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Review

A Review on the Biotechnological Applications of the Operational Group *Bacillus amyloliquefaciens*

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Abstract: Bacteria under the operational group *Bacillus amyloliquefaciens* (OG*Ba*) are all Gram-positive, endospore-forming, and rod-shaped. Taxonomically, the OG*Ba* belongs to the *Bacillus subtilis* species complex, family Bacillaceae, class Bacilli, and phylum Firmicutes. To date, the OG*Ba* comprises four bacterial species: *Bacillus amyloliquefaciens*, *Bacillus siamensis*, *Bacillus velezensis* and *Bacillus nakamurai*. They are widely distributed in various niches including soil, plants, food, and water. A resurgence in genome mining has caused an increased focus on the biotechnological applications of bacterial species belonging to the OG*Ba*. The members of OG*Ba* are known as plant growth-promoting bacteria (PGPB) due to their abilities to fix nitrogen, solubilize phosphate, and produce siderophore and phytohormones, as well as antimicrobial compounds. Moreover, they are also reported to produce various enzymes including α-amylase, protease, lipase, cellulase, xylanase, pectinase, aminotransferase, barnase, peroxidase, and laccase. Antimicrobial compounds that able to inhibit the growth of pathogens including non-ribosomal peptides and polyketides are also produced by these bacteria. Within the OG*Ba*, various *B. velezensis* strains are promising for use as probiotics for animals and fishes. Genome mining has revealed the potential applications of members of OG*Ba* for removing organophosphorus (OPs) pesticides. Thus, this review focused on the applicability of members of OG*Ba* as plant growth promoters, biocontrol agents, probiotics, bioremediation agents, as well as producers of commercial enzymes and antibiotics. Here, the bioformulations and commercial products available based on these bacteria are also highlighted. This review will better facilitate understandings of members of OG*Ba* and their biotechnological applications.

Keywords: plant growth-promoting bacteria; biocontrol agent; enzymes; antimicrobial compounds; probiotics; bioremediation; *Bacillus amyloliquefaciens*; *Bacillus velezensis*; *Bacillus siamensis*; *Bacillus nakamurai*

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1. Introduction

In 1943, a Japanese scientist, Juichiro Fukumoto, first isolated *Bacillus amyloliquefaciens* from the soil. The species is named after its unique character because it produced (*faciens*) a liquefying (*lique*) α-amylase (*amylo*) [1,2]. Later, *B. amyloliquefaciens* was combined with the closely related *Bacillus subtilis* and *Bacillus licheniformis* into the *B. subtilis* species complex, based on phylogenetic and phenetic evidence [3]. From the *B. subtilis* species complex, it can be further sub-grouped into the operational group *B. amyloliquefaciens* (OG*Ba*) that

comprises four bacterial species; the soil-borne *B. amyloliquefaciens*, the plant-associated *Bacillus siamensis* and *Bacillus velezensis*, and a black-pigment-producing strain *Bacillus nakamurai* [4].

Previously, several bacterial species of the OG*Ba*, namely *B. amyloliquefaciens* subsp. *plantarum*, *Bacillus methylotrophicus* and *Bacillus oryzicola,* were reclassified as strains of *B. velezensis* [5]. Genome-based and gene-derived phylogenetic analyses revealed that *B. velezensis* belongs to a conspecific group consisting of *B. velezensis*, *B. amyloliquefaciens* subsp. *plantarum* FZB42 (reclassified as *B. velezensis* FZB42) and *B. methylotrophicus*. However, *B. velezensis* is distinct from the closely related species of *B. amyloliquefaciens* and *B. siamensis* [4]. To date, a plethora of bacterial whole-genome sequences (WGS) from members of OG*Ba* have been deposited into the National Center Biological Information (NCBI) database (Table S1). As confirmed taxonomically in 2019, 223 genomes belonged to *B. velezensis*, 19 belonged to *B. amyloliquefaciens*, 10 belonged to *B. siamensis* and 2 belonged to *B. nakamurai* [6].

The members of OG*Ba* are found in various niches including soil, plants, food, animal faeces and aquatic environments [4]. Currently, genome mining has revealed their applicability as plant growth-promoters, biocontrol agents, probiotics, bioremediation agents as well as producers of commercial enzymes and antibiotics [7,8]. Therefore, knowledge of the biology of the OG*Ba* is imperative to understanding the special qualities of the group. This review focused on the biotechnological applications of the bacterial strains belonging to the OG*Ba*.

2. An Overview of the OG*Ba*

2.1. Identification and Characterization

Bacterial species from the OG*Ba* are all Gram-positive bacteria and motile by peritrichous flagella. They are endospore-forming bacteria from the *B. subtilis* species complex. For many years, the speciation of OG*Ba* within the *B. subtilis* species complex has been uncertain, often leading to erroneous and variable results. They are difficult to distinguish using classical taxonomy parameters: morphological and physiological characteristics, cell wall compositions, 16S ribosomal RNA sequence, guanine–cytosine (G+C) content, fatty acid methyl esters (FAME) and DNA–DNA hybridization (DDH) [9]. Therefore, the taxonomic status of the bacterial species belonging to the OG*Ba* is constantly causing confusion to researchers, especially for non-professional taxonomy researchers.

It is worth mentioning that some studies have used protein-coding genes in order to further ascertain the degree of relatedness of the OG*Ba* within the *B. subtilis* species complex [10,11]. The highly conserved DNA gyrase subunit B (*gyrB*), signal transduction histidine kinase CheA (*cheA*) and RNA polymerase β-subunit (*rpoB*) were used for the study of speciation within the *B. subtilis* species complex before the advent of multilocus sequence analysis (MLSA) [11–13]. The taxonomical status of the members of OG*Ba* has been solved by genome-based [4] and gene-derived [14] phylogeny analyses. The OG*Ba* comprised four species: (i) *B. amyloliquefaciens*; (ii) *B. siamensis*; (iii) *B. velenzensis*; and (iv) *B. nakamurai*, as confirmed by cladistic analysis (Figure 1; Table 1).

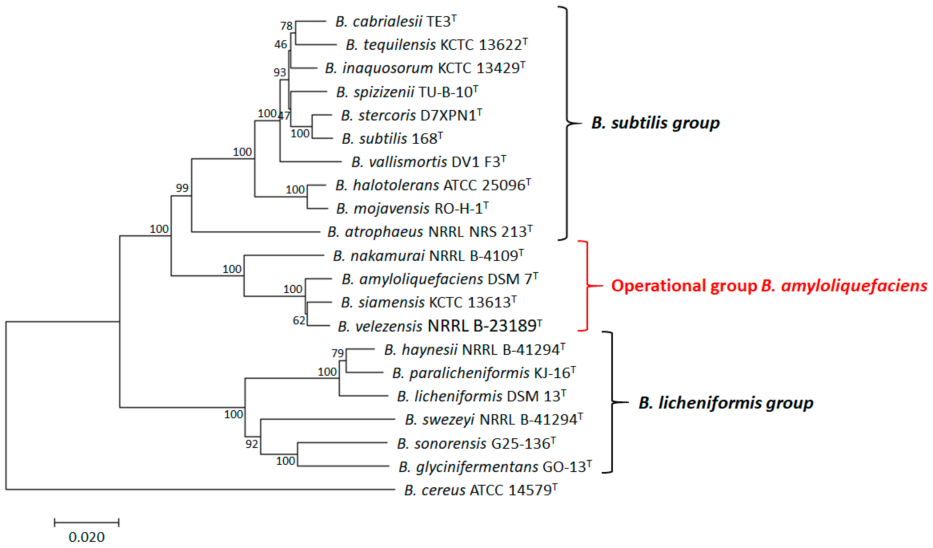

Figure 1. Neighbor-joining phylogenetic tree based on complete *rpoB* nucleotide sequences of bacterial species under the *B. subtilis* species complex. Evolutionary analyses were conducted using the MEGAX software [15]. The optimal tree with the sum of branch length = 0.66533958 is shown. The evolutionary distances were computed using the *p*-distance method. Bootstrap values, based on 1000 repetitions, are indicated at the branch points. The analysis involved 19 nucleotide sequences. There were 3534 positions in the final dataset. Bar, 0.02 substitutions per nucleotide position. *Bacillus cereus* ATTC 14579^T was used as the outgroup.

Table 1. Characterizations of bacterial species under the operational group *Bacillus amyloliquefaciens.*

Characterization		*B. amyloliquefaciens*	*B. siamensis*	*B. velezensis*	*B. nakamurai*
Type Strain		DSM 7^T / ATCC 23350^T / F^T	KCTC 13613^T / PD-A10^T / BCC 22614^T	NRRL B-23189^T / CR-502^T / CECT 5686^T / LMG 22478^T	NRRL B-41091^T / CCUG 68786^T
Isolation Source		Soil and industrial α-amylase fermentations	Salted crab (*poo-khem*) in Thailand	Brackish water sample from the river Velez at Torredelmar in Ma'laga, southern Spain	Soil in Tierra del Fuego, Argentina
Size		0.7–0.9 × 1.8–3.0 µm	0.3–0.6 × 1.5–3.5 µm	0.5 × 1.5–3.5 µm	0.74–0.93 × 1.39–2.04 µm
Endospore		Oval spores are central or paracentral in unswollen sporangia	Ellipsoidal spores are central or sub-terminal positions in swollen sporangia	Ellipsoidal spores are paracentral or sub-terminal positions in unswollen sporangia	Ellipsoidal spores are central in unswollen sporangia
G + C Content (mol %)		44.6	41.4	46.1–46.4	43.8
Growth Temperature		Optimal growth temperature is 30–40 °C. No growth occurs below 15 °C or above 50 °C.	Optimal growth temperature is 37 °C. Growth occurs at 4 °C and 55 °C.	Grow within the temperature range of 15–45 °C	Grow within the temperature range of 17–50 °C, with an optimum of 37 °C
NaCl Resistance (*w/v*)		Growth occurs with 0–10% NaCl	Growth occurs with 0–14% NaCl	Growth occurs with 0–12% NaCl	Growth occurs with 0–9% NaCl
Substrate Utilization	Tyrosine	-	-	-	+
	Citrate	+	-	-	+
Fermentation (acid)	Lactose	+	+	+	-
	Trehalose	+	-	+	+
Reference		[1]	[16]	[17]	[18]

Note: All the bacterial species are able to metabolize casein, gelatin, starch, fructose, cellobiose, glucose, glycerol, maltose, mannitol, raffinose, salicin and sucrose. Symbol: +, positive result; -, negative result.

2.2. Ecology, Isolation and Cultivation

The ability to produce endospores when facing harsh conditions allowed the members of the operational group to survive in various niches including soil, animal faeces, plants, food, bee products, drugs, air, and the aquatic environments (Table S1). Evidently, the members of OG*Ba* had been directly isolated from rare dormant volcanic soils [19], mango orchards [20] and animal faeces [21,22]. They had also been isolated from plant parts including fruits (such as lemons [23] and apples [24]), roots (such as Peruvian ground cherry [25] and peanut roots [26]) and leaves (such as lucerne [27] and camphor leaves [28]).

Moreover, traditional fermented foods including bibimbap [29], douchi [30], and doenjang [31] were reported as the sources of isolation of bacteria from this operational group. They also were isolated from bee products [32–34], heroin [35], and air [36]. In other related studies, bacteria of this operational group have been isolated from water [37], seawater [38] and sea sediment [39]. Chicken [40] and fish intestines [41] were also reported as the sources of origin for members of this operational group.

Generally, the members of OG*Ba* are cultivated routinely in Luria–Bertani (LB) medium at 30–37 °C aerobically [11,16,17]. Some members of OG*Ba* such as *B. nakamurai* grew well on nutrient agar (NA), trypticase soy agar (TSA), Reasoner's 2A agar (R2A) and tryptone glucose yeast extract agar (TGY) at 30 °C for two days [18]. Moreover, *B. velezensis* and *B. siamensis* were also reported to grow well on TSA at 37 °C and 32 °C, respectively [16,17].

2.3. Genome and Its Arrangement

In 2019, 254 bacterial strain genomes which had been deposited in the NCBI database were reported as belonging to the OG*Ba* [6]. Some of the examined strains were found to contain plasmids (Table S1). Most of the reported strains had only one plasmid, except for *B. velezensis* 157, *B. velezensis* DKU_NT_04, and *B. velezensis* NJAU-Z9 (all contained two plasmids), and *B. velezensis* LB002 (which contained three plasmids). Interestingly, some studies have focused on the functionality of the genes carried by the plasmid. For instance, the *B. velezensis* S499 plasmid, pS499, was reported as containing a *rap-phr* cassette. This cassette encoded for the regulator aspartate phosphatase (*rap*) and the Rap regulatory peptide (*phr*) with a role in governing protease secretion, growth and motility, biofilm formation and production of surfactin [42]. Meanwhile, *B. amyloliquefaciens* LL3 plasmid, pMC1, has a 6.8 kbp plasmid that includes a *rap* which is not homologous to the pS499 [42]. The hypothetical *rap* and the origin of replication of the pMC1 plasmid were cloned into the pKSV7, vector which brought about the production of plasmid-cured strains. The plasmid-cured strains have increases in glutamate-independent poly-γ-glutamic acid production by 6% as compared to the *B. amyloliquefaciens* LL3 [43].

Genome analysis allowed for further biological studies on the members of OG*Ba*. The genomic and metabolic features of the members of the group were similar; however, species-specific features including secondary metabolite biosynthesis-related and energy metabolism-related genes were also identified [4,44]. Secondary metabolite biosynthesis-related genes are enriched in *B. velezensis*, whereas energy metabolism-related genes are enriched in *B. amyloliquefaciens*. In the core-genome, *B. velezensis* harbors more genes involved in the biosynthesis of antimicrobial compounds as well as genes involved in $_{D}$-galacturonate and $_{D}$-fructuronate metabolisms compared to *B. amyloliquefaciens* and *B. siamensis*. Moreover, a xanthine oxidase gene cluster that is involved in metabolizing xanthine and uric acid to glycine and oxalureate was found in the core-genome of all the members of the group. Pan-genome analysis revealed the abilities of members of OG*Ba* to metabolize diverse carbon sources aerobically or anaerobically. Their abilities to produce various metabolites such as lactate, ethanol, xylitol, diacetyl, acetoin, and 2,3-butanediol were also identified [44]. In addition, genome analysis suggested that the regions of genomic plasticity controlled the function and structure of the genome and governed the adaptations to different niches [45]. Genome analysis also enabled the prediction of uncharacterized gene clusters and assessed the capabilities of members of OG*Ba* to produce antimicrobial compounds [6].

3. The Importance and Applications of the OG*Ba*

3.1. Plant Growth Promoters and Biocontrol Agents in Agriculture

In the agricultural sector, the biocontrol strategy has received great attention because it provides safe, environmentally friendly, long-lasting, and inexpensive alternatives [46]. The characterizations of the bacterial strains from the OG*Ba* as biocontrol agents were determined based on their abilities to improve plant growth and health [47]. These abilities involve multiple mechanisms including direct (improve plant growth) and indirect (improve plant health) mechanisms (Figure 2). Direct mechanisms involve nitrogen fixation, phosphate solubilization, siderophore production and phytohormone production (e.g., indole-3-acetic acid (IAA) and enzymes such as 1-amyclocyclopropane-1-carboxylate (ACC) deaminase). It has been reported that the co-inoculation of *B. velezensis* S141 with *Bradyrhizobium diazoefficiens* USDA110 into soybean resulted in enhanced nodulation and nitrogen fixation efficiency by producing larger nodules [48]. In another related study, the members of OG*Ba* were able to solubilize phosphate, and produce IAA, ACC deaminase and siderophores [49–51].

Meanwhile, the indirect mechanism is mainly due to their biocontrol activities attributed to the production of antimicrobial compounds in response to biotic stress [52]. The members of OG*Ba* produced antimicrobial compounds such as hydrogen cyanide (HCN) and cyclic lipopeptides such as surfactin used to inhibit the growth of pathogenic microbes [53,54]. The interactions of biocontrol agents with plant roots enhance plant resistance against some competing microbes including pathogenic bacteria, fungi and viruses. This phenomenon is termed as induced systemic resistance (ISR) [6,55].

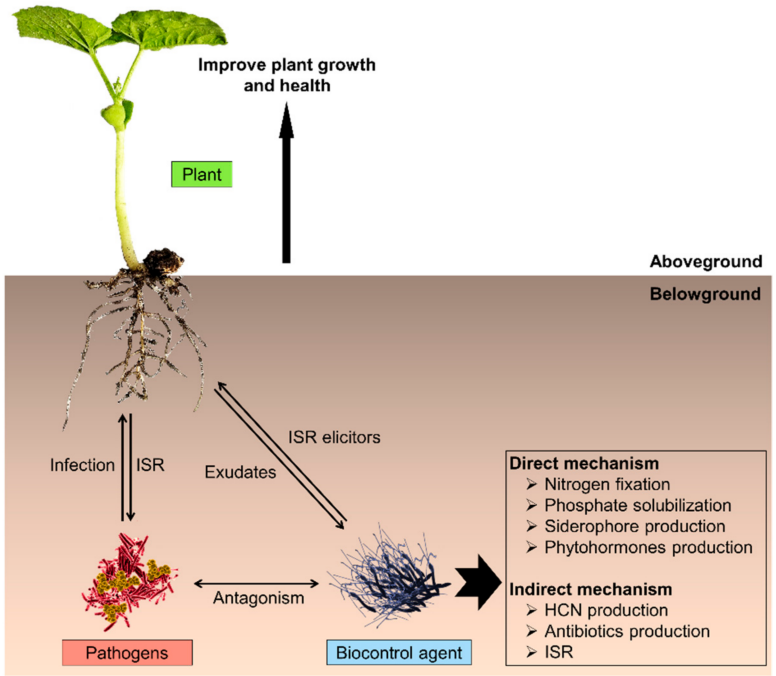

Figure 2. The biological control interactions. The illustration depicts the interactions between biocontrol agents, plant pathogens, and plants. The biocontrol agent colonized the plant root surface and produced antimicrobial compounds such as surfactin. In the plant rhizosphere, antibiosis and nutrient competition interaction suppressed the growth of pathogens. Due to the production of antimicrobial compounds and in the simultaneous presence of pathogens, the induced systemic resistance (ISR) is enhanced. Thus, this mediated the defense response of the plant towards pathogens and consequently improved plant growth and the defense mechanism against pathogens.

The members of OG*Ba* were proven to provide advantages to the agricultural sector by contributing to plant pathogen disease suppression. In plant disease management, the members of OG*Ba* acted as plant growth-promoting bacteria (PGPB) that aid in the devel-

opment of plants and reduce the proliferation of plant pathogens (Table 2). The secretion of antimicrobial compounds such as surfactin from PGPB was suggested to trigger the pathways of ISR which contributed to the suppressive effect of plant immunity [56,57]. Surfactin was determined to act as elicitors of plant immunity and enhance resistance towards further pathogenesis in plants [47]. In the lettuce rhizosphere, increased production of surfactin by *B. velezensis* FZB42 in the axenic system was suggested to contribute to the disease suppression towards *Rhizoctonia solani* infection [53]. Similarly, the treatment using *B. velezensis* FZB42 in tobacco plants was suggested improve ISR and enhance plant height and fresh weight, while lowering the disease severity rating of the tobacco mosaic virus (TMV) [58].

Table 2. Plant pathogen suppression by members of the operational group *Bacillus amyloliquefaciens* in various plant species.

PGPB Strain	Disease and Pathogen	Plant Species	Reference
B. siamensis KCTC 13613	*R. solani* *Botrytis cinerea* *Micrococcus luteus*	*Arabidopsis thaliana*	[59]
B. velezensis 83	Anthracnose disease	*Zea mays* *A. thaliana*	[20]
B. velezensis 1B-23	*Clavibacter michiganensis* subsp. *michiganensis*	*Solanum lycopersicum*	[60]
B. velezensis B25	*Fusarium verticillioides*	*Z. mays*	[61]
B. velezensis BTLK6A	*Magnaporthe oryzae Triticum*	*Triticum aestivum*	[62]
B. velezensis BTS 4			
B. velezensis CC09	Powdery mildew disease	*T. aestivum*	[28]
B. velezensis CGMCC 11640	*Botryosphaeria dothidea*	*Carya cathayensis*	[63]
B. velezensis Co1-6	*Verticillium dahliae* *R. solani* *Fusarium culmorum* *Ralstonia solanacearum*	*Matricaria chamomilla*	[64]
B. velezensis GB1	*Valsa mali*	*Malus domestica*	[65]
B. velezensis GH1-13	*Fusarium fujikuroi* *R. solani* *Xanthmonas oryzae*	*Oryza sativa*	[49]
B. velezensis GQJK49	*F. solani*	*Lycium barbarum* L.	[66]
B. velezensis GYL4	Anthracnose disease	*Cucumis sativus* L. cv. *Chunsim*	[67]
B. velezensis J-5	*B. cinerea*	*S. lycopersicum*	[68]
B. velezensis JK	*M. oryzae*	*O. sativa*	[69]
B. velezensis L-1	*Botryosphaeria berengeriana*	*Pyrus communis*	[70]
B. velezensis LM2303	*Fusarium graminearum*	*T. aestivum*	[71]
B. velezensis M27	*Sclerotinia sclerotiorum*	*Lactuca sativa* L.	[72]
B. velezensis NJAU-Z9	*Fusarium oxysporum* f. sp. *niveum* *Ralstonia solanacearum*	*Capsicum annuum* L.	[73]
B. velezensis NJN-6	*F. oxysporum* f. sp. *cubense*	*Musa* sp.	[74]
B. velezensis OEE1	*F. solani*	*Olea europaea* L.	[75]
B. velezensis P42	Bacterial wilt and early blight diseases	*S. lycopersicum*	[76]
B. velezensis PG12	Apple ring rot disease	*Malus domestica*	[24]
B. velezensis TrigoCor1448	*Fusarium* head blight disease	*T. aestivum*	[77]
B. velezensis UCMB5113	*Alternaria brassicae* *B. cinerea* *Leptosphaeria maculans* *Verticillium longisporum*	*Brassica napus*	[78]
B. velezensis XK-4-1	*Verticillium* wilt disease	*Gossypium* sp.	[79]
B. velezensis ZF2	*Corynespora* leaf spot diseases	*C. sativus*	[80]

Bacterial species from the OG*Ba* are used in bioformulations. For instance, the bacterial strain *B. velezensis* FZB42 had been established as a model strain for plant growth promotion and as a biocontrol agent [55]. In 2019, tomato seeds coated with gum arabic as adhesive along with liquid bioformulations containing *B. velezensis* FZB42 showed great inhibitory effects against *Fusarium solani* infections under in vitro conditions. Increments in germination percentage and germination rate as compared with the control were also reported [81].

To date, there are a few bioformulations containing bacterial species from the OG*Ba* available on the market (Table 3), such as SERENADE® (Bayer Crop Science, Germany) which contains *B. velezensis* QST 713 (previously *B. subtilis* QST 713) and Double Nickel 55™ (Certis Columbia, MD USA) which contains *B. velezensis* D747 (previously *B. amyloliquefaciens* D747) [55]. The application of SERENADE® together with Fracture fungicide (CEV, Portugal), which contains BLAD polypeptide, had shown notable success in controlling *Botrytis* blossom blight disease infection in blueberries [82]. Application of Double Nickel 55™ was found to be effective in controlling white mold in snap beans caused by *Sclerotinia sclerotiorum*. Double Nickel 55™, a biofungicide, was approved for organic vegetable production by the National Organic Program and Organic Materials Review Institute [83].

Table 3. Some commercial products containing the members of the operational group *Bacillus amyloliquefaciens* available on the market.

Bacterial Strain	Commercial Product	Company	Description
B. velezensis QST 713 (previously *B. subtilis* QST 713)	SERENADE Max	Bayer Crop Science, previously AgraQuest	EPA-registered biofungicide. Controls and suppresses fungal pathogens on foliage and in the soil
	SERENADE SOIL®	Bayer Crop Science, previously AgraQuest	EPA-registered biofungicide for food crops
	CEASE®	BioWorks, Inc., Victor, New York, U.S.A.	Aqueous suspension biofungicide for leafy and fruiting vegetables, herbs and spices, and ornamentals
B. velezensis FZB42 (previously *B. amyloliquefaciens* FZB42)	RhizoVital® 42	ABiTEP GmbH, Berlin, Germany	Biofertilizer, plant-growth-promoting activity, provides protection against various soil-borne diseases
	FZB24® TB	ABiTEP GmbH, Berlin, Ger-many	Plant growth-promoting agent for plant strengthening
	Taegro®	Syngenta, Basel, previously Novozyme, Davis, California, and Earth Biosciences	EPA-registered biofungicide for use in North America
B. velezensis GB03 (previously *B. subtilis* GB03)	Kodiak™	Bayer Crop Science, North Carolina, NC	EPA-registered biological seed treatment fungicide with demonstrable PGR activity. Efficient in cotton, beans, and vegetables
	Companion	Growth Products Ltd., White Plains, NY	EPA-registered biofungicide that prevents and controls plant diseases
B. velezensis D747 (previously *B. amyloliquefaciens* D747)	Double Nickel 55™	Certis Columbia, MD, U.S.A.	EPA-registered biofungicide for control or suppression of fungal and bacterial plant
	Amylo-X®	Certis Columbia, MD USA/Intrachem Bio Italia SpA	Biocontrol of *Botrytis* and other fungal diseases of grapes, strawberries, and vegetables, and bacterial diseases, such as fire blight in pome fruit and PSA in kiwi fruit

Apart from the aforementioned uses, the members of OG*Ba* have also been applied as biocontrol agents against parasitic nematodes and protist pathogens. In 2008, *B. velezensis* FZB42 was reported to reduce nematode eggs in roots, juvenile worms in soil and plant galls on tomato [84]. Genomic study revealed that the whole genome of *B. velezensis* FZB42 encoded a diverse spectrum of different antimicrobial compounds able to suppress harmful nematodes living within the plant rhizosphere [85]. In controlling the protist pathogen,

B. velezensis HB-26 (previously *B. amyloliquefaciens* HB-26) showed promising capability for controlling *Plasmodiophora brassicae*, a root-infecting protist that causes clubroot disease in brassica species. Many antimicrobial compounds showing specific activities against *P. brassicae* were found in the genome of *B. velezensis* HB-26 [86]. Overall, much more focus is still needed to fulfill the understanding of the molecular basis for the ability of members of OG*Ba* to inhibit nematodes and protists beyond in silico genomic studies. Understanding such attributes will help to shed light on the functionalities as well as the biological roles of antimicrobial compounds from OG*Ba* not only for improved plant growth but as biocontrol agents to minimize the proliferation of plant pathogens including viruses, bacteria, fungus, nematodes, and protists.

3.2. Source of Commercial Enzymes

Microbial enzymes such as α-amylase, protease, and lipase have been used in various biotechnological applications including textile applications, feed industry, food industry, and organic synthesis [87–89]. The U.S. Food and Drug Administration (FDA) in 1999 reported that enzymes such as α-amylase and protease originating from *B. subtilis* are Generally Recognized as Safe (GRAS) for use as direct food ingredients [90]. As members of the *B. subtilis* species complex, OG*Ba* bacteria are a potent bacterial group due to their abilities to produce various types of enzymes including α-amylase, protease, lipase, cellulase, xylanase, pectinase, aminotransferase, barnase, peroxidase, and laccase (Table 4).

Table 4. Various types of enzymes produced by members of the operational group *Bacillus amyloliquefaciens*.

Bacterial Species	Enzymes	Reference
B. amyloliquefaciens KCP2	α-amylase and protease	[91]
B. amyloliquefaciens NRRL 942	α-amylase	[92]
B. siamensis JJC33M	α-amylase	[93]
B. velezensis 157	α-amylase, cellulase, xylanase and pectinase	[94]
B. velezensis 275	Cellulase, xylanase, peroxidase, and laccase	[95]
B. velezensis AP194	Pectinase	[96]
B. velezensis AP214	Pectinase	[96]
B. velezensis GZB	Laccase	[97]
B. velezensis JJ-D34	α-amylase, protease and cellulase	[98]
B. velezensis Jxnuwx-1	Protease	[99]
B. velezensis SB1216	Barnase	[100]
B. velezensis SPZ1	Lipase	[101]
B. velezensis SYBC H47	Aminotransferase	[102]
B. velezensis ZL918	α-amylase	[103]

3.3. Antimicrobial Compounds Producer

The increment in the global antibiotic-resistant pathogens has led to the exploration of compounds with alternative therapeutic strategies [104]. The members of OG*Ba* were reported to produce antimicrobial compounds used in the suppression of pathogens [45]. The antimicrobial compounds produced by the member of OG*Ba* have been reviewed previously [8,105]. The members of OG*Ba* produced some important antimicrobial compounds (Figure 3), including non-ribosomal peptides (surfactin, fengycin, bacillomycin-D, bacilysin and bacillibactin) and polyketides (bacillaene, macrolactin and difficidin) [6,105].

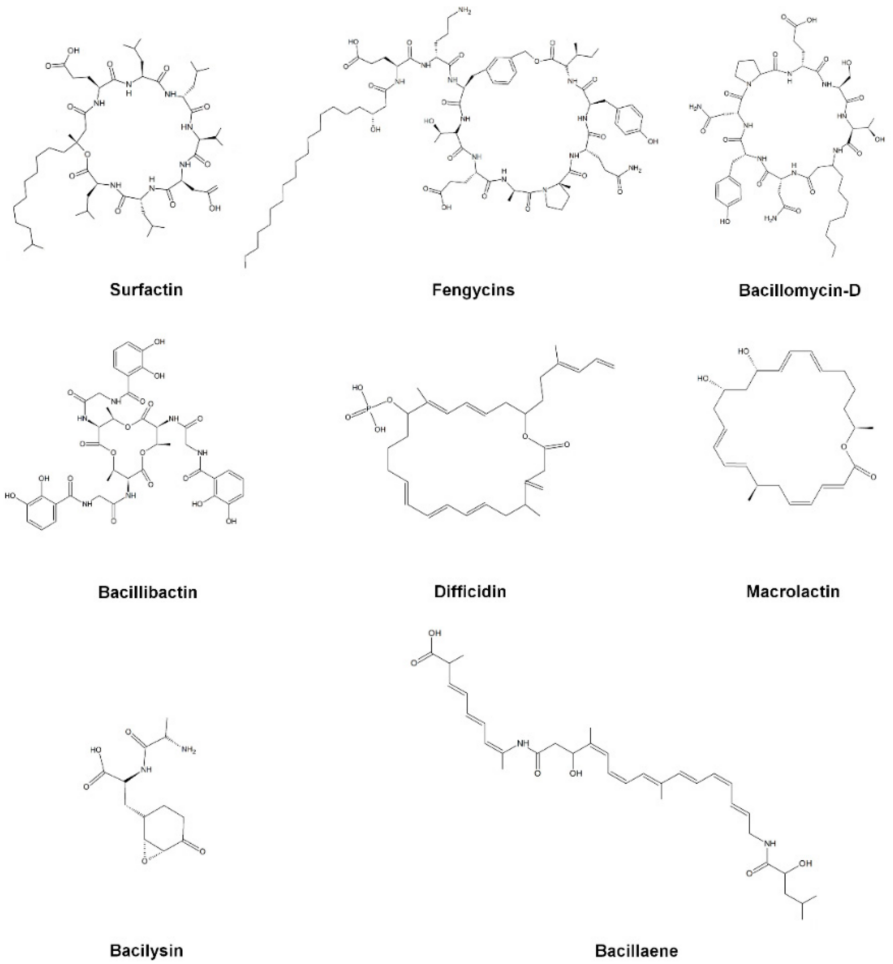

Figure 3. Antimicrobial compounds produced by members of the operational group *Bacillus amyloliquefaciens.*

Non-ribosomal peptides produced by bacteria and fungi contain two or more moieties derived from amino acids [106]. The mode of action of non-ribosomal peptides involves the disruption to the cell membrane and inhibition on the transfer of peptidoglycan precursors to bactoprenol pyrophosphate [107]. In 2019, surfactins from *B. velezensis* 9D-6 were found to inhibit the in vitro growth of bacteria (*B. cereus*, *C. michiganensis*, *Pantoea agglomerans*, *Ralstonia solanacearum*, *Xanthomonas campestris* and *Xanthomonas euvesicatoria*) and fungi (*Alternaria solani*, *Cochliobolus carbonum*, *F. oxysporum*, *F. solani*, *Gibberella pulicaris*, *Gibberella zeae*, *Monilinia fructicola*, *Pyrenochaeta terrestris* and *R. solani*) pathogens [108]. In another related study, in silico genomic study of *B. siamensis* JFL15 had gene clusters involved in the biosynthesis of antimicrobial compounds. The LC–MS/MS analysis confirmed the presence of iturin A and bacillomycin F. Both compounds showed strong antifungal activities against *Magnapothe grisea*, *R. solani* and *Colletotrichum gloeosporioides*, as analyzed under in vitro conditions [109]. Moreover, the presence of fengycin, bacilysin, and bacillibactin had also been reported from *B. velezensis* OSY-S3 that showed inhibition activities against *Listeria innocua*, *Escherichia coli*, *Penicillium* sp., *Cladosporium* sp., and *Staphylococcus aureus* [110].

Polyketides are biopolymers of acetate and other short carboxylates that are biosynthesized by polyketide synthases, a natural metabolite produced by microorganisms and plants which possess various antifungal and antibacterial activities [111,112]. Since the discovery of polyketides (e.g., streptomycin in 1950), the exploration of new polyketides has assisted pharmaceutical companies in isolating new antibiotic-producing strains as the main sources of antibiotics [113]. Antibacterial polyketides including bacillaene, macrolactin and difficidin were reported from *B. velezensis* OSY-GA1 [109]. Moreover, *B. velezensis* YJ11-1-4 isolated from doenjang exhibited good antimicrobial activities against bacterial

(*B. cereus*, *E. coli*, *Listeria monocytogenes* and *S. aureus*) and fungal (*Aspergillus flavus* subsp. *flavus*) foodborne pathogens. Genomic analysis reveals the presence of antibiotic biosynthesis operons including bacillaene, macrolactin and difficidin in the genome of *B. velezensis* OSY-GA1 [114]. Additionally, four new glycosylated macrolactin compounds, namely macrolactins O, P, Q and R, had been isolated from the liquid cultures of *B. velezensis* AH159-1. These compounds inhibited *S. aureus* peptide deformylase and also showed antibacterial activities against *E. coli* and *S. aureus* [115].

3.4. Potential as Probiotics

Probiotics are live microbial feed supplements that benefit the host animal by improving the microbial balance. Probiotics have become increasingly popular due to continuously expanding scientific evidence pointing to their beneficial effects on both humans and animals [116]. Within the OG*Ba*, some *B. velezensis* strains are reported to display probiotic potential and have been applied as probiotics for animals [117]. For instance, *B. velezensis* H57 (previously *B. amyloliquefaciens* H57) isolated from lucerne was first investigated in the research to prevent fungal spoilage of hay [118]. Because it is an endospore-forming bacterium able to produce antimicrobial compounds, *B. velezensis* H57 was commercialized as a spoilage control agent under the product name HayRite™ (Biocare and BASF, Australia). Interestingly, sheep and cattle fed on HayRite™ showed improvements in digestibility and nitrogen retention leading to increased weight gain [118]. Genomically, the potential of *B. velezensis* H57 to synthesize antimicrobial compounds including surfactin (*srfABCD*), iturin (*ituABCD*), bacillomycin D (*bmyABC*), fengycin (*fenABCDE*), macrolactin (*mlnABCDEFGHI*), difficidin (*dfnABCDEFGHIJ*) and bacillaene (*baeEDLMNJRS*) were suggested to facilitate the probiotic effects of *B. velezensis* H57 [27]. In another related study, *B. velezensis* FTC01 manifested itself as a probiotic [119]. Genes coding for hydrolases (peptidases, phytases and glycosidases) that can improve feed digestion and prevent intestinal disorders are present in the genome of *B. velezensis* FTC01. Additionally, peptidylprolyl isomerase (*prsA*) gene (a gene that is involved in bacterial adhesion and signaling of biofilm formation in the host gut) was also found. Moreover, in silico genome analysis of *B. velezensis* FTC01 proved the presence of gene clusters involved in the synthesis of antimicrobial peptides. Similarly, gene clusters involved in the synthesis of antimicrobial peptides were also found in the genome of *B. velezensis* JT3-1, a probiotic strain isolated from faeces of the domestic yak [21]. The antimicrobial activity of *B. velezensis* JT3-1 was confirmed using an antimicrobial assay. Strain JT3-1 manifested strong antagonistic activities against various intestinal pathogenic flora including *L. monocytogenes*, *S. aureus*, *E. coli*, *Salmonella typhimurium*, *Mannheimia haemolytica*, *Staphylococcus hominis*, *Clostridium perfringens* and *Mycoplasma bovis*.

B. velezensis B-1895 (previously *B. amyloliquefaciens* B-1895) has been commercially used as a probiotic in the fish industry, particularly for *Alburnus leobergi* [120,121]. Its probiotic potential was proven thought the Ames test (reported as non-mutagenic) and antimicrobial activities (against *Streptococcus intermedius* and *Porphyromonas gingivalis*). Moreover, the endospores of *B. velezensis* B-1895 were found tolerant to 0.3% (*w/v*) bile salts and survived incubation for 4 h in MRS broth at pH 2.0–3.0. Overall, the results suggested the potential of *B. velezensis* B-1895 as a fish probiotic [122]. In another related study, *B. velezensis* JW also manifested itself as a fish probiotic [123]. Strain JW showed antibacterial activities against a broad range of bacterial fish pathogens (*Aeromonas hydrophila*, *Aeromonas salmonicida*, *Lactococcus garvieae*, *Streptococcus agalactiae* and *Vibrio parahemolyticus*). Dietary administration of *B. velezensis* JW induced an immune response in *Carassius auratus*. The immune-related genes in *C. auratus* such as interferon gamma gene (IFN- γ), tumor necrosis factor-α (TNF-α), interleukin-1 (IL-1), interleukin-4 (IL-4) and interleukin-10 (IL-10) were found to be upregulated by *B. velezensis* JW-supplemented diets. It is noteworthy that *C. auratus* fed with *B. velezensis* JW-supplemented diets showed improvements in survival rate after *A. hydrophila* infection. This was supported genomically by the presence of antimicrobial gene clusters in the genome of *B. velezensis* JW [122]. Moreover, a potential probiotic effect of *B. velezensis* V4 on the growth performance of *Oncorhynchus mykiss*

had also been investigated [124]. Cell-free supernatant of *B. velezensis* V4 with anti-*A. salmonicida* was shown to contain antimicrobial compounds including iturin, macrolactin and difficidin. The mortality rate of *O. mykiss* was reduced by 27% and the weight gain ratio was increased by 71% through the 1% (*v/w*) addition of *B. velezensis* V4. Overall, the findings demonstrated that *B. velezensis* V4 was an effective probiotic in *O. mykiss*.

The commercialization of *B. amyloliquefaciens* as a probiotic in aquaculture is not as common compared to its agricultural applications (Table 3). Ecobiol® Soluble Plus, is one of the commercial probiotic products reported as containing *B. amyloliquefaciens* at a concentration of 10^9 CFU/g, specifically formulated for applications in poultry and swine, as well as in aquaculture. There was research conducted on the commercial probiotic Ecobiol® Soluble to observe its positive effects on the biofloc culture of *Litopenaeus vannamei* and its benefits on water quality, growth performance and the immune system of shrimps. Three doses of probiotic (9.48×10^4, 1.90×10^5 and 3.79×10^5 CFU/g) were applied to the culture water for 42 days. At the end of the trial, there was no significant improvement in the water quality. However, it showed notable changes in the immune system of the shrimp. As compared to the control treatment, there was an increase in the total protein concentration and granular hemocytes, and a decrease in the cell number with apoptosis in the hemolymph in all treatments. Therefore, other than being mixed with feed, *B. amyloliquefaciens* in the commercial probiotic Ecobiol® Soluble Plus could also be applied directly to the culture system; this research proved it provided better resistance to shrimps against the outbreak of pathogens in shrimp biofloc systems [125].

There is much ongoing research on the development and formulations of bacterial strains belonging to the OG*Ba* as potential probiotics for commercialization purposes in the aquaculture industry. Most of the studies have emphasized probiotic feed formulations, feeding trials on a small scale before moving to field trials. For instance, dietary inclusion of *B. amyloliquefaciens* at 10^6 CFU/g fed to zebra fish improved the expression levels of metabolism-related genes, enzyme activities and oxidative stress-related genes in the fish liver as well as enhanced their immune resistance against pathogenic *A. hydrophila* and *S. agalactiae*. In addition, the strain of *B. amyloliquefaciens* used in this study was able to express recombinant xylanase, an important enzyme that aided in better feed digestibility and efficiency [126]. In another related study, the administration of *B. amyloliquefaciens* (1×10^9 CFU/g), together with *Spirulina platensis* in formulated diet for tilapia, improved growth performance and feed utilization after a 60 day feeding trial. The mRNA level of the *TNF-α* gene and the transcription of *SOD* were considerably higher in tilapia fed with dietary *B. amyloliquefaciens* and *S. platensis* compared to the control group [127]. Moreover, *B. amyloliquefaciens* at a concentration of 10^6 CFU/mL provided significant protection to juvenile blue swimming crabs, *Portunus pelagicus*, when challenged with *Vibrio harveyi* in in vivo trials [128]. Nevertheless, further studies are necessary, mainly on probiotic formulation along with larger field trials, to strengthen the outcomes in order to be able to commercialize bacterial strains belonging to the OG*Ba* for aquaculture use.

In vivo and field trials are critical in probiotic development. Occasionally, there were negative outcomes in in vivo studies which were carried out based upon the positive results acquired from the preliminary in vitro assays, which indicated the possibility of negative correlations between trials in vitro and in vivo. Hence, it is crucial to understand and to optimize various conditions in in vivo studies or field trials including the probiotic formulation which may affect the survival, colonization, proliferation, and interaction of the probiotic with the host in a certain environment [129].

3.5. Potential as Bioremediation Agents

The use of microorganisms as bioremediation agents has become a burgeoning trend [130]. To date, most research focused on the plant growth-promoting activity and antimicrobial compounds of OG*Ba* is as described above. Interestingly, in 2019, *B. amyloliquefaciens* YP6 was reported to exhibit both plant growth-promoting activity and broad-spectrum organophosphorus pesticide (OP) removal [131]. In silico genome analysis of *B.*

amyloliquefaciens YP6 found it to contain a variety of promising genes, including phosphorus solubilizing and OP-degrading related genes (*pho*D, *pho*A, *phr*C, *pho*E, *ycs*E, *bcr*C and *yva*K), indole-3-acetic acid synthesis related genes (*amh*X, *cge*E and *eps*M), and siderophores synthesis related genes (*ent*B, *men*F, *ent*C and *ent*A). The results hinted at the potential application of *B. amyloliquefaciens* YP6 in agricultural and environmental remediations. Overall, much more focus is still needed to understand the OP-degrading related genes beyond in silico genome analysis. Therefore, it is necessary to conduct further studies to determine the in vitro functional genomics and the OP-degrading enzyme activities of the members of OG*Ba*. Understanding such attributes will help to shed light on the applicability of the OG*Ba* in OPs degradation and in the bioremediation processes as a whole.

4. Concluding Remark and Future Perspectives

In conclusion, the progress of the research on the biotechnological applications of bacterial species that belong to OG*Ba* is remarkable. The bacteria are important not only industrially, but also environmentally. A plethora of studies have addressed the abilities of the members of OG*Ba* as plant growth-promoters, biocontrol agents, probiotics, bioremediation agents as well as producers of commercial enzymes and antibiotics. Moreover, the use of the bacteria in optimized bioformulations as well as the demonstration of the great success of the commercialized products give us hope towards more sustainable agricultural and aquacultural industries. Owing to the listed biotechnological applications and potentials, more research should be done focusing on the integration of system biology data derived from genomics, phenomics, proteomics, metabolomics and fluxomic analyses in order to expand our basic understanding on the versatility of the members of OG*Ba*. Enabling the prediction of cellular functions and metabolites produced by the members of this operational group could provide fundamental knowledge towards the enhancement of the applications of their potentials in biotechnology and bioprocessing for the benefit of all.

Supplementary Materials: The following are available online at https://www.mdpi.com/2076-2607/9/3/614/s1: Table S1. Bacterial strains from the operational group *Bacillus amyloliquefaciens*.

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