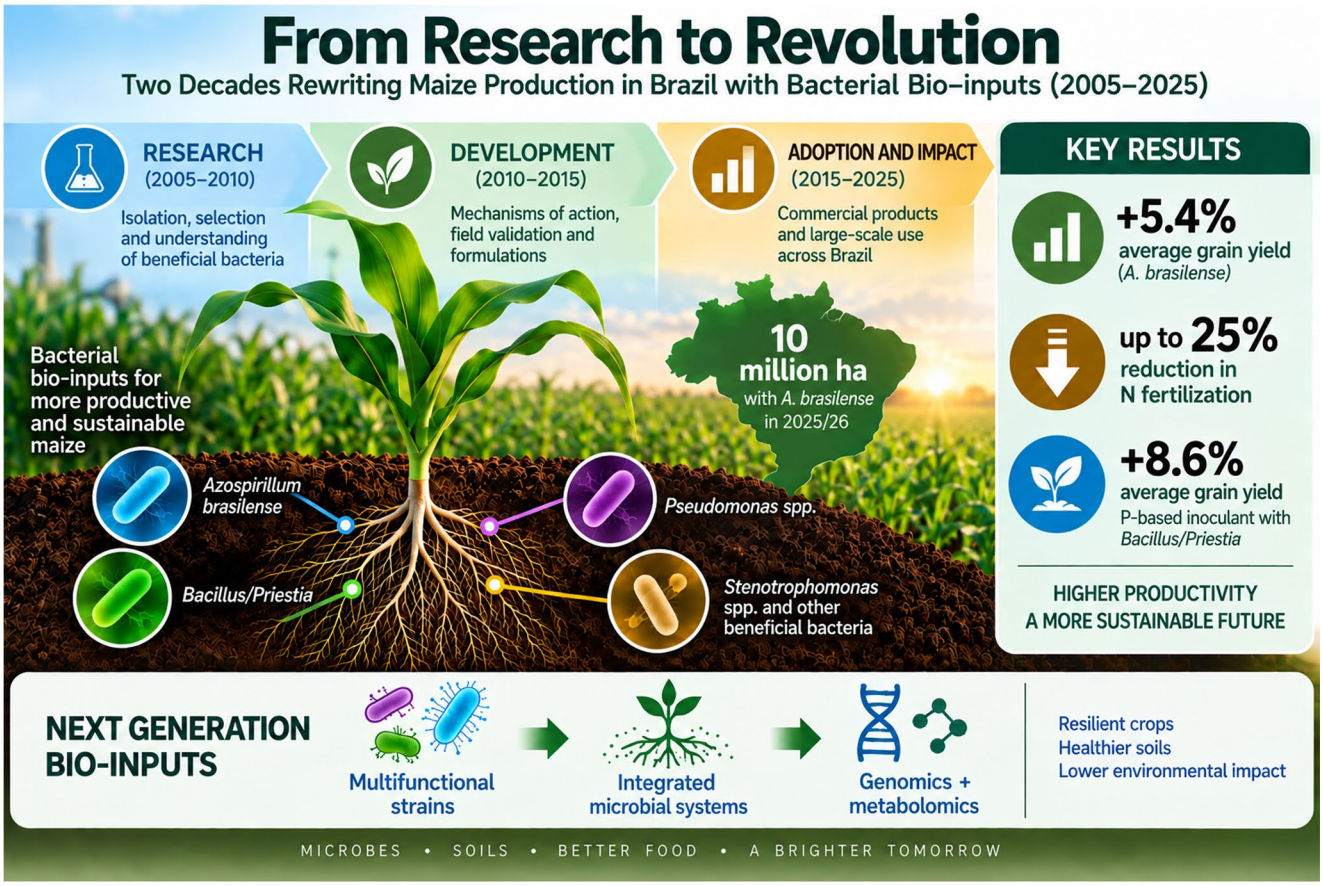
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Graphical Abstract



Highlights

- Brazil transformed bacterial bio-inputs for maize from research into large-scale technologies
- *Azospirillum brasilense* inoculants reached 10 million ha, increasing grain yield by 5.4% on average
- *A. brasilense* can reduce N fertilization by up to 25% without compromising yield
- A P-based inoculant with *Bacillus*/*Priestia* increased maize grain yield by 8.6% on average
- Multifunctional microbial systems emerge as a new frontier for sustainable maize nutrition.microbial systems emerge as a new frontier for sustainable maize nutrition

Keywords Biological Nitrogen Fixation · Phytohormones · Phosphate Solubilization · Biocontrol · *Azospirillum* · *Bacillus*

1 Introduction

Maize (*Zea mays* L.) holds a central position in Brazilian agriculture, with an estimated cultivated area of 21.9 million hectares and total production projected at 138.4 million tons for the 2025/26 growing season (Conab 2026), consolidating Brazil as the world's third-largest producer. The crop plays a strategic role in food security, animal feed production, ethanol generation, and the supply of industrial raw materials. The crop demands large quantities of nitrogen (N), a nutrient that, when supplied exclusively through synthetic fertilizers, imposes rising costs on producers and environmental risks that increasingly call into question the viability of conventional production models.

The industrial synthesis of nitrogenous fertilizers via the Haber-Bosch process consumes approximately 2% of global energy and accounts for roughly 1.44% of annual CO_2 emissions (Kyriakou et al. 2020). In Brazil, dependence on fertilizer imports represents approximately 85% of national consumption, constituting a significant economic and commercial vulnerability (Brasil 2022). Globally, crops use only 50% of the applied nitrogen effectively (Govindasamy et al.

2023), and nitrogen use efficiency in maize averages only 33% worldwide (Davies et al. 2020), resulting in losses through volatilization, leaching, and denitrification that contribute to aquifer contamination, surface water pollution, and N_2O emissions (Govindasamy et al. 2023).

In this context, plant growth-promoting bacteria (PGPB) emerge not merely as a promising alternative, but as a solution already proven at commercial scale. These microorganisms establish beneficial associations with the host plant through complementary and synergistic mechanisms: (*i*) biological nitrogen fixation (BNF); (*ii*) phytohormone production; (*iii*) phosphate solubilization; (*iv*) siderophore synthesis; (*v*) ACC-deaminase activity; (*vi*) induction of systemic resistance (ISR); (*vii*) rhizosphere microbiome modulation; and (*viii*) biocontrol of phytopathogens (Baatsen et al. 2025; Ercole et al. 2026; Figueiredo et al. 2025; Fukami et al. 2018a; Glick 2012; Vasques et al. 2024a). The multiplicity of these mechanisms, frequently acting simultaneously within a single strain, confers upon PGPB a degree of multifunctionality unprecedented among conventional agricultural inputs.

Brazil occupies a leading position globally in this field. Research on PGPB in grasses dates back to the 1970s and 1980s, with the pioneering studies of Dr. Johanna Döbereiner on *Azospirillum* spp. (Döbereiner 1979), but a marked intensification occurred from the 2000s onward, driven by advances in molecular tools, the development of stable commercial formulations, and growing awareness of agricultural sustainability. The registration of *A. brasilense* strains Ab-V5 and Ab-V6 in Brazil and the launch of the first commercial inoculant in 2009 marked the inflection point of this trajectory (Hungria et al. 2010; Santos et al. 2021), paving the way for an increasingly sophisticated generation of bio-inputs grounded in genomic mining, validated metabolomics, and high-throughput phenotypic screening.

This review synthesizes and critically evaluates the accumulated knowledge on PGPB in maize in Brazil over the period of 2005–2025, two decades that transformed *A. brasilense* from a research subject into a consolidated technology. Brazil also witnessed the emergence of a new generation of multifunctional microorganisms with the potential to redefine the foundations of nutrition and protection for the crop. The principal microorganisms studied, the mechanisms of action elucidated, the agronomic outcomes reported, the remaining knowledge gaps, and the prospects for the next technological frontier of bio-inputs are all identified and discussed. Although highlighting Brazil successful experience, the strategies and outcomes can be applied to all countries, and not only for the maize crop, redefining the use of biologicals in agriculture.

2 Maize Production and the Adoption of Bacterial Bio-Inputs in Brazil (2005–2025)

The two decades covered by this review coincide with the period in which Brazilian maize production and the commercial use of bacterial bio-inputs expanded simultaneously. Table 1 compiles, season by season, the national planted area, grain production and average yield of maize reported by Conab together with the area treated with *A. brasilense* inoculants and the corresponding adoption rates reported by Kynetec/FarmTrak (2026), so that the two trajectories can be read against each other rather than in

Table 1 Brazilian maize planted area, grain production and average yield, and area treated with *Azospirillum brasilense* inoculants, by growing season (2014/15 to 2025/26). Adoption rate is the percentage of the cultivated area of each crop that received inoculant; average yield was calculated as total production divided by planted area. Inoculant use in the second crop was not recorded for 2014/15. nd, not available; ha, hectare; Mt, million tonnes

Season	Maize area (M ha)	Maize production (Mt)	Average yield (kg ha^{-1})	Treated area, summer crop (1,000 ha)	Adoption, summer crop (%)	Treated area, second crop (1,000 ha)	Adoption, second crop (%)	Total treated area (1,000 ha)
2014/15	15.8	84.7	5,360	75.8	1.77	nd	nd	75.8
2015/16	15.8	66.5	4,211	59.8	1.66	324.6	3.18	384.4
2016/17	17.3	97.9	5,656	427.0	9.29	1,736.1	14.17	2,163.1
2017/18	16.0	80.7	5,046	409.0	11.05	2,147.3	17.10	2,556.3
2018/19	17.8	100.1	5,622	470.6	12.37	2,480.8	21.49	2,951.4
2019/20	18.5	102.6	5,546	576.3	15.81	2,841.8	21.54	3,418.1
2020/21	19.8	87.1	4,400	803.7	20.46	3,374.2	24.14	4,177.9
2021/22	21.6	113.1	5,245	1,018.1	21.55	5,239.0	34.39	6,257.1
2022/23	22.3	131.9	5,926	964.6	21.52	6,772.2	41.04	7,736.8
2023/24	21.0	115.5	5,500	971.8	24.51	7,595.6	45.45	8,567.4
2024/25	21.5	141.2	6,567	857.3	23.74	6,989.2	43.67	7,846.5
2025/26	21.9	138.4	6,320	1,116.6	28.40	8,909.8	50.94	10,026.4

Sources: Brasil (2024) and Conab (2026) for the maize series; Kynetec/FarmTrak (2026), unpublished data, for treated area and adoption rate

isolation. Production for the seasons up to 2022/23 is taken from the compilation of Conab data published by the Ministry of Agriculture and Livestock (Brasil 2024), which disaggregates the first, second and third crops.

Three features of Table 1 deserve comment. First, the expansion of the treated area was concentrated in the second (winter) crop, which rose from 324.6 thousand hectares in 2015/16 to 8,909.8 thousand hectares in 2025/26, and in which the adoption rate reached 50.9%; in the summer crop, adoption remained below 30% throughout the period. This asymmetry is agronomically coherent: the second crop is sown after soybean, is more frequently exposed to water deficit and to reduced topdressing N rates, and is therefore the environment in which the growth-promotion mechanisms discussed in Sect. 4 are most likely to be expressed. Second, the inflection between 2020/21 and 2021/22 in the treated area coincides with the constraints on synthetic fertilizer supply described in Sect. 3.1, indicating that adoption responded not only to agronomic performance but also to input price and availability. Third, national average yield and total production increased over the same interval, but the two series must not be read as cause and effect.

National yield gains over 2005–2025 result from the simultaneous advance of genetics, no-till systems, sowing calendar, crop protection, fertilization and mechanization, of which inoculation is one component among several, and the aggregate national series cannot isolate its individual contribution. What can be attributed with confidence to inoculation is the incremental response measured in controlled comparisons within the same experiment. In the meta-analysis of Barbosa et al. (2022), covering 103 field trials in 54 locations across ten states, inoculation with Ab-V5 and Ab-V6 increased grain yield by 5.4% on average; in the multi-environment network of Hungria et al. (2022), comprising 30 experiments in 13 locations over ten years, the increase was 3.1%, with the inoculated treatment receiving 75% of the recommended N statistically equivalent to the non-inoculated treatment receiving 100%. For *Bacillus*-based phosphate-solubilizing formulations, field trials across eight Brazilian states recorded average increases of 8.6% in maize (Oliveira et al. 2020). These effect sizes, and not the national production series, are the appropriate basis for quantifying the agronomic contribution of bacterial bio-inputs; the national series in Table 1 provides the production context within which that contribution has been scaled up.

Read jointly, the two sets of data show that the technology was adopted during a period of continuous expansion of the crop and reached, in the second crop, approximately half of the cultivated area, which places bacterial bio-inputs among the most widely adopted agricultural biotechnologies in Brazilian maize. The economic and environmental magnitude of this adoption, estimated by the avoided-cost method, is presented in Sect. 3.1 and summarized in Fig. 1.

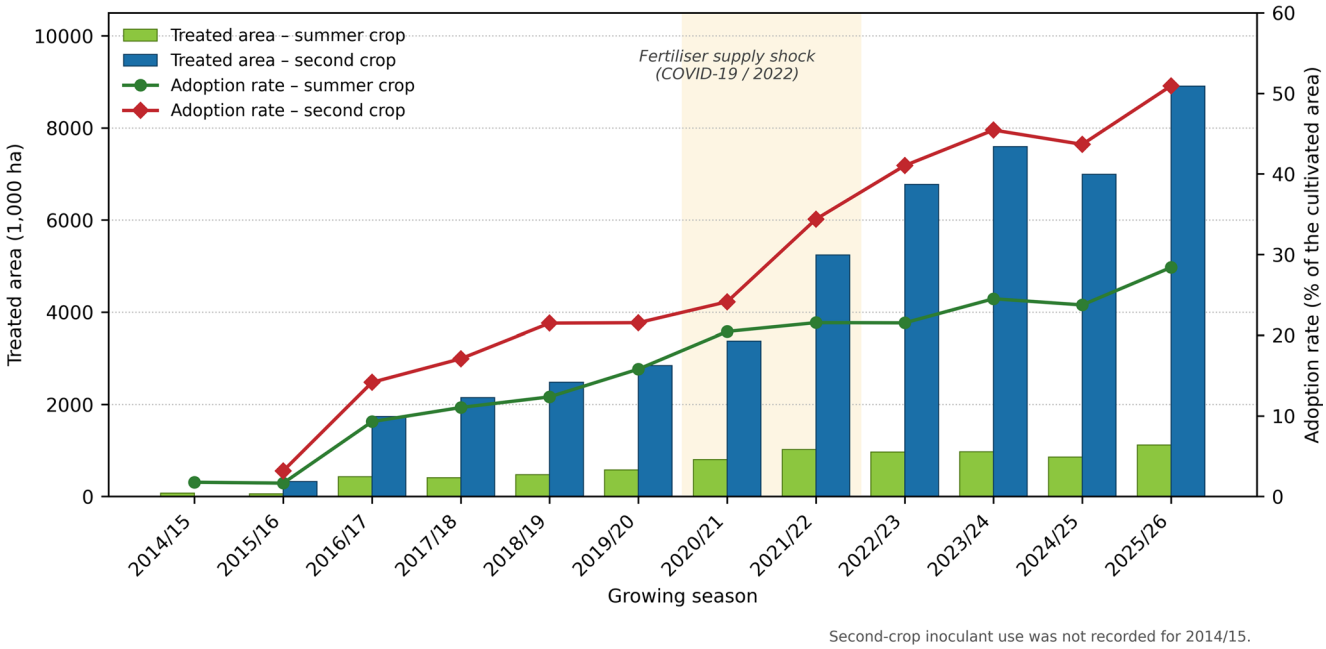


Fig. 1 Estimated current and potential economic and environmental impact of the biological nitrogen fixation (BNF) associated with *Azospirillum brasilense* inoculants in Brazilian maize. Upper panel, the avoided-cost pathway; lower panels, the current situation compared with full adoption across the total Brazilian maize area. Method and input values as described in Sect. 3.1 (Hungria et al. 2022; Telles et al. 2023; Kynetec/FarmTrak 2026). NUE, nitrogen use efficiency; Mt CO_2-eq, million tonnes of carbon dioxide equivalent

3 Main Microorganisms Identified

3.1 *Azospirillum brasilense*

Azospirillum brasilense represents the most extensively studied microorganism in maize in Brazil, with particular emphasis on strains Ab-V5 (=CNPSo 2083) and Ab-V6 (=CNPSo 2084), natural variants selected by Empresa Brasileira de Pesquisa Agropecuária (Embrapa): Centro Nacional de pesquisa da soja (Embrapa Soja) and Universidade Federal do Paraná (UFPR) in the late 1990s (Hungria et al. 2010, 2022; Hungria and Nogueira 2019; Santos et al. 2020, 2021). The strain designations CNPSo 2083 and CNPSo 2084 refer to accession numbers in the Culture Collection of Embrapa Soja (CNPSo). These strains underwent a rigorous selection program encompassing laboratory, greenhouse, and field evaluations over a total of ten years of research prior to their commercial release (Hungria et al. 2010). Worldwide the species is probably also the main one studied with the maize crop.

The trajectory of *A. brasilense* strains Ab-V5 and Ab-V6 constitutes a paradigmatic case of successful biotechnological development, demonstrating how rigorous scientific research, extensive validation, and effective technology transfer can yield transformative impact in agriculture. Santos et al. (2021) document the process from the outset of *Azospirillum* strain prospecting at Embrapa Soja in 1996, in the state of Paraná, through eight years of evaluations under laboratory, greenhouse, and field conditions, comprising 17 field experiments conducted in two different edaphoclimatic conditions. The process culminated with the identification of Ab-V5 and Ab-V6 as elite strains, natural variants of *A. brasilense* Sp7 (=ATCC 29145), effective for both maize and wheat (*Triticum aestivum* L.), and in the launch of the first commercial inoculant in 2009.

In the analysis by Santos et al. (2021), the authors identified the following critical success factors for *A. brasilense*: (*i*) high-quality science with rigorous multicentric validation; (*ii*) a competitive and accessible technology transfer model; (*iii*) attractive cost-effectiveness; (*iv*) ease of use integrated into existing agronomic practices; and (*v*) the cultural receptiveness of Brazilian farmers already familiar with bio-inputs through the longstanding tradition of soybean inoculation. This success story established a replicable model for the development of new bio-inputs and demonstrates that, when technology is effective and well communicated, farmers are receptive and capable of adopting microbiological innovations at scale, contributing simultaneously to agricultural productivity and sustainability.

Also according to Santos et al. (2021), from a genomic standpoint, Ab-V5 comprises 6,934,595 bp and Ab-V6, 7,197,196 bp; both carry structural genes for BNF (*nif/fix*), yet the species is particularly distinguished by its phytohormone production, with genes for the synthesis of indole-3-acetic acid (IAA), salicylic acid (SA), gibberellin (GA3) (predominantly detected in strain Ab-V5, though also detected in Ab-V6 in the presence of tryptophan), and jasmonic acid (JA) under certain conditions (Fukami et al. 2017). In the same study, the authors reported that inoculation, both via seed and foliar application, induced upregulation of oxidative stress genes (*APX1*, *APX2*, *CAT1*, *SOD2*, *SOD4*) in leaves and defense genes (*PR1*, *prp2*, *prp4*) in roots, suggesting that the benefits of *A. brasilense* inoculation are associated with both phytohormone production and the induction of systemic resistance to biotic and abiotic stresses. An important functional distinction is that Ab-V5 harbors an active quorum sensing (QS) system, whereas Ab-V6 compensates for this absence through greater IAA production, resulting in complementary agronomic efficiencies when the two strains are used in combination (Fagotti et al. 2019).

Regulatory registration of both strains with MAPA (Ministério da Agricultura, Pecuária e Abastecimento; Brazilian Ministry of Agriculture, Livestock and Food Supply) took place in 2009, followed by non-exclusive licensing to multiple inoculant-producing companies (Hungria and Nogueira 2019). This enabled rapid commercial dissemination with exponential adoption growth: from approximately 384,000 ha in 2015/16 to 10.0 million ha in 2025/26 (Table 1; Fig. 2), with adoption rates of 50.9% in the second crop and 28.4% in the summer crop in 2025/26 (Kynetec/FarmTrak 2026).

The rapid growth in the inoculant market consolidates *A. brasilense* as an important bio-input in Brazilian agriculture, driven by an expanding portfolio of registered products and increasing adoption by farmers across diverse production systems. The pronounced increase observed between the 2020/21 and 2021/22 seasons in treated area, from 803.7 to 1,018.1 thousand hectares in summer crop and from 3,374.2 to 5,239.0 thousand hectares in second crop (Fig. 2), can be attributed to a combination of factors: suppressed supply of synthetic fertilizers during the COVID-19 pandemic and as an effect of the Russia–Ukraine conflict in February 2022, which redirected interest toward bio-inputs. As a result, there was an accelerated expansion of companies in the sector, as well as the entry of multinational corporations into the market. The relative stabilization observed in summer crop between 2022/23 and 2023/24 (964.6 to 971.8 thousand ha) suggests a period of market consolidation, whereas the second crop continued its upward trajectory, reaching 7,595.6 thousand hectares in 2023/24 before receding to 6,989.2 thousand hectares in 2024/25. By 2025/26, treated area reached 1,116.6 thousand hectares in summer crop and 8,909.8 thousand hectares in second crop, with adoption

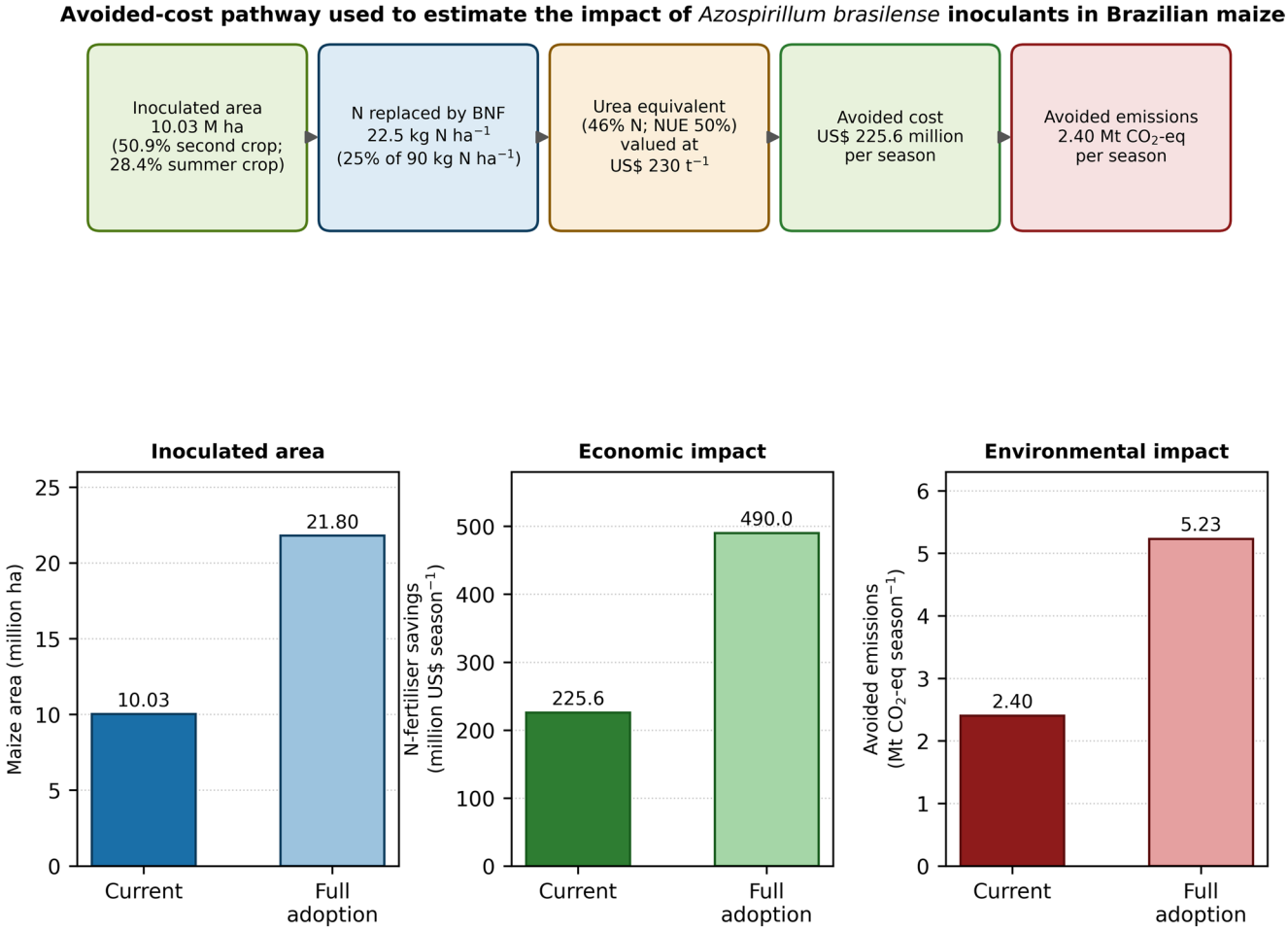


Fig. 2 Area treated with *Azospirillum brasilense* inoculants and adoption rate in Brazilian maize, from the 2014/15 to the 2025/26 growing season. Bars, treated area (left axis); lines, adoption rate (right axis); green, summer crop; blue, second crop. The shaded band marks the seasons of constrained synthetic fertilizer supply discussed in Sect. 3.1. Second-crop data were not recorded for 2014/15. Source: Kynetec/FarmTrak (2026), unpublished data.

rates of 28.4% and 50.9%, respectively, further consolidating *A. brasilense* as the leading bacterial bio-input in Brazilian maize production (Kynetec/FarmTrak 2026). The renewed increase recorded in the 2025/26 season may be partially associated with geopolitical tensions in the Middle East, which once again constrained the global supply of synthetic fertilizers and stimulated demand for biological alternatives.

The viability of partial replacement of mineral nitrogen fertilizer by *A. brasilense* inoculation in maize was robustly demonstrated by Hungria et al. (2022), in a study comprising 30 field experiments across 13 Brazilian locations over ten years. The authors evaluated treatments combining inoculation with strains Ab-V5 and Ab-V6 with different topdressing nitrogen rates (0, 50, 75, and 100% of 90 kg N ha^{-1} as urea, applied approximately 35 days after emergence). Inoculation significantly increased grain yield by 3.1% on average, with consistent responses across subtropical and tropical conditions, clay and sandy soils, and varying organic carbon contents. The most agronomically relevant finding was the statistical equivalence between the inoculated treatment receiving 75% of the recommended N and the non-inoculated treatment receiving 100%, indicating that 22.5 kg N ha^{-1} of topdressing N-fertilizer could be reduced without yield penalty. The authors attributed these effects primarily to improvements in root system architecture promoted by IAA production from the inoculant strains, which enhances the efficiency of water and nutrient uptake, including that of the applied mineral N-fertilizer.

Following the methodological approach proposed by Telles et al. (2023) for estimating the economic and environmental value of BNF in Brazilian agriculture, and based on

the finding that inoculation with *A. brasilense* can replace up to 25% of the recommended mineral nitrogen dose (equivalent to 22.5 kg N ha^{-1} at a standard rate of 90 kg N ha^{-1}) while maintaining equivalent grain yield (Hungria et al. 2022), it is possible to estimate the current impact of *A. brasilense* based inoculants in Brazilian maize. Using the avoided-cost method, whereby the N contributed by BNF is converted into its equivalent in urea (46% N), adjusted for a nitrogen use efficiency of 50%, and valued at the prevailing market price (US$ 230 t^{-1}), the 10.03 million hectares currently inoculated (second crop: 50.9%; summer crop: 28.4%; Kynetec/FarmTrak 2026) represent an estimated saving of approximately US$ 225.6 million in synthetic nitrogen fertilizers per season, with a corresponding reduction of 2.40 million tons of CO_2-equivalent greenhouse gas emissions (Fig. 1). If adopted across the entire Brazilian maize cultivated area (approximately 21.8 million hectares), the potential savings would reach US$ 490 million per season, with a reduction of 5.23 million tons of CO_2-eq, reinforcing the strategic role of *A. brasilense* inoculants in sustainable and low-carbon maize production systems.

The scale of research on *A. brasilense* following its registration in Brazil is considerable. Barbosa et al. (2022) conducted a meta-analysis encompassing 60 scientific publications, comprising 103 field trials distributed across 54 locations in ten main maize-producing states of the country. The trials were carried out under diverse edaphoclimatic conditions, covering Cerrado soils, Latosols, and Argisols, different management systems (no-till and conventional tillage), and varying technological production levels. The meta-analysis results showed average increases of 5.4% in grain yield, 12.1% in root dry mass, 4.3% in leaf N concentration, and 3.6% in grain N content, with positive effects observed across all yield ranges and edaphoclimatic conditions evaluated. Seed inoculation with peat based inoculant (+9.5%) outperformed liquid formulations (+5.5%), and foliar application showed a significant effect only when carried out at growth stages V2–V3 (+3.1%). The authors concluded that inoculation with *A. brasilense* Ab-V5 and Ab-V6 represents a consolidated biotechnological tool for increasing the yield and nutritional value of maize under Brazilian tropical and subtropical conditions.

A new *A. brasilense* strain has been attracting attention as a promising bio-input candidate: HM053, that corresponds to strain Ab-V2, studied by Hungria et al. (2010). Pedrosa et al. (2019) evaluated the potential of HM053 as a maize inoculant in four field trials across three regions of Paraná, south of Brazil. HM053 is also a derivative of strain Sp7 (=ATCC 29145), capable of fixing nitrogen constitutively and excreting ammonium even in the presence of high NH_4^+ concentrations. In trials with a basal N application of 30 kg N ha^{-1}, inoculation with HM053 increased grain yield by 4.7 to 29% (460 to 1,769 kg ha^{-1}), outperforming Ab-V5 in three out of the four locations. According to the authors, at two sites in the 2013 growing season, plants inoculated with HM053 and receiving 30 kg N ha^{-1} achieved yields statistically equivalent to the non-inoculated treatment receiving 160 kg N ha^{-1}, indicating the strain's potential for a significant reduction in N-fertilization. However, it should be noted that the study used only strain Ab-V5 as a commercial reference, excluding Ab-V6, a strain recognized for its superior capacity for phytohormone production, particularly auxins, which contribute significantly to plant growth promotion (Hungria et al. 2010).

3.2 *Bacillus* spp

The genus *Bacillus* stands out among PGPB by its remarkable versatility of action mechanisms and its capacity to form endospores resistant to adverse conditions of temperature, ultraviolet radiation, and desiccation, a property that confers stability to commercial formulations and extends their viability under storage and application conditions (Vasques et al. 2024b). In the Brazilian agricultural context, the genus accounts for approximately 80% of the bio-input market dedicated to biological control, with applications estimated across tens of millions of hectares, while the segment focused on plant growth promotion reached more than six million hectares in just five years. This impressive growth reflects increasing recognition of the multifunctional potential of selected strains, whose benefits to the plant operate through direct and indirect pathways simultaneously (Vasques et al. 2024b).

Genomic mining and metabolic profiling of elite strains deposited in the Embrapa Soja Culture Collection, including *B. velezensis* CNPSo 2657, *B. altitudinis* CNPSo 2658, and *B. safensis* CNPSo 2725, confirmed IAA and Indole-3-butyric acid (IBA) production by all three strains, with *B. velezensis* CNPSo 2657 being the only one to also synthesize abscisic acid (ABA), and revealed that from 8.28 to 18.03% of their genomes are dedicated to biosynthetic gene clusters (BGCs) of secondary metabolites, the highest proportion among *Bacillus* species studied, including 20 clusters with similarity to compounds antifungal such as fengycin and antibacterial such as bacillaene, difficidin, macrolactin (Ercole et al. 2026). The same study identified an average of 79 CAZymes per genome in the *Bacillus* strains analyzed, carbohydrate-active enzymes encompassing glycoside hydrolases and glycosyl transferases as predominant classes, providing the enzymatic basis for rhizosphere substrate degradation and reinforcing the biocontrol potential of these species.

In another study, Ercole et al. (2024) performed whole-genome sequencing of three *B. velezensis* strains isolated

from maize roots in southern Brazil (LGMB12, LGMB319, and LGMB426) and demonstrated in vitro antagonistic activity against four fungal phytopathogens relevant to maize: *Fusarium graminearum*, *F. verticillioides*, *Colletotrichum graminicola*, and *Stenocarpella* sp. Genome mining via antiSMASH revealed that on average 16.2% of the genome is dedicated to secondary metabolite BGCs, a proportion substantially higher than the 5–8% typically reported for the *Bacillus* genus. Among the nine BGC clusters common to all strains, those with similarity to surfactin, fengycin, macrolactin H, bacillaene, bacillibactin, difficidin, and bacilysin were identified, with strain LGMB12 harboring two additional clusters for iturin and bacillomycin D, consistent with its superior antagonistic performance in paired culture assays. Phosphate solubilization systems (alkaline phosphatases *phoA* and *phoD*, and inorganic pyrophosphatase *ppa*) and genes for siderophore production (*dhbABCEF*), IAA biosynthesis, and biofilm formation were also identified across all genomes, reinforcing the multifunctional profile of these strains as bio-input candidates for maize (Ercole et al. 2024). Indeed, the multiple multifunctional properties of *Bacillus* were comprehensively reviewed by Vasques et al. (2024b).

The capacity for biocontrol of fungal phytopathogens constitutes another central attribute of the genus, with particular relevance for maize. The strain of Collection Embrapa Milho e Sorgo (CNPMS), *B. velezensis* CNPMS-22, isolated from a Cerrado soil from Sete Lagoas, Minas Gerais, demonstrated in vitro antifungal activity against ten species of phytopathogenic fungi, with inhibition rates of 54.5 to 76.2% in dual culture assays and up to 97.6% through volatile organic compounds (VOCs) in inverted plate assays (Figueiredo et al. 2025). Scanning electron microscopy (SEM) revealed that the contact with CNPMS-22 caused twisting, wrinkling, and rupture of *Fusarium verticillioides* hyphae, with 56% broken hyphae in treated samples versus 0% in controls and evidenced the formation of bacterial biofilm adhered to fungal hyphae. In vivo biocontrol was confirmed both in greenhouse conditions, where seed treatment with CNPMS-22 increased plant survival in *F. verticillioides*-infested soil from 34.4% to 87.5%, matching the efficacy of the chemical fungicide Captan, and under field conditions, where maize grain yield with CNPMS-22 (8,340.93 kg ha^{-1}) was statistically equivalent to that obtained with chemical fungicide (8,219.25 kg ha^{-1}) and significantly superior to untreated controls. Genomic analysis of CNPMS-22 identified three non-ribosomal lipopeptide clusters, surfactin, fengycin, and iturin, along with genes for extracellular hydrolytic enzymes, VOCs, and ISR in plants, revealing the molecular basis of the strain's antifungal arsenal (Figueiredo et al. 2025).

In another study, within the Bacilli class, *B. velezensis* CNPSo 2384, isolated from landrace maize grown under low-input conventional systems in southern Brazil, demonstrated outstanding plant growth-promotion abilities, improving shoot biomass by 45%, root biomass by 27%, root length by 120%, and root specific length by 85% compared with the non-inoculated control, surpassing the reference strain *A. brasilense* Ab-V5 (Fagotti et al. 2026).

Vasques et al. (2026) confirmed and extended this scenario by evaluating 100 strains from the Embrapa Soja Culture Collection under water stress conditions. Of the ten characteristics assessed in vitro, only *Bacillus* species demonstrated satisfactory growth in media with water activity of 0.897 at 40 °C, the five strains exhibiting this profile all belonged to this genus, reflecting the endospore-forming capacity that confers resistance to temperature extremes, pH variation, and radiation. In greenhouse experiments, *B. velezensis* CNPSo 2384 stood out for producing the greatest root volume across all treatments (13.86 mL per plant), surpassing even the irrigated control (11.92 mL), with a photosynthetic rate 51% higher than the non-inoculated control under water restriction in the second experiment. *B. subtilis* CNPSo 2606 and *Bacillus* sp. CNPSo 2723 completed the trio of strains identified as candidate bio-inputs for drought tolerance, reinforcing *Bacillus* as the most promising genus for conditions of increasing water deficit associated with climate change. In parallel, *B. velezensis* and *B. subtilis* strains isolated from the Caatinga biome, a semiarid environment subject to severe water restriction, demonstrated growth under low water activity, exopolysaccharide production, and siderophore synthesis, indicating potential for the development of bio-inputs targeting crop resilience under water-deficit conditions (Ferreira et al. 2025).

The prospection of *Bacillus* strains adapted to water stress conditions has gained increasing attention in the context of Brazilian tropical agriculture. Ferreira et al. (2025) genomically characterized five strains isolated from Caatinga biome soils in the state of Ceará: two belonging to *B. velezensis* (6E9 and 5D5) and three to *B. subtilis* (2E7, 1A11, and 1H10), collected from five distinct municipalities and deposited in the Embrapa Milho e Sorgo - Collection of Multifunctional and Phytopathogenic Microorganisms (CMMF) under accession numbers BRM051761, BRM051757, BRM051747, BRM051734, and BRM051737, respectively. Strain selection was based on functional attributes relevant to water-deficit tolerance: all demonstrated growth under low water activity (520 and/or 780 g/L sorbitol) and in vitro exopolysaccharide production. Genomes ranged from 3.89 to 4.29 Mb, with G+C content between 43.59 and 46.70%. Taxonomic classification confirmed by the TYGS server revealed Fast ANI values of 98.07–98.10% relative to reference strain JS25R for

B. velezensis strains, and 98.35–98.51% relative to ATCC 11,774 for *B. subtilis* strains. Although no plant trial data are presented, the genomic and phenotypic characteristics described indicate the potential of these strains for developing bio-inputs targeting crop resilience in semiarid regions, broadening the microbial germplasm diversity available for inoculant breeding programs in Brazil.

In another study of bacteria tolerant to water stress, a bacterium found in the rhizosphere of mandacaru (*Cereus jamacaru*), a cactus native to the Caatinga region of Brazil, has entered the Brazilian market to help maize crops withstand drought. The rhizobacterium *B. aryabhattai* (reclassified as *Priestia aryabhattai*) enhances plant resilience and adaptive capacity under water stress. The biostimulant, commercialized under the trade name Auras® (*P. aryabhattai* CMAA 1363), can promote crop growth even under drought conditions. In a controlled greenhouse study on maize, Barbosa et al. (2026) evaluated the effects of Auras® under both well-watered and drought stress conditions. Treatment with CMAA 1363 alleviated water stress by increasing leaf relative water content and the activities of antioxidant enzymes (superoxide dismutase, catalase, and ascorbate peroxidase), while simultaneously reducing electrolyte leakage and proline accumulation. Protection of the photosynthetic apparatus was evidenced by the preservation of chlorophyll molecules and improvements in transient chlorophyll fluorescence parameters. Under both water regimes, significant improvements in morpho-agronomic parameters were observed, positively correlated with an increase in root system dry mass.

Studies with endophytic strains isolated from maize reinforced this multifunctional potential. Ribeiro et al. (2018) evaluated four *Bacillus* strains: *B. subtilis* (B1920, B2084, and B2088) and *B. pumilus* (B1923), isolated from roots, leaves, and xylem sap of maize grown in Cerrado Oxisol, and found that all solubilized iron phosphate (Fe-P), the predominant and least soluble form of P in highly weathered tropical soils. Three of the four strains produced carboxylate-type siderophores and high IAA levels in the presence of tryptophan, with production ranging from 3.2 to 61.6 µg mL^{-1}. Under greenhouse conditions, strains B2084 and B2088 increased shoot biomass by approximately 55% and N, P, and K contents by 30, 50, and 70%, respectively, in soil without phosphate fertilization, demonstrating that the synergistic combination of multiple growth-promotion mechanisms amplifies the effects on the host plant (Ribeiro et al. 2018).

Phosphate solubilization represents one of the most thoroughly studied mechanisms within the genus *Bacillus* applied to maize. The best-documented example in Brazil is the BiomaPhos® formulation, containing *B. megaterium* CNPMS B119 (reclassified as *Priestia megaterium*) and *B. subtilis* CNPMS B2084, developed by Embrapa Milho e Sorgo and launched for maize in 2019 and has since obtained registration for several legume and non-legume crops, now covering more than 7 million hectares in the 2025/2026 growing season (Oliveira et al. 2020, 2025). Both strains produce siderophores, acid and alkaline phosphatases, phytase, and form biofilm, with calcium phosphate solubilization capacity superior to that of iron phosphate (Oliveira et al. 2025). In field trials conducted with BiomaPhos® inoculation across eight Brazilian states, this formulation yielded average productivity increases of 8.6% in maize and 6.3% in soybean (Oliveira et al. 2020). However, in high built-fertility soils, such as the clayey Latosol in Sete Lagoas used by Oliveira et al. (2025), inoculation with the same formulation did not result in significant grain yield increases, though it did alter rhizosphere microbial diversity and root architecture parameters depending on the growing season. This finding underscores that the efficacy of *Bacillus*-based inoculants is strongly context-dependent, modulated by soil nutrient availability, seasonal climatic conditions, and host plant genotype (Oliveira et al. 2025).

3.3 *Pseudomonas* spp

Among the species studied as bio-inputs for maize, *Pseudomonas fluorescens* stands out for its metabolic versatility and multifunctionality, combining multiple growth-promoting mechanisms with robust biocontrol capabilities (Bonotto et al. 2025; Ercole et al. 2026; Vasques et al. 2026). The review by Bonotto et al. (2025) systematizes that this efficiency results from the combination of multiple mechanisms: phosphate solubilization via organic acids, phytohormone production (IAA through the tryptophan pathway), siderophore synthesis with chelating and antimicrobial activity, and ACC-deaminase activity that reduces ethylene-mediated stress. The indirect biocontrol aspect warrants particular emphasis: *Pseudomonas* produces a diversified antimicrobial arsenal, including phenazines, pyrrolnitrin, and hydrogen cyanide, effective against common maize phytopathogens such as *Fusarium* spp. and *R. solani*. Additionally, in Bonotto et al. (2025), its capacity to ISR in the host plant via the jasmonic acid/ethylene pathway creates an additional layer of lasting protection against biotic stresses. An innovative aspect highlighted in the literature is the potential of *Pseudomonas* spp. in co-inoculations with other PGPB: combination with *A. brasilense* demonstrated superior effects over individual applications, while association with *Bacillus* spp. provides functional complementarity, with *Bacillus* performing more strongly under water stress and high temperature conditions and *Pseudomonas* excelling in siderophore production, phosphate solubilization, and biocontrol (Bonotto et al. 2025; Vasques et al. 2026).

In the context of bioprospecting new strains to compose a next-generation of bio-inputs, Ercole et al. (2026) characterized genomically and metabolomically six elite strains of the Embrapa Soja culture collection, including *Pseudomonas* sp. CNPSo 2799, identified as a probable new species, with ANI of 80.78% and dDDH of 24.60% relative to the closest described species *Pseudomonas brassicacearum*, well below the 95–96% and 70% thresholds used as species demarcation criteria. This strain presented the largest repertoire of BGCs in comparison to the other five strains studied (*Chromobacterium violaceum* CNPSo 1954; *Pantoea agglomerans* CNPSo 2602; *B. velezensis* CNPSo 2657; *Bacillus altitudinis* CNPSo 2658; *Bacillus safensis* CNPSo 2725), encompassing at least 33 clusters corresponding to 12.32% of the total genome, including 14 with high similarity to known compounds, among them 2,4-diacetylphloroglucinol, histicorrugatine, corpeptin, nunapeptin, and kolossin, alongside numerous clusters with no correspondence to any described molecule, indicating high potential for the synthesis of novel metabolites. Metabolomic analysis confirmed production of IAA, IBA, and IPA (indole-3-pyruvic acid) and the genome revealed genes for biofilm formation and siderophore production. Together with *B. velezensis* CNPSo 2657, *Pseudomonas* sp. CNPSo 2799 was the unique strain with representatives of CAZymes across all six functional classes identified, indicating superior enzymatic versatility for polysaccharide degradation and remodeling in the rhizosphere (Ercole et al. 2026). In a field study, inoculation of maize with the strain *P. fluorescens* CNPSo 2719, resulted in average grain yield increases of 29% under standard technological input levels and of 31% under high technological input levels, even with a 25% reduction in the N topdressing rate (Sandini et al. 2019).

3.4 *Stenotrophomonas* spp

Beyond the most extensively studied genera (*Azospirillum*, *Bacillus*, *Pseudomonas*), Brazilian biodiversity has revealed other promising genera of PGPB. In a bioprospecting study conducted with rhizospheric isolates from maize in Brazil, Ercole et al. (2021) screened 282 isolates and selected eleven candidates with the highest plant growth-promoting performance in greenhouse assays. Among these, isolate LGMB417, identified as *Stenotrophomonas* sp., represented a noteworthy result, as *Stenotrophomonas* accounted for only 2.91% of the total collection. Among the eleven selected isolates, LGMB417 was the only one to simultaneously yield positive results for biological nitrogen fixation in both the molecular detection of the *nifH* gene and the biochemical assay, in addition to phosphate solubilization (presence of *pqqC*), IAA production (presence of *ipdC*), and synthesis of cellulase, pectinase, urease, and esterase. This metabolic multifunctionality confers to the isolate a particularly versatile profile, compatible with activity across multiple fronts of growth promotion and biocontrol.

In addition, Ercole et al. (2021) further noted that bacteria of the genus *Stenotrophomonas* are frequent colonizers of the rhizospheres of diverse crops and may play relevant roles in biogeochemical processes such as the sulfur and nitrogen cycles, reinforcing the biotechnological potential of LGMB417 as a bio-input candidate for maize, subject to species-level identification and safety validation for commercial use. The broader significance of *Stenotrophomonas* as a PGPB genus is further supported by Ercole et al. (2025), who identified it among the bacterial genera capable of quorum sensing-mediated biocontrol, a mechanism by which bacteria coordinate gene expression in response to cell density to suppress phytopathogens and regulate biofilm formation, highlighting the indirect plant protection potential of this genus beyond its direct growth-promoting traits.

Extending this line of investigation to endophytic communities, Fagotti et al. (2026) isolated and characterized 83 endophytic bacteria from stems of landrace maize grown under low-input and organic cropping systems in southern Brazil, identifying eight *Stenotrophomonas* isolates distributed across all three agricultural management systems evaluated. Among them, *Stenotrophomonas* spp. CNPSo 2326 was particularly noteworthy for its outstanding capacity to synthesize indolic compounds even in the absence of tryptophan, reaching 6.44 µg mL^{-1}, the highest value among all isolates under that condition, suggesting the activity of tryptophan-independent IAA biosynthesis pathways, which may be especially relevant under field conditions where tryptophan availability is limited.

3.5 Other Bacteria

While most studies on PGPB in maize in Brazil focus on rhizobacteria that colonize the root surface, a special category of microorganisms has been attracting increasing attention: endophytic bacteria. Ercole et al. (2025) highlight that these microorganisms, capable of internally colonizing plant tissues without causing disease symptoms, offer unique advantages over traditional rhizobacteria, including greater stability in the interaction with the host plant and direct access to plant-derived signaling compounds.

Endophytic bacteria benefit from their internal location, which reduces competition with soil microbiota and favors the direct production of bioactive compounds within plant tissues. Genera such as *Herbaspirillum* and *Burkholderia*, as well as certain *Bacillus* strains, have demonstrated internal colonization capacity in maize and other grasses, acting through multiple mechanisms (Ercole et al. 2025; Fagotti et al. 2026). Among the mechanisms described for endophytic

PGPB, ACC-deaminase activity, which cleaves the ethylene precursor and thereby reduces its concentration under stress conditions, has been highlighted as particularly relevant for drought and salinity tolerance (Ercole et al. 2025). Regarding future perspectives, the authors emphasize the importance of identifying strains adapted to specific ecological niches, especially in light of the challenges posed by climate change.

On the other hand, Ikeda et al. (2020) conducted a comprehensive bioprospecting study in soils of Paraná, isolating 173 bacterial strains from maize rhizosphere and roots, subjecting them to multiple functional screening (in vitro) and greenhouse validation. Characterization revealed that 70.5% of the strains produced siderophores, 56.5% solubilized phosphate, and 53.7% were positive for both traits; of those, 63.4% also produced IAA and exhibited BNF capacity, demonstrating the functional richness of the microbiota associated with maize. Twelve elite bacterial strains were identified, their performance as inoculation of maize plants was confirmed under greenhouse conditions. Through hierarchical selection based on multifunctionality (≥3 PGPB properties) and activity intensity, these strains promoted, in greenhouse assays, increases of 44–62% in total biomass and 48–69% in root development compared to the non-inoculated control, with performance equivalent to or superior to the commercial strain *A. brasilense* Ab-V5. The elite strains were identified as belonging to the genera *Cellulosimicrobium*, *Enterobacter*, *Stenotrophomonas* and *Bacillus*.

Another genus with relevant biotechnological potential, still underexplored in agricultural applications, is *Chromobacterium*. Strain *C. violaceum* CNPSo 1954, isolated from the waters of the Rio Negro, in the Brazilian Amazon, was genomically and metabolomically characterized by Ercole et al. (2026). The genus *Pantoea* has also been attracting growing interest as a PGPB, although its characterization as a growth-promoting agent coexists with records of pathogenicity in certain species. Strain *P. agglomerans* CNPSo 2602, isolated from rice rhizosphere in Seville, Spain, was also characterized by Ercole et al. (2026) as endophytic, with genes associated with N metabolism, biofilm formation, siderophore production, and phosphate solubilization.

Methylobacterium symbioticum is a pink-pigmented, strictly aerobic, and facultatively methylotrophic *Alphaproteobacteria* originally isolated from spores of the arbuscular mycorrhizal fungus *Glomus iranicum* var. *tenuihypharum* (Pascual et al. 2020). Unlike classical associative diazotrophic bacteria used in maize, which colonize the rhizosphere and are applied via seed treatment, *M. symbioticum* colonizes predominantly the phyllosphere and has been applied via foliar spraying. Greenhouse and field trials have reported that inoculation of *M. symbioticum* allowed reductions in mineral N rates in maize without yield loss, accompanied by lower nitrate reductase activity in inoculated plants compared to controls, which was interpreted by the authors as indicative of partial substitution of mineral N by BNF (Pascual et al. 2020; Vera et al. 2024). However, this interpretation was not supported by direct experimental evidence, such as measurements of ^{15}N, N balance or acetylene reduction activity (ARA).

The genome of the strain *M. symbioticum* SB0023/3^T revealed the complete absence of the *nifHDKENB* genes required for biosynthesis and assembly of a functional nitrogenase. Three structurally and phylogenetically related forms of nitrogenase are known, the Mo-nitrogenase, the V-nitrogenase, and the Fe-only nitrogenase, all sharing a conserved minimum gene set consisting of *nifH*, *nifD*, *nifK*, *nifE*, *nifN*, and *nifB* as the core genetic requirement for N_2 fixation (Mus et al. 2018). The strain carries only *nifH*-like genes encoding a protochlorophyllide reductase subunit L and a chlorophyllide *a* reductase subunit X, both involved in bacteriochlorophyll biosynthesis, and therefore lacks this minimum gene set required for N_2 fixation (Giller et al. 2024). Any agronomic responses observed upon inoculation should therefore be attributed to other growth-promoting mechanisms described for the *Methylobacterium* genus. Among these, cytokinin production stands out as a particularly distinctive trait: a comprehensive survey of 46 *Methylobacterium* strains revealed that all representatives of the genus produce cytokinins in vitro, with *trans*-zeatin (tZ) consistently detected as the predominant and most biologically active form, at levels that surpass those reported for other plant growth-promoting bacteria (Palberg et al. 2022). This capacity to biosynthesize unusually high levels of tZ, a form structurally identical to cytokinins endogenously produced by plants, enables *Methylobacterium* to stimulate cell division and modulate host development independently of any contribution from BNF. Additional growth-promoting mechanisms described for the genus include auxin biosynthesis from L-tryptophan, ACC-deaminase activity, and siderophore production (Giller et al. 2024).

4 Mechanisms of Action

4.1 Biological Nitrogen Fixation

BNF in grasses has been the subject of systematic research in Brazil since the 1950s, when the first studies on diazotrophic bacteria associated with the rhizosphere of tropical grasses revealed fundamental differences relative to temperate regions, notably the occurrence of at least six nitrogen-fixing bacterial species, as well as stimulatory effects of plants on these microbial populations (Döbereiner 1968). Among the associations described at the time, those of

Beijerinckia spp. with sugarcane and *Azotobacter paspali* with *Paspalum notatum* stood out, as the dependence of the bacteria on the host plant indicated a close relationship that conceptually anticipated what would later be characterized as a diazotrophic association (Döbereiner 1968). A decisive advance came in the 1970s with the development of the semi-solid NFb (N-free broth) medium and the introduction of the acetylene reduction assay, which enabled the isolation and characterization of *Azospirillum lipoferum* and *A. brasilense* from roots of tropical grasses (Baldani and Baldani 2005; Döbereiner and Pedrosa 1987).

The BNF process is catalyzed by the nitrogenase enzyme complex, composed of two main subcomponents: the Fe protein (dinitrogenase reductase) and the MoFe protein (dinitrogenase), the catalytic site of the reaction. This is a highly energy-demanding process whose expression is strictly regulated according to nitrogen and oxygen availability (Döbereiner and Pedrosa 1987; Mus et al. 2018). In *A. brasilense*, expression of the *nifA* gene, the transcriptional activator of the nitrogenase structural genes, displays regulation distinct from that of other diazotrophs, being synergistically repressed by ammonium and oxygen (Baldani and Baldani 2005). The agronomic relevance of BNF promoted by *A. brasilense* in cereals was progressively documented in Brazil.

Under field conditions, experiments with strains Ab-V5 and Ab-V6 in maize and wheat demonstrated significant increases in macro and micronutrient uptake (N, P, K, Zn, and Cu), with yield gains of up to 27% in maize and 31% in wheat. These gains were attributed mainly to root development favored by IAA production and other growth regulators, rather than to BNF (Hungria et al. 2010). This understanding is reinforced by the so-called "multiple mechanisms theory" (Fukami et al. 2018a). In the Brazilian Cerrado, factorial trials evaluating inoculation with *A. brasilense* (Ab-V5 and Ab-V6), N sources, and topdressing N rates demonstrated that inoculation in the absence of topdressing N promoted a significant increase in maize yield, with an increment of 2700 kg ha^{-1} relative to the non-inoculated control without N fertilization (Kaneko et al. 2019). However, the interaction between inoculation and high mineral N rates (135–180 kg ha^{-1} topdressing) resulted in reduced leaf N concentration and yield in inoculated plots, suggesting that high mineral N availability may negatively interfere with the nitrogenase activity and *Azospirillum* mediated root development (Kaneko et al. 2019).

Araújo et al. (2015) evaluated, under field conditions in Dourados, state of Mato Grosso do Sul, central-west Brazil, the effect of N fertilization combined with inoculation with *A. brasilense* strains Ab-V5 and Ab-V6 and *Herbaspirillum seropedicae* strain Z-94 on agronomic parameters, yield, and nutritional status of maize. The authors found that inoculation combined with N fertilization positively influenced ear fresh weight and diameter, number of grains per ear, shoot dry mass, grain yield, and leaf chlorophyll content, with yield increases of up to 6.82% relative to the non-inoculated, unfertilized control, and of 27.64% increase in shoot dry mass in the *H. seropedicae* + 120 kg ha^{-1} N treatment. Leaf N, P, K, and Zn contents were positively influenced by the treatments, with a notable 52.73% increase in leaf N content in the *A. brasilense* + 120 kg ha^{-1} N treatment relative to the control. The authors concluded that inoculation combined with only 30 kg ha^{-1} N yielded results similar to those obtained with the maximum rate of 120 kg ha^{-1} N, suggesting the potential for reducing synthetic nitrogen fertilizer use in maize through inoculation with diazotrophic bacteria.

These results reinforce the importance of calibrating nitrogen fertilization in systems that incorporate biological inoculants, to maximize the benefits of BNF and the other growth-promotion mechanisms at play (Araújo et al. 2015; Fukami et al. 2018a; Kaneko et al. 2019).

4.2 Phytohormones

Phytohormone synthesis is a central mechanism of growth promotion by PGPB and has been reviewed in detail elsewhere (Orozco-Mosqueda et al. 2023); the general biology is therefore not repeated here, and this section is restricted to the findings obtained with strains used or prospected for maize in Brazil. Two points from that general framework are retained because they condition the interpretation of the Brazilian data: 80–90% of the PGPB strains studied synthesize IAA, and the physiological response of the plant can rarely be attributed to a single phytohormone (Orozco-Mosqueda et al. 2023).

In this context, Fukami et al. (2018b), through metabolomic analyses by Ultra-High-Performance Liquid Chromatography coupled with High-Resolution Tandem Mass Spectrometry (UHPLC-HRMS/MS) of cell-free metabolites of *A. brasilense* Ab-V5 and Ab-V6, found that strain Ab-V6 synthesized 233% more IAA and 50% more SA than Ab-V5, while JA was detected at very low concentrations, below 1.0 µg L^{-1}. The authors further demonstrated that, under normal conditions, inoculation with these strains induces plant protection through the simultaneous activation of the JA and SA signaling pathways, corresponding respectively to induced systemic resistance and systemic acquired resistance. Under salt stress, protection occurs predominantly via the SA and ABA pathways, evidencing the mechanistic plasticity of PGPB in response to environmental conditions (Orozco-Mosqueda et al. 2023).

Recent advances in the metabolomic characterization of PGPB have revealed that the phytohormonal profile of

agronomically relevant strains extends well beyond the widely studied IAA. Ercole et al. (2026) combined genomic and metabolomic prospection of six elite strains (described elsewhere in this review) and quantified 14 phytohormones and precursors in bacterial cell-free metabolites (CFMs). Five of these compounds were detected in the CFMs, and IAA was the only phytohormone identified in all strains, with concentrations ranging from 0.60 µg mL^{-1} (*P. agglomerans* CNPSo 2602) to 24.87 µg mL^{-1} (*C. violaceum* CNPSo 1954).

Also in the study of Ercole et al. (2026), IPA, a key precursor in IAA biosynthesis via the tryptophan-dependent pathway, was detected exclusively in the CFMs of *C. violaceum* CNPSo 1954 (175.55 µg mL^{-1}) and *B. safensis* CNPSo 2725 (11.32 µg mL^{-1}), at concentrations exceeding those of IAA itself, suggesting that the precursor may have been partially channeled into alternative metabolic routes. IBA, a precursor of IAA in plant tissues, was detected in all three *Bacillus* strains and in *Pseudomonas* sp. CNPSo 2799, with concentrations between 6.53 and 8.47 µg mL^{-1} and no statistically significant differences among these strains. ABA was detected exclusively in the CFMs of *B. velezensis* CNPSo 2657 (1.44 µg mL^{-1}), constituting one of the rare records of bacterial production of this phytohormone, generally synthesized by plants via the carotenoid pathway, with relevant implications for the induction of abiotic stress tolerance, in line with the modulatory role of ABA described by Orozco-Mosqueda et al. (2023). A finding of methodological and interpretive significance concerns the discrepancy between genomic potential and metabolic expression: *P. agglomerans* CNPSo 2602 possesses multiple genes associated with IAA biosynthesis, including *iaaH*, *iad*, *aldH*, and *ipdC*, yet produced the lowest IAA concentration among all strains and showed complete tryptophan depletion in the CFMs, suggesting that the precursor may have been diverted to other metabolic routes. This result reinforces the argument of Orozco-Mosqueda et al. (2023) that most PGPB possess multiple IAA biosynthesis pathways with intersections among them, and that gene presence alone does not guarantee equivalent metabolic expression, highlighting the need for metabolomic validation as an indispensable step in the bioprospection and development of next-generation bio-inputs.

The stimulation of root growth and architecture by phytohormones produced by PGPB (particularly auxins) has direct agronomic consequences beyond biomass accumulation. An expanded and more branched root system enhances the plant's capacity to explore soil volume and absorb nutrients, including those derived from mineral fertilization. Martins et al. (2018) demonstrated this effect in maize grown in a sandy Cerrado Oxisol, where inoculation with *A. brasilense* (strains AbV5+AbV6 and Sp245) increased total urea-^{15}N recovery by up to 71% compared to the non-inoculated control, reaching 58% total fertilizer-N recovery in shoots. Notably, the grain yield increases attributed to *A. brasilense* inoculation (>1,000 kg ha^{-1}) exceeded those obtained with urea-N fertilization (475–876 kg ha^{-1}), reinforcing that PGPB-mediated root growth promotion can improve the conversion of fertilizer inputs into harvestable product. The authors attributed this effect partly to the bacteria's known capacity to produce indoles and other plant growth regulators, which likely enhanced root exploration of the soil profile and mitigated the impact of dry spells characteristic of the Cerrado region on nutrient uptake.

4.3 Phosphate Solubilization

Inorganic phosphate solubilization is of particular relevance in Brazilian tropical soils, which are characterized by high P adsorption capacity and a predominance of iron and aluminum phosphates in Latosols and Argisols. Pioneering work conducted at Embrapa Milho e Sorgo demonstrated that solubilization capacity is highly variable among bacterial species and isolates: in a screening of 371 colonies from the rhizosphere of maize grown in a Cerrado Oxisol, the most efficient bacterial isolates for tricalcium phosphate solubilization were *Bacillus* sp. B17 (solubilizing 67% of total P) and *Burkholderia* sp. B5 (58.5% of total P), the latter associated with the largest pH reduction to 4.46 in the growth solution (Oliveira et al. 2009). Among isolates evaluated for organic P mineralization, *P. megaterium* CNPMS B119 showed relevant phytate mineralization activity coupled with acid phosphatase production, while the greatest overall diversity of phosphate-solubilizing microorganisms was consistently observed in the rhizosphere of P-efficient maize genotypes (L3 and BRS3060), suggesting that P acquisition efficiency in these cultivars may be partially mediated by the selective recruitment of solubilizing microorganisms (Oliveira et al. 2009). More recently, field experiments confirmed that inoculation with a bioinoculant containing *P. megaterium* CNPMS B119 and *B. subtilis* CNPMS B2084 increased P-resin availability by 46.2% and root surface area by 31.5% in the first growing season, with higher grain P and K concentrations observed in the second season, although grain yield did not differ significantly between inoculated and non-inoculated treatments under high soil P availability (Oliveira et al. 2025).

Subsequent studies with endophytic *Bacillus* strains isolated from maize revealed that Fe-P solubilization, the predominant and least soluble form in Brazilian Oxisols, ranged from 34.25 to 52.22 mg P L^{-1}, with a significant negative correlation between solubilized P and final medium pH

($r = -0.84$; $p < 0.05$) (Ribeiro et al. 2018). Strains CNPMS B2084 (*B. subtilis*, isolated from leaf tissue) and B2088 (*B. subtilis*, isolated from root tissue) produced gluconic acid as the mechanism associated with solubilization; the growth and nutrient-uptake responses obtained with these strains are presented in Sect. 3.2.

The specificity for phosphate solubilization was confirmed by Vasques et al. (2026) in a comprehensive screening of 100 strains: only seven strains solubilized calcium phosphate, five of which belonged to the genus *Pseudomonas* (CNPSo 2222, 2604, 2719, 2878, and 4140), one to *P. agglomerans* CNPSo 2602, and one to *Gluconacetobacter azotocaptans* CNPSo 2783. This result, with only 7% positivity among 100 strains, demonstrates that phosphate solubilization is a rare and genus-specific trait more likely to be encountered in *Pseudomonas*, which has direct implications for bioprospection strategies: systematically collecting and screening representatives of this genus maximizes the probability of identifying phosphate solubilizers with bio-input potential.

4.4 ACC-Deaminase

The enzymology of 1-aminocyclopropane-1-carboxylate (ACC) deaminase (EC 3.5.99.7), encoded by the *acdS* gene, has been extensively reviewed (Glick et al. 2007; Glick 2014; Shahid et al. 2023; Orozco-Mosqueda et al. 2023) and is summarized here only to the extent required to interpret the Brazilian data: bacteria carrying *acdS* take up root-exuded ACC and cleave it into α-ketobutyrate and ammonia, lowering endogenous ethylene and preserving root growth under abiotic stress, and this activity operates in a self-reinforcing loop with bacterial IAA, which would otherwise raise ACC synthase transcription and ethylene production. The trait is taxonomically widespread, having been documented for *Pseudomonas* spp., *Bacillus* spp., *Enterobacter* spp., *Azotobacter* spp. and *Agrobacterium* spp. in association with tolerance to water deficit, salinity and heavy metals (Shahid et al. 2023).

In the Brazilian context, Vasques et al. (2026) identified 38 (out of 100) ACC-deaminase producers distributed across 15 genera: *Achromobacter*, *Agrobacterium*, *Azospirillum*, *Bacillus*, *Bradyrhizobium*, *Chromobacterium*, *Delftia*, *Ensifer*, *Methylobacterium*, *Neorhizobium*, *Paenibacillus*, *Pantoea*, *Paraburkholderia*, *Pseudomonas*, and *Rhizobium*. *Pseudomonas* harbored the greatest number of strains (six), followed by *Agrobacterium* and *Bradyrhizobium* (four each). In greenhouse experiments with maize under water restriction, IAA production and ACC-deaminase activity were highlighted as central mechanisms to increase drought tolerance (Vasques et al. 2026).

4.5 Siderophores

The chemistry and classification of siderophores, and their dual role in iron acquisition and in the deprivation of phytopathogenic fungi, have been comprehensively reviewed (Beneduzi et al. 2012; Scavino and Pedraza 2013; Saha et al. 2016) and are not restated here. What is specific to maize is that, as a member of the *Poaceae*, the crop uses Strategy II for iron acquisition, exuding non-proteinogenic phytosiderophores that form Fe^{3+}–phytosiderophore complexes internalized by high-specificity transporters (Scavino and Pedraza 2013); bacterial siderophores act complementarily by mobilizing Fe^{3+} in the rhizospheric apoplast. Sharma and Johri (2003) demonstrated that seed inoculation of maize with siderophore-producing *Pseudomonas* sp. strains GRP3A and PRS9 resulted in significant increases in root and shoot growth variables under Fe limitation, with the greatest values of length and dry mass observed at 10 µM Fe^{3+} combined with the bacterial inoculants, providing direct evidence of the contribution of siderophores to iron nutrition in maize grown in calcareous soil. Pyoverdines produced by fluorescent *Pseudomonas* and citric acid-based siderophores found in genera such as *Bacillus* and *Rhizobium* are among the best-documented examples of this interaction with the crop (Scavino and Pedraza 2013).

In the screening study already referenced in this review, Vasques et al. (2026) identified 30 siderophore-producing strains distributed across 11 genera: *Agrobacterium* (3), *Azoarcus* (1), *Azospirillum* (1), *Bacillus* (2), *Bradyrhizobium* (2), *Chromobacterium* (3), *Delftia* (1), *Paenibacillus* (1), *Paraburkholderia* (2), *Pseudomonas* (12), and *Rhizobium* (2). Siderophore production was evaluated by the halo/colony ratio on King B medium supplemented with chrome azurol S (CAS), with readings at 24 and 72 h of incubation, to capture differences in halo development between fast- and slow-growing strains. After 72 h, *Rhizobium giardinii* CNPSo 171 and *Pseudomonas* sp. CNPSo 2625 presented the highest halo/colony ratios. The predominance of *Pseudomonas*, with 12 producer strains, is consistent with the specialized literature, which recognizes this genus as an efficient synthesizer of pyoverdines in soils with low iron availability (Scavino and Pedraza 2013). Additionally, *A. brasilense* has been reported to synthesize siderophores that limit Fe availability to phytopathogens, and one strain of the genus was among the siderophore producers identified in the Brazilian screening discussed above, a mechanism that may confer additional competitive advantage in the rhizosphere of tropical soils, complementing the multifunctional roles already documented throughout this review (Fukami et al. 2018a; Vasques et al. 2026).

4.6 Benzoxazinoids

Recent discoveries concerning the mechanisms governing the association between grasses and PGPB were elucidated by Baatsen et al. (2025), who unveiled the role of benzoxazinoids (BXs) as signaling molecules in the maize–*Azospirillum* interaction. BXs are secondary metabolites naturally secreted by the roots of grasses such as maize, wheat, and rye, traditionally known for their defensive functions against herbivores and pathogens. Using transcriptomic approaches and chemotaxis assays, the researchers demonstrated that *A. brasilense* strain Ab-V5 (CNPSo 2083), exhibits an intense and specific chemotactic response to BXs, particularly DIMBOA and MBOA. This chemical attraction directs bacteria toward the roots, facilitating mutual recognition and optimizing root colonization. RNA-Seq analyses revealed that exposure to BXs induces upregulation of genes related to chemotaxis, flagellar motility, aromatic compound metabolism, and biofilm formation, evidencing a coordinated molecular response for the establishment of the symbiosis (Baatsen et al. 2025).

Nevertheless, BX-mediated signaling represents only one layer of a complex chemical dialogue between maize roots and rhizosphere bacteria. A comprehensive understanding of the full repertoire of molecular signals governing plant–bacteria recognition, including root exudate composition, strain-specific receptor systems, and host genotype-dependent variation, remains a critical frontier. Advancing this knowledge will be essential for the rational selection of elite bacterial strains and the development of maize genotypes with enhanced responsiveness to inoculation, ultimately improving the agronomic performance and consistency of bacterial bio-inputs under field conditions.

4.7 Biocontrol

The use of bio-inputs for the biocontrol of phytopathogens, including fungi, bacteria, nematodes, and pests, has been growing rapidly and with increasing structural diversification in Brazil, positioning the country as a global leader in this segment. Biological crop protection products totaled R$ 5.3 billion in sales in 2025, a 15% increase over the previous year, with treated area reaching 117 million hectares, a 46% advance over 2024, and the market has nearly sextupled since 2020 (CropLife Brasil 2026). The most striking expansion occurred in nematode biocontrol: bionematicides grew 60% in treated area, adding 16 million hectares in a single year, consolidating themselves as a mature market integrated into sustainable management protocols for major crops. Biofungicides, in turn, recorded the highest value growth across the entire sector, reaching R$ 1.4 billion with a 41% expansion, driven directly by increasing pressure from complex diseases such as white mold and rust in large-scale crops (CropLife Brasil 2026).

In Brazil, 142 products based on *Bacillus* spp. are registered as biofungicides and 96 as bionematicides (ANPIIBIO 2026), with products registered for nematode control that also demonstrate intrinsic root protection capacity showing efficacy against soilborne fungi such as *Fusarium* spp., evidencing the multifunctionality of a next generation of biological agents. Bacterial solutions are expected to continue dominating the market over the next decade, with new formulations containing multiple microorganisms and a broad range of target organisms. In this context, PGPB with biocontrol capacity gain strategic relevance, and understanding the molecular mechanisms by which they suppress phytopathogens, including antifungal lipopeptide production, lytic enzymes, volatile organic compounds, biofilm formation, and induction of systemic resistance, becomes an indispensable condition for the development of more effective bio-inputs (Compant et al. 2005; Diniz et al. 2024; Figueiredo et al. 2025).

One main biocontrol mechanism of PGPB is the production of lytic enzymes, particularly chitinases (EC 3.2.1.14), which cleave the β-1,4-glycosidic bonds of chitin, the main structural component of fungal cell walls; the evidence for this mechanism across bacterial genera and pathosystems was compiled by Compant et al. (2005) and is not detailed here.

In the specific context of biocontrol in maize, in the study already cited in this review with *B. velezensis* and *Paenibacillus ottowii*, Figueiredo et al. (2025) identified, through manual and bioinformatic analysis, genes encoding chitinase, cellulase, β-1,3−1,4-glucanase, phosphodiesterases, extracellular proteases (dihydrolipoamide dehydrogenase, oxalate decarboxylase), subtilisin, and serine proteases. The remaining components of this antifungal arsenal, namely the lipopeptide clusters, volatile organic compounds, biofilm and ISR genes, together with the greenhouse and field performance of the strain, are presented in Sect. 3.2 (Figueiredo et al. 2025).

Diniz et al. (2024) characterized chemically and genetically the lipopeptides produced by three *B. velezensis* strains (CT02, IM14, and LIS05) and one *P. ottowii* strain (LIS04) against *F. verticillioides* CML2778. Analysis by UPLC-ESI-QTOF-MS identified, in the *B. velezensis* strains, lipopeptides of the fengycin A and B and surfactin families, with iturin A additionally detected in LIS05 and IM14; for *P. ottowii* LIS04, fusaricidins A, B, C, D/E, and A1 were identified, along with five novel lipopeptides with no prior description in the literature. The mechanism of action of these molecules is based on their amphiphilic nature, a lipid-peptide structure that interacts with cell membranes, altering their configuration and leading to cell lysis and death.

The ultrastructural effects were documented by SEM: control hyphae appeared intact, smooth, and of uniform thickness, while hyphae treated with the cell-free supernatant of all four strains were dehydrated, distorted, ruptured, and showed membrane cavitation. Chemometric analysis (PLS-DA) demonstrated that surfactin and the novel lipopeptides of *P. ottowii* were the compounds with the greatest discriminating power among the groups. The *Bacillus* strains, particularly CT02 grown in TSB medium, showed the highest antifungal activity, while *P. ottowii* LIS04 required 100% CFS concentration to achieve ≥ 50% inhibition of *F. verticillioides* growth.

The biocontrol mechanism exerted by these bacteria therefore involves not only direct lysis of the pathogen by lipopeptides and hydrolytic enzymes, but also the activation of induced systemic defense responses in the plant, mediated by VOCs, biofilm adhered to roots, and regulation of cellular water and solute transport, contributing simultaneously to plant protection and growth promotion (Figueiredo et al. 2025). Compant et al. (2005) describe that PGPB-mediated ISR operates predominantly through the jasmonic acid/ethylene pathway, with accumulation of pathogenesis-related proteins (PR proteins), including endogenous plant chitinases, PR-1, PR-2, and peroxidases, creating an amplified and systemic biocontrol effect.

The systematic genomic characterization of CAZymes in PGPB represented an important methodological advance for understanding biocontrol at the molecular level. Ercole et al. (2026) identified an average of 79 CAZymes per genome in six elite strains, distributed across six functional classes: glycoside hydrolases (GHs), glycosyltransferases (GTs), polysaccharide lyases (PLs), carbohydrate esterases (CEs), auxiliary activities (AAs), and carbohydrate-binding modules (CBMs). GHs and GTs accounted for more than 50% of the total repertoire. *P. agglomerans* CNPSo 2602 presented the greatest number of CAZymes (93), while *B. velezensis* CNPSo 2657 and *Pseudomonas* sp. CNPSo 2799 were the only strains with representatives across all six classes, as the other *Bacillus* strains lacked auxiliary activities, and *C. violaceum* and *P. agglomerans* lacked polysaccharide lyases and/or carbohydrate-binding modules. These data provide the genomic basis for explaining the enzymatic activity detected in soils inoculated with PGPB, connecting biochemical soil indicators to the molecular mechanisms of the responsible bacteria.

4.8 Peptides of Microbial Origin

Non-ribosomal peptides (NRPs) are synthesized by non-ribosomal peptide synthetases (NRPS) independently of the ribosome, a route that allows the incorporation of non-canonical amino acids and confers cyclic structures and bioactivities unavailable to ribosomally synthesized proteins; their general chemistry and mode of action have been reviewed by Ranjan et al. (2023) and are not repeated here. The lipopeptides most relevant to maize pathosystems are surfactin, iturin and fengycin, which act by membrane disintegration, pore formation and loss of membrane integrity respectively, and bacillibactin, an NRP with siderophore function (Ranjan et al. 2023). Consistent with these findings, genome analysis of *B. velezensis* CNPSo 2384, strain isolated from maize, revealed eight biosynthetic gene clusters encoding NRPs and polyketides, underscoring the biocontrol potential of Brazilian native *Bacillus* strains (Fagotti et al. 2026). In the genus *Chromobacterium*, violacein is a tryptophan-derived compound synthesized by an NRPS enzymatic complex, with documented anti-microbial, anti-parasitic, and insecticidal activities, and is also the characteristic purple pigment of the species (Ercole et al. 2026). These compounds constitute a central component of the biocontrol arsenal of PGPB.

Ercole et al. (2026) provided the first systematic characterization of NRPS-type BGCs in six elite Brazilian PGPB strains, revealing the breadth of this peptidic arsenal. *B. velezensis* CNPSo 2657 presented clusters with high similarity to bacilysin, macrolactin H, bacillibactin, and fengycin, along with clusters like difficidin and bacillaene. *B. altitudinis* CNPSo 2658 exhibited clusters like bacilysin and lichenysin, while *B. safensis* CNPSo 2725 showed high similarity to bacillibactin, bacillibactin E and F, peptides with siderophore function. *C. violaceum* CNPSo 1954 revealed clusters related to viobactin, violacein, and chromobactin, along with indole-type and NRP-metallophore clusters. *P. agglomerans* CNPSo 2602 presented clusters like frederiksenibactin and desferrioxamine E, both iron-chelating compounds with siderophore and biocontrol functions. *Pseudomonas* sp. CNPSo 2799 stood out with the largest absolute repertoire of BGCs (33 clusters, 12.32% of the genome), including clusters with high similarity to 2,4-diacetylphloroglucinol, histicorrugatin, corpeptin, nunapeptin, and kolossin, along with numerous clusters with no correspondence to known compounds, indicating strong potential for the discovery of novel bioactive molecules. The systematic presence of NRPS-type BGCs across all strains studied reinforces that biocontrol mediated by bioactive peptides is a central property of elite PGPB, with direct implications for the development of multifunctional bioinputs for Brazilian maize.

The integration of results described in the preceding sections allows a systemic reading of the mechanisms by which PGPB promote the growth and protection of maize. Figure 3 graphically synthesizes this multiplicity of actions, bringing together the eight principal mechanisms documented in the literature for the period 2005–2025: biological nitrogen

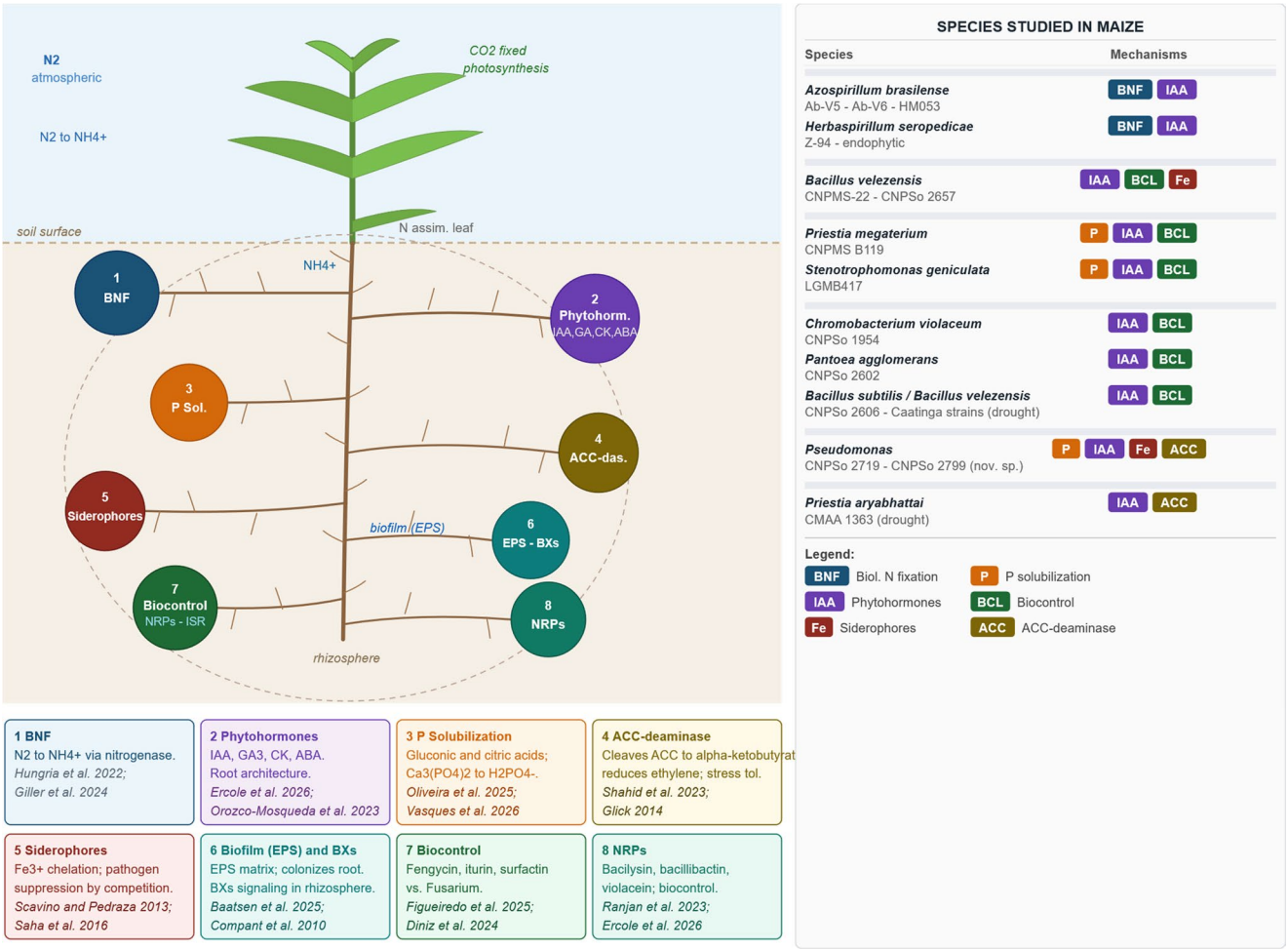


Fig. 3 Mechanisms of action of bacterial bio-inputs in the maize (Zea mays L.) rhizosphere studied in Brazil (2005–2025): 1 biological nitrogen fixation; 2 phytohormones and benzoxazinoid signalling; 3 inorganic phosphate solubilization; 4 ACC-deaminase; 5 siderophores; 6 biofilm (EPS) and benzoxazinoids; 7 biocontrol; 8 non-ribosomal peptides. Each mechanism is described in Sect. 4. The lateral panel lists the best-characterized bacterial species in maize in Brazil and the mechanisms confirmed for each strain. ABA, abscisic acid; ACC, 1-aminocyclopropane-1-carboxylate; BXs, benzoxazinoids; CK, cytokinins; EPS, exopolysaccharides; GA3, gibberellic acid; IAA, indole-3-acetic acid; NRPs, non-ribosomal peptides

fixation (BNF), phytohormone production, phosphate solubilization, ACC-deaminase activity, siderophore synthesis, benzoxazinoids and biofilm formation (exopolysaccharides, EPS), biocontrol of phytopathogens and non-ribosomal peptide (NRP) production. The lateral panel of the figure presents the best-characterized bacterial species in maize in Brazil, with indication of the confirmed mechanisms for each strain studied.

4.9 Effects on Soil Nutrient Status and Rhizosphere Functioning

Most Brazilian studies on bacterial bio-inputs in maize have quantified the nutritional status of the plant rather than that of the soil, and this asymmetry needs to be stated explicitly before the available evidence is summarized. The plant-side evidence is consistent. Under field conditions, inoculation with Ab-V5 and Ab-V6 increased the uptake of N, P, K, Zn and Cu in maize and wheat (Hungria et al. 2010); the meta-analysis presented in Sect. 3.1 recorded higher leaf N concentration and grain N content (Barbosa et al. 2022); and in Mato Grosso do Sul, inoculation combined with 120 kg ha^{-1} N increased leaf N content by 52.73% relative to the control, with positive effects also on leaf P, K and Zn (Araújo et al. 2015). In a sandy Cerrado Oxisol, inoculation increased total urea-^{15}N recovery by up to 71%, reaching 58% of applied fertilizer N recovered in shoots (Martins et al. 2018), which is the most direct Brazilian demonstration that PGPB improve the capture of nutrients already present in the system rather than simply adding them.

Evidence on soil attributes themselves is far more restricted and is essentially confined to phosphorus: the

acidification, solubilization and field data presented in Sect. 4.3 show that inoculation can raise P availability in the soil and not only in the plant (Oliveira et al. 2009, 2025; Ribeiro et al. 2018), and the genomic basis for the enzymatic activity detected in inoculated soils is given by the CAZyme repertoire described in Sect. 4.7 (Ercole et al. 2026).

Two limitations should therefore be acknowledged. First, no long-term Brazilian dataset yet reports the effect of continuous inoculation on soil chemical attributes such as organic carbon, cation exchange capacity, base saturation or the N and P balances of the system; the available results refer to single seasons or to specific fractions such as P-resin. Second, where soil P availability is already high, as in the built-fertility Latosol of Sete Lagoas, the effect on grain yield disappears even though root and rhizosphere parameters are altered (Oliveira et al. 2025), which indicates that changes in soil nutrient status mediated by bio-inputs are conditional on the initial fertility of the site. Establishing long-term monitoring of soil fertility indicators under inoculation is, in our view, one of the most consequential gaps for the next decade of research on bio-inputs in Brazilian maize.

5 Commercial Formulations of Bacterial Bio-Inputs for Maize in Brazil

Because the scale of use described in Sect. 2 rests on products rather than on strains alone, the characteristics of the commercial formulations available in Brazil are summarized in Table 2. Four categories can be distinguished.

Table 2 Principal commercial and pre-commercial bacterial bio-input formulations used in maize in Brazil. Blank cells indicate data not reported in the cited sources. CFU, colony-forming units; ha, hectare; MAPA, Ministério da Agricultura, Pecuária e Abastecimento (Brazilian Ministry of Agriculture, Livestock and Food Supply); PGCit, poly(glycerol citrate)

Formulation / product	Microbial composition	Carrier and application route	Guaranteed concentration	Adoption / scale	Reported agronomic effect in maize	Reference
A. brasilense inoculants (registered with MAPA in 2009; non-exclusive licensing)	*A. brasilense* Ab-V5 (=CNPSo 2083)+Ab-V6 (=CNPSo 2084)	Peat or liquid; seed, in-furrow or foliar (V2–V3)	1×10^8 to 2×10^8 CFU g^{-1} or mL^{-1}	10.03 million ha in 2025/26	+5.4% grain yield (meta-analysis); peat+9.5% vs. liquid+5.5%; foliar at V2–V3+3.1%; +3.1% with 25% reduction of topdressing N	Hungria et al. 2010; Hungria and Nogueira 2019; Barbosa et al. 2022; Hungria et al. 2022; Fukami et al. 2016; Alves et al. 2026; Kynetec/FarmTrak 2026
BiomaPhos® (launched 2019)	*P. megaterium* CNPMS B119+*B. subtilis* CNPMS B2084	Seed treatment		>7 million ha in 2025/26	+8.6% grain yield across eight states; +46.2% soil P-resin and +31.5% root surface area; no yield response in high-P soil	Oliveira et al. 2020, 2025
Auras®	*P. aryabhattai* CMAA 1363	Biostimulant			Alleviation of water stress; higher leaf relative water content and antioxidant enzyme activity; increased root dry mass	Barbosa et al. 2026
Bacillus-based biological control products	*Bacillus* spp. (142 biofungicide and 96 bionematicide registrations)	Seed, in-furrow and foliar		117 million ha treated (all crops, 2025)	Suppression of soilborne fungi including *Fusarium* spp.	ANPIIBIO 2026; CropLife Brasil 2026
B. velezensis CNPMS-22 (pre-commercial)	*B. velezensis* CNPMS-22	Seed treatment		Experimental	Plant survival in *F. verticillioides*-infested soil raised from 34.4% to 87.5%; field yield equivalent to chemical fungicide	Figueiredo et al. 2025
PGCit–trehalose encapsulated powder (experimental)	*A. brasilense* Ab-V5	Dry powder; seed treatment	$>10^8$ CFU g^{-1} for >180 days (lyophilized)	Experimental	4.76×10^4 CFU $seed^{-1}$ recovered from agrochemical-treated seeds vs. no recovery with liquid inoculant	Alves et al. 2026
Foliar *Methylobacterium* products	*M. symbioticum*	Foliar spraying			Reported reductions in mineral N rate without yield loss; no *nifHD-KENB* genes, so effects not attributable to BNF	Pascual et al. 2020; Vera et al. 2024; Giller et al. 2024

The first comprises inoculants based on *A. brasilense* Ab-V5 and Ab-V6, registered with the Ministry of Agriculture in 2009 and licensed non-exclusively to multiple manufacturers (Hungria and Nogueira 2019; Santos et al. 2021). Two carriers dominate: peat-based and liquid formulations, generally guaranteeing between 1×10^8 and 2×10^8 CFU g^{-1} or mL^{-1} (Alves et al. 2026). The carrier is agronomically relevant and not merely logistical, since peat-based seed inoculation outperformed liquid formulations in the meta-analysis presented in Sect. 3.1 (Barbosa et al. 2022). Registered application routes include seed treatment, in-furrow application and foliar spraying, which were shown to be equally effective in four Brazilian locations, allowing a 25% reduction in the complementary N rate without yield loss, with the caveat that excessive in-furrow or soil doses may inhibit plant growth (Fukami et al. 2016).

The second category comprises phosphate-solubilizing formulations, of which BiomaPhos®, containing *P. megaterium* CNPMS B119 and *B. subtilis* CNPMS B2084, is the Brazilian reference. Its registration history, scale of use and yield response are presented in Sect. 3.2 (Oliveira et al. 2020, 2025).

The third category comprises formulations aimed at abiotic stress, exemplified by Auras®, based on P. aryabhattai CMAA 1363, whose physiological effects under water deficit are described in Sect. 3.2 (Barbosa et al. 2026).

The fourth comprises *Bacillus*-based biological control products, with 142 registrations as biofungicides and 96 as bionematicides in Brazil (ANPIIBIO 2026), within a biological crop protection market that reached R$ 5.3 billion in sales and 117 million hectares treated in 2025 (CropLife Brasil 2026).

The main technological bottleneck of these formulations is the maintenance of cell viability above 10^8 CFU g^{-1} or mL^{-1} during storage and their compatibility with the fungicides and insecticides applied to seed, which can drastically reduce viability (Santos et al. 2020). The experimental encapsulated formulation developed for Ab-V5 illustrates the direction of current development and is described in Sect. 7 (Alves et al. 2026).

6 From Single-Strain Inoculants to Multi-Strain Formulations

The transition from single-strain to multi-strain preparations is a question that the Brazilian record is unusually well placed to answer, and the evidence is summarized here.

Strictly speaking, the commercial trajectory in Brazilian maize did not begin with a single-strain product. The inoculant registered in 2009 already combined two strains, Ab-V5 and Ab-V6, and the rationale for the combination was functional complementarity rather than redundancy: Ab-V5 harbours an active quorum sensing system that Ab-V6 lacks, while Ab-V6 compensates through greater auxin production, synthesizing 233% more IAA and 50% more salicylic acid than Ab-V5 (Fukami et al. 2018b; Fagotti et al. 2019). Because the meta-analytic mean of 5.4% and the multi-environment mean of 3.1% both refer to this dual-strain product (Barbosa et al. 2022; Hungria et al. 2022), the Brazilian yield record for *Azospirillum* is, from the outset, a record for a two-strain formulation.

The clearest evidence that combining strains adds productivity comes from BiomaPhos®. The two component strains are not interchangeable: both produce siderophores, acid and alkaline phosphatases, phytase and biofilm, but their solubilization profiles differ, with calcium phosphate solubilized more efficiently than iron phosphate (Oliveira et al. 2025), and *P. megaterium* CNPMS B119 additionally shows phytate mineralization coupled with acid phosphatase production (Oliveira et al. 2009), while *B. subtilis* CNPMS B2084 was selected for Fe-P solubilization through gluconic acid and for high IAA production (Ribeiro et al. 2018). The yield response of this two-strain formulation, reported in Sect. 3.2, is higher than the means reported for the dual Azospirillum product, although the two figures come from different experimental networks and are not directly comparable.

Beyond registered products, the case for consortia now rests on an explicit functional partition of traits among genera. The screening of 100 strains of the Embrapa Soja Culture Collection, detailed in Sect. 4.3 to 4.5, shows that phosphate solubilization, ACC-deaminase activity and siderophore production are concentrated in Pseudomonas, whereas growth at low water activity and high temperature was restricted to Bacillus (Vasques et al. 2026). Genomic and metabolomic characterization of six elite strains reached the same conclusion from the opposite direction: no single strain carried the full functional repertoire, with the largest BGC repertoire in *Pseudomonas* sp. CNPSo 2799, the only record of bacterial abscisic acid production in *B. velezensis* CNPSo 2657, and the highest IAA concentration in *C. violaceum* CNPSo 1954 (Ercole et al. 2026). Consistent with this partition, co-inoculation of *Pseudomonas* with *A. brasilense* produced effects superior to the individual applications, and the association of *Pseudomonas* with *Bacillus* is functionally complementary, with *Bacillus* performing better under water stress and high temperature and *Pseudomonas* under iron limitation and phosphate solubilization (Bonotto et al. 2025; Vasques et al. 2026).

Two qualifications are necessary. First, direct field comparisons between single-strain and multi-strain treatments within the same experiment remain scarce in maize in Brazil, so the productivity gains reported for two-strain products

cannot yet be formally partitioned between the effect of combining strains and the effect of strain identity. Second, increasing the number of components increases formulation complexity, compatibility requirements and regulatory burden, and none of the studies reviewed here evaluated the stability of consortia of more than two strains under commercial storage conditions. Resolving these two points is, in our assessment, the immediate priority for establishing multi-strain formulations on the same evidentiary footing as the dual-strain products already in use.

7 Challenges and Future Perspectives

Despite consistently positive results, the response to bio-input inoculation in maize displays variability associated with the genetic background of the host. It is worthwhile mentioning that inconsistency in results is a recognized feature of PGPB contributions in non-legumes, and a major factor is variability due to plant genotype. Indeed, plant genotype affects host-microbe interactions even in highly effective symbioses such as soybean–*Bradyrhizobium*, where differences of up to twofold in nodule number, nodule dry weight and total nitrogen accumulated in tissues have been reported among cultivars grown under the same soil conditions, and yield differences of up to 27% have been observed in field experiments with cultivars belonging to the same maturity group (Hungria and Bohrer 2000). The genetic architecture underlying these differences is complex and quantitative in nature: mapping studies in soybean identified genomic regions associated with nodulation and nitrogen fixation traits, but each region explained only a small proportion of total phenotypic variation, reflecting the strong influence of environmental conditions on the expression of these traits (Santos et al. 2013). Therefore, the conclusion is that any contribution of PGPB can be affected by the plant genotype, from highly effective symbioses to lower contribution of rhizosphere bacteria.

Furthermore, developing formulations that maintain high cell viability ($>10^8$ CFU mL^{-1} or g^{-1}) over extended periods and are compatible with agrochemicals applied via seed treatment represents a persistent technological challenge. Systemic fungicides and insecticides can drastically reduce bacterial cell viability, including when pre-applied to seeds (Santos et al. 2020). Strategies to overcome this limitation include: (*i*) encapsulation of cells in biodegradable polymers; (*ii*) in-furrow application; and (*iii*) foliar spraying at early development stages (Alves et al. 2026; Fukami et al. 2016).

Regarding encapsulation, Alves et al. (2026) developed a powder formulation containing strain Ab-V5 encapsulated in a poly(glycerol citrate) (PGCit) and trehalose matrix, comparing three drying methods: (*i*) convection oven drying, (*ii*) lyophilization, and (*iii*) spray drying. The PGCit polymer was synthesized from glycerol and citric acid, naturally occurring components present in biological systems, chosen for its balance between polymerization yield, water solubility, and bacterial cell protection. The encapsulation process reduced the initial concentration of approximately 1.13×10^{10} CFU g^{-1} of the mixture to the range of 10^8 to 10^9 CFU g^{-1} in the resulting powders, a loss attributed to non-encapsulated bacteria and to incomplete protection offered by the matrix during drying. Even so, the concentrations obtained are compatible with those of commercial *A. brasilense* based bio-inputs marketed in Brazil, which generally range between 1×10^8 and 2×10^8 CFU g^{-1} or mL^{-1}.

Regarding storage stability, the three methods differed substantially (Alves et al. 2026). The spray-dried formulation showed a significant reduction in viability as early as seven days, stabilizing at around 10^7 CFU g^{-1} through 180 days, a result attributed to the small particle size generated by this process (mean diameter of approximately 4.60 µm), comparable to bacterial cell size, which may offer insufficient protection. The oven-dried formulation maintained statistically stable viability for up to 28 days, with a more pronounced decline from 70 days onward, though remaining superior to spray drying over the same period. The lyophilized formulation stood out by maintaining significantly higher viability than the other methods at all time points evaluated, preserving values above 10^8 CFU g^{-1} for more than 180 days. This result was attributed to the lower stress imposed on cells during the process, the formation of larger and more homogeneous particles, and the cryoprotective effect of trehalose, which prevents the gel-fluid phase transition of lipid bilayers during freezing.

In the cell recovery analysis on seeds, the lyophilized formulation was tested on untreated maize seeds and on seeds pre-treated with commercial fungicide and insecticide (Alves et al. 2026). After 2 h of drying, viable cells were recovered at approximately 5.19×10^4 CFU $seed^{-1}$ from untreated seeds and 4.76×10^4 CFU $seed^{-1}$ from agrochemical pre-treated seeds. After 24 h, values were 2.31×10^4 and 3.01×10^4 CFU $seed^{-1}$, respectively, indicating that neither prolonged drying time nor pesticide exposure significantly compromised bacterial recovery. In contrast, the liquid inoculant used as control did not allow the recovery of viable cells under any of the conditions tested, with counts below the detection limit in all treatments. These results demonstrate the protective potential of the PGCit-trehalose matrix against the adverse conditions on seed surfaces and against the toxic effects of chemical treatments (Alves et al. 2026).

Regarding alternative application routes, Fukami et al. (2016) demonstrated, in field experiments conducted at four locations in Brazil with maize and wheat, that foliar

and in-furrow inoculation with *A. brasilense* was as effective as seed inoculation, allowing a 25% reduction in the complementary nitrogen fertilizer rate without yield loss. The authors noted, however, that excessive inoculant doses applied in-furrow or to the soil may exert an inhibitory effect on plant growth, highlighting the need for precise dose adjustment according to the application method. Furthermore, foliar application is emerging as an alternative for better results; however, care must be taken during preparation, and other products should not be mixed into the application solution.

8 Conclusion

Two decades of research on plant growth-promoting bacteria in maize in Brazil have produced a robust body of knowledge, technologies validated at commercial scale, and a scientific trajectory that positions the country at the global forefront of agricultural bio-inputs. The substantial volumes of inoculants commercialized annually, and the growing adoption rates translate, at industrial scale, decades of rigorous science conducted under Brazilian tropical and subtropical conditions.

Azospirillum brasilense, particularly strains Ab-V5 and Ab-V6, has consolidated itself as a paradigmatic case of successful agricultural biotechnology, with consistent gains in grain yield, root mass, and the demonstrated possibility of reducing N fertilization across hundreds of field trials. To this consolidated prominence, the role of *Bacillus* spp. as a strategic component of bio-inputs for Brazilian maize has been increasingly added. The trajectory of BiomaPhos®, the first nationally developed commercial inoculant formulated with native phosphate-solubilizing bacteria, exemplifies how bioprospecting from efficient tropical genotypes can generate technologies with their own edaphoclimatic identity, although its efficacy has proven highly context-dependent on soil fertility conditions, reinforcing that the greatest benefits of bio-inputs occur under nutritional limitation or stress.

The distinctive contribution of this review lies in the systematic incorporation of advances in omics approaches and next-generation bioprospecting. The field has advanced well beyond *Azospirillum*: the metabolic arsenal of *Bacillus* spp., the unprecedented genomic repertoire of *Pseudomonas* spp., including a putative new species (CNPSo 2799), another highlight is the bacterial genus *Stenotrophomonas* spp., capable of performing biocontrol mediated by quorum sensing, in addition to its direct growth-promoting characteristics, and finally, the phytohormonal and biocontrol potential of *C. violaceum* reveals a functional diversity that remains largely underexplored. A central methodological advance of this review is the recognition that genomic potential and actual metabolic expression do not always coincide, a critical gap in earlier studies based exclusively on phenotypic screening that only metabolomic validation can overcome.

Co-inoculation emerges as a central strategy of the next generation of bio-inputs for maize. The functional complementarity among species acting in biological nitrogen fixation, phytohormone production, phosphate solubilization, siderophore synthesis, and biocontrol provides the scientific basis for multifunctional formulations capable of acting simultaneously on plant nutrition, protection, and stress tolerance. The discovery of the role of root signaling molecules in the chemotactic attraction of specific bacteria opens a new frontier: the possibility of integrating plant breeding and microbiology to select genotypes with greater capacity to recruit and benefit from precision microbial consortia.

The remaining challenges are known, but now more clearly defined. Encapsulated formulations in biodegradable matrices offer a promising solution for compatibility with chemical seed treatments and storage stability, a technological bottleneck that has historically limited large-scale adoption. Artificial intelligence, integrated with high-resolution metagenomics and metabolomics platforms, represents a promising emerging tool for predicting the performance of microbial consortia under specific edaphoclimatic conditions, overcoming the trial-and-error approach that still dominates inoculant development.

The trajectory of PGPB in maize in Brazil demonstrates that rigorous basic science, multicentric validation, and efficient technology transfer can transform soil microorganisms into tools of measurable economic and environmental impact. With the genomic, metabolomic, and agronomic framework built over the past two decades, and with *Bacillus* consolidated as the second pillar of bio-inputs alongside *Azospirillum*, Brazil possesses the unique conditions to lead the next transition: from single-strain inoculation toward integrated, intelligent microbial systems adapted to tropical conditions, capable of redefining the foundations of nutrition and protection in Brazilian maize.

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Data Availability Not applicable. This article is a bibliographic review and does not report original data.

Declarations

Declaration on Generative AI Use During the preparation of this manuscript/study, the authors used ChatGPT for the purpose of generating the graphical abstract. The authors have reviewed and edited the output and take full responsibility for the content of this publication.

Competing interests The authors declare no competing interests.

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