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Review

Biosynthesis of Gamma-AminoButyric Acid (GABA) by *Lactiplantibacillus plantarum* in Fermented Food Production

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Abstract: In recent decades, given the important role of gamma-aminobutyric acid (GABA) in human health, scientists have paid great attention to the enrichment of this chemical compound in food using various methods, including microbial fermentation. Moreover, GABA or GABA-rich products have been successfully commercialized as food additives or functional dietary supplements. Several microorganisms can produce GABA, including bacteria, fungi, and yeasts. Among GABA-producing bacteria, lactic acid bacteria (LAB) are commonly used in the production of many fermented foods. *Lactiplantibacillus plantarum* (previously *Lactobacillus plantarum*) has a long history of natural occurrence and safe use in a variety of food products. This LAB species provides functional properties to various fermented foods by producing a variety of bioactive compounds, including GABA. The present review aims, after a preliminary excursus on the function and biosynthesis of GABA, to provide an overview on the current uses of microorganisms and in particular of *L. plantarum* in the production of GABA, with a detailed focus on fermented foods.

Keywords: *Lactobacillus plantarum*; functional food; L-glutamate decarboxylase; lactic acid bacteria

1. Introduction

Gamma (γ)-Aminobutyric acid (GABA), also named 4-aminobutyric acid, is a four carbon non-protein amino acid that is widely distributed in a wide variety of organisms including algae, bacteria, fungi, animals, plants, and cyanobacteria [1–7].

Over the last several decades GABA has attracted great attention due to its different positive effects on mammalian physiology [8–10].

As known, GABA is the most common inhibitory neurotransmitter in human central nervous system [11]. Furthermore, besides being an important antidepressant [12], GABA also performs other functions including neuroprotective, anti-inflammatory, antioxidant and antihypertensive effects [10], enhancement of immunity under stress conditions [13], prevention of cancer cell proliferation [14], prevention of diabetic conditions [15], and cholesterol-lowering effect [16].

GABA ubiquitously exists in various foods such cereals, tea, vegetables, and fruits [17]. However, the content of GABA in dietary ingredients is relatively low [17,18]. Consequently, there has been an increase in studies to find ways to increase GABA contents in foods over the years [8,19]. Currently, GABA is mainly produced through chemical synthesis [20], plant enrichment [21], or microbial fermentation [3].

Microbial synthesis of GABA may be much more promising than chemical synthesis methods since the former is characterized by high specificity, environmental friendliness and cost-effectiveness [3].

In addition, GABA production by beneficial and pro-technological microorganisms has the potential to increase the functional effect of some fermented foods and beverages [19,22]. So far, various studies have confirmed that several microorganisms like fungi, bacteria, and yeasts can produce GABA via fermentation [3,9,23].

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Lactic Acid Bacteria (LAB) are Gram-positive bacteria which are not only widely distributed in nature and naturally existing in traditional fermented foods, but also extensively involved in industrial food fermentations because they are generally recognized as safe (GRAS) [24,25]. The LAB, besides all beneficial and technological properties, are capable of producing a high level of GABA [26–28]. Therefore, LAB that produce GABA could be exploited for the manufacture of health-promoting GABA-enriched food products [22].

Lactiplantibacillus plantarum (formerly *Lactobacillus plantarum*) is a LAB species with high ecological and metabolic adaptability [29,30]. This bacterium is capable of inhabiting a range of ecological niches including fermented foods [31,32] and also the animal and human gastrointestinal tract [33,34]. In addition, some strains belonging to this species are also proposed as animal or human probiotics [33–37]. *L. plantarum* is used as a starter culture in fermentation of raw materials from plant and animal origin, where it contributes to enhance sensorial quality and shelf life of the fermented products [38–42]. Some *L. plantarum* strains also increase the functional properties of various fermented foods by producing a variety of bioactive compounds, including GABA [26,43].

The present review aims, after a preliminary excursus on the function and biosynthesis of GABA, to provide an overview on the current uses of microorganisms and in particular of *L. plantarum* in the production of GABA, with a detailed focus to fermented foods.

2. GABA biosynthesis

In mammalian neural and non-neural tissues, GABA is synthesized in the cytoplasm of the presynaptic neuron and glial cells from the precursor glutamate by the enzyme glutamate decarboxylase, an enzyme which uses vitamin B6 (pyridoxine) as a cofactor [44]. Alternate sources of GABA include putrescine, spermine, spermidine and ornithine, which produce GABA via deamination and decarboxylation reactions, while L-glutamine is an additional source of glutamic acid via deamination [2].

In plants, GABA is an endogenous signaling molecule involved in various physiological and biochemical processes that plays an important role in the promotion of plant growth and development, and relates to the plant metabolism in response to environmental stresses as well as pathogen and insect attacks [1,45,46]. A high concentration of GABA increases plant stress tolerance by improving photosynthesis, inhibiting reactive oxygen species (ROS) generation, activating antioxidant enzymes, and regulating stomatal opening in drought stress [47].

In microorganisms, GABA is biosynthesized in the cells through the decarboxylation of L-glutamate catalyzed by glutamate decarboxylase (GAD; EC4.1.1.15) with pyridoxal-5′-phosphate (PLP) as a cofactor (Figure 1).

GAD is encoded by *gadA* or *gadB* genes in bacterial cells. Glutamate is transported into a cell through an antiporter, and then the decarboxylation occurs. Finally, the GABA product is secreted from the cell by the glutamate/GABA antiporter, which is encoded by *gadC* gene [48].

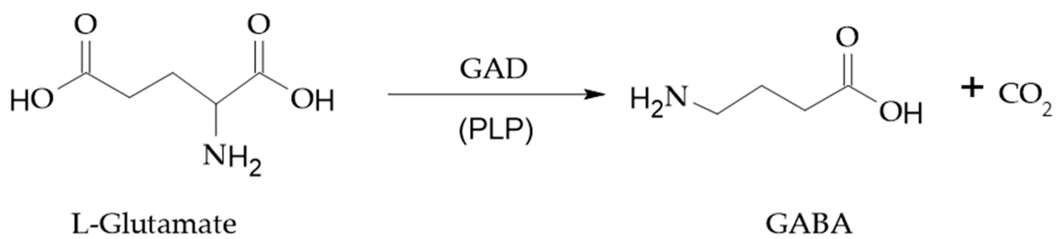

Figure 1. GABA production from L-glutamate by glutamate decarboxylase (GAD) with pyridoxal-5′-phosphate (PLP) as a cofactor.

These microorganisms metabolize GABA through a conserved pathway of enzymes known as the GABA shunt [49]. The GABA shunt is characterized by a group of enzymes that convert GABA to succinate to fuel the tricarboxylic acid (TCA) cycle in the production of energy and essential metabolic intermediates as carbon skeletons for the cell (Figure 2). In both microbial and mammalian species, GABA is produced from L-glutamate through a GAD enzyme-mediated decarboxylation [50].

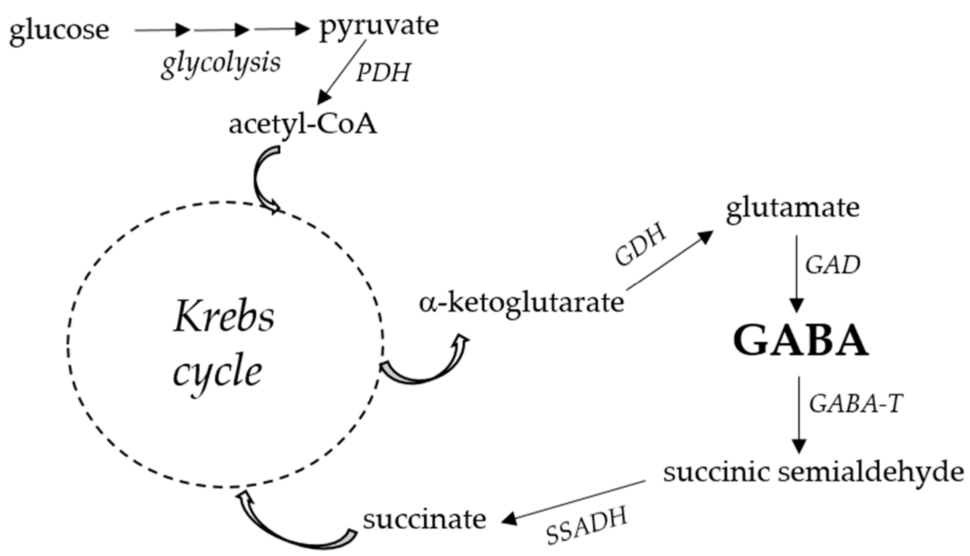

Figure 2. Metabolic pathway of GABA production from the TCA cycle (adapted from Sahab et al. [19]). For higher clarity, this scheme reports only enzymes and relevant substrates/products, omitting coenzymes and other compounds involved in the reactions showed. Abbreviations: PDH, pyruvate dehydrogenase; GDH, glutamate dehydrogenase; GAD, glutamate decarboxylase; GABA-T, GABA transaminase; SSADH, succinic semialdehyde dehydrogenase.

3. GABA, an ancestral molecule

Although doubts currently remain about the role that some neurotransmitters might play as signal molecules within the bacterial communities themselves, for sure, GABA is considered an important molecular signaling agent, ubiquitous in nature [51].

GABA is produced by bacteria [3,52] fungi [53,54], plants [55,56], vertebrate animals and invertebrates [57–59]. Using the same terms in molecular language among various species orders means having part of the language in common.

GABA-mediated interregnum communication has been observed between algae and invertebrates [60], plants and fungi [61], plants and insects [62], plants and bacteria [63].

Therefore, GABA is a signal molecule, ubiquitous in nature, also produced by Archaea which possesses homologous enzymes for GABA biosynthesis [64].

Due to this pervasive presence in biological kingdoms and ecosystems, we tend to consider the GABA molecule more as a ubiquitous signaling molecule than as a specific synaptic neurotransmitter [50].

Thus, to try to understand microbial GABA signaling, one must place oneself in the view that the genesis and evolution of bacterial GABA signaling was structured outside the human body.

4. Production of GABA by Microorganism

GABA can be obtained not only from natural sources but also through plant enrichment, chemical synthesis, enzymatic process and microbial metabolism [9,65]. Due to the low GABA content in natural animal- and plant- associated food products, high GABA-producing microorganisms are of great importance to produce food-grade GABA and GABA-rich fermented foods via fermentations [66].

The biosynthesis of GABA by microorganisms is safe and eco-friendly, and provides the possibility of production of new naturally fermented health-oriented products [23,67].

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5. Production of GABA by Fungi

Other than bacteria, various yeasts and molds, that both belong to the kingdom of fungi, have also been reported to as able to produce GABA.

Some *Rhizopus oligosporus* and *R. oryzae* strains have been shown to produce GABA during tempeh fermentation (fermented soybean) [68].

Similarly, *R. monosporus* strain 5351 has been reported to increase GABA content in soybean and mung bean [69,70].

Marine yeasts *Pichia guilliermondii* and *P. anomala* isolated from the Pacific Ocean off Japan have high GABA-producing abilities [71,72].

Actinomucor elegans AS 3.227 has been reported to increase the GABA concentration in SUFU (traditional fermented soybean food from China) manufacturing using solid-state fermentation [73].

Glutamic acid decarboxylase has also been identified in yeasts such as *Saccharomyces cerevisiae* and *Kluyveromyces marxianus* isolated from fermented product [74–76].

Wild yeast, such as *Kazachstania unispora, Sporobolomyces carnicolor, Sporobolomyces ruberrimus, Nakazawaea holstiiand Pichia scolyti*, isolated from wild flowers, also have GAD activity [77].

Aspergillus oryzae NSK is a GABA-generating mould used as a starter culture to ferment rice koji for sake production and soy sauce koji [78–82].

Cai et al. demonstrated that oats fermented by *A. oryzae* var. *effuses* 3.2825, *A. oryzae* 3.5232 and *R. oryzae* 3.2751 can be recommended as tempeh-like functional foods with higher GABA [83].

In other studies, *Monascus pilosus* IFO 4520 [84] and *M. purpureus* CCRC 31615 [85] increases the content of γ-aminobutyric acid (GABA) during the production of beni-koji and red mold rice fermented.

6. Production of GABA by bacteria

GABA is naturally synthesized by several bacteria. Indeed, not all strains within one species can produce GABA, as the ability depends on the presence of GAD genes and glutamate/GABA antiporter [86].

Bacillus is commonly reported bacteria that can produce GABA [87,88]. Besides *Bacillus*, *Corynebacterium glutamicum* was found to produce endogenous L-glutamate [89], *Streptomyces bacillaris* and *Str. cinereus* were reported to increase the GABA content in fermented tea [90]. Otaru et al. have shown that human intestinal *Bacteroides* are able to synthesize GABA [91].

Recent studies revealed that the increased level of GABA in the human gut could be derived by the ability of the intestinal microbiota or ingested probiotic, such *Bacteroides* and some LAB (*Bifidobacteria* and *Lactobacilli*), to metabolize dietary monosodium glutamate [91–93]. Therefore, numerous research has been directed towards isolating and characterizing GABA-producing bacteria to be used as starters for the production of GABA-enriched fermented food [3].

Because of the GRAS status, LABs are widely used in the production of fermented foods [25] and acts as potential probiotic cultures. Actually, in addition to pro-technological functions, LAB also offer beneficial functions such as antioxidant and antimicrobial activities, as well as the formation of bioactive compounds as the GABA [94,95].

Therefore, the use of GABA-producing LABs has been considered a promising possibility in order to increase the nutritional, functional, sensory and technological properties of some fermented food products [8,26,96].

GABA can be biosynthesized by various LAB strains mainly belonging to the genera of Lactobacillus, Lactococcus, Pediococcus, Leuconostoc, Bifidobacterium, Enterococcus, Streptococcus, Weissella, Lacticaseibacillus, Lactiplantibacillus and recently, Levilactobacillus and Secundilactobacillus [28,97–103].

Nowadays, *Lactobacillus plantarum* (recently, reclassiflied as *Lactiplantibacillus plantarum*). is among the main LAB species proposed to be used as probiotic starter cultures to produce GABA in the fermented food and beverage industry [35,104,105].

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7. Production of GABA by *L. plantarum*

Among GABA-producing LAB, *L. plantarum* is a facultative heterofermentative species with high adaptability to many different conditions, being isolated from various ecological niches including milk, fruit, cereal crops, vegetables, bee bread and fresh meat [106,107]. This extremely versatile LAB species is a normal inhabitant of the gastro-intestinal tract of insects, fish and mammals, including humans [108–110]. *L. plantarum* is widely employed in industrial fermentation and processing of raw foods, "generally recognized as safe" (GRAS) and has qualified presumption of safety (QPS) status [111]. The intrinsic characteristics of *L. plantarum* are the basis of its versatility and success in industrial applications, not only as a starter culture but also as a probiotic [38,39,112].

In recent years, many researchers have studied *L. plantarum* for its ability to synthesize GABA using the GAD system.

Only *L. brevis* possesses two GAD genes that produce isozyme GADs among the LABs examined so far [113,114]. Glutamic acid decarboxylase (GAD) system encoded by the gad operon is responsible for glutamate decarboxylation and GABA secretion in bacteria and consists of two important elements: Glu/GABA antiporter *gadC* and the glutamate decarboxylase enzyme encoded either by *gadA*, *gadB* genes [115]. This system converts glutamate into GABA and while doing so consumes protons thus maintaining cytosolic pH homeostasis [114].

Unlike *L. brevis*, *L. plantarum* has only one GAD coding enzyme in its genome, the *gadB* and there may not be a specific glutamate/GABA antiporter (gadC) gene [115].

In a study conducted by Nakatani et al. on the genome of *L. plantarum* KB1253 it has been found that this strain contains two *gadB* genes coding for glutamate decarboxylase [116].

Many studies showed that *L. plantarum* can produce appreciable amounts of GABA, so there must be a transporter responsible for transporting glutamate and GABA in and out of the cell. A glutamate/gamma-aminobutyrate transporter family protein coded by the *yjeM* gene can be the best candidate for such a transporter [117]

Further investigation, conducted by Surachat et al. indicates that *L. plantarum* is a key GABA-producing species in nature, since almost all strains were encoded GAD operon in their genome [118].

However, the production of GABA varies among various LAB strains and is affected by several factors as pH value of culture medium, fermentation temperature, fermentation time, L-glutamic acid concentration, PLP, media additives, carbon source, nitrogen source) [3,66,96,119]. An optimum between these parameters could potentially result in an applicable and cost-effective fermentation for the food industry [3,94].

In recent years, many researchers have studied *L. plantarum* in particular for its ability to synthesize GABA in several media culture (Table 1).

Table 1. GABA production by *Lactiplantibacillus plantarum* (previously *Lactobacillus plantarum*) in different culture media.

Microorganism	Isolation Source	Culture medium	GABA production	Comments	Refs
L. plantarum C48	cheese	MRS	16.0 mg/kg	Survival and GABA production in simulated GI conditions	[97]
L. plantarum CCARM 0067	CCARM	CDM	≈700 mM (48h)	Anti-proliferative and anti-metastatic activity in HT-29/5FUR cell line	[14]
L. plantarum DM5	Marcha of Sikkim	MRS + 100 mM MSG	not quantified	GABA production has been qualitatively identified by the TLC	[120]
L. plantarum KCTC 3103	Unknown	MRS modified	0.67 g/L	Two-stage fermentation: cell grown (stage 1); GABA production (stage 2)	[121]

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L. plantarum K154	kimchi	broth fortified with skim milk and 2% MSG	15.53 mg/mL	Co-culture with *Ceriporia lacerata*	[122]
L. plantarum EJ2014	Rice bran	SM	19.8 g/L	Optimization of production by the addition of yeast extract	[119]
L. plantarum K154	kimchi	MRS + 30 g/L MSG	0.2 g/L	Potential probiotic: good resistance to vancomycin and polymyxin B, tolerance to bile juice and low pH	[123]
L. plantarum Taj-Apis362	honeycomb and stomach of honeybee	MRS + 50 mM MSG	7.15 mM	culture temperature of 36 °C, initial pH of 5.31 and incubation time of 60 h	[124]
L. plantarum 45a	cambodian fermented foods	MRS + 2% MSG	20.34 mM	Two other strains of *L. plantarum* capable of synthesizing GABA have been identified: 44d (16.47 mM GABA) and 37e (5.63 mM GABA)	[125]
L. plantarum FNCC 260	indonesian fermented foods	MRS + 25-100 mM MSG	809.2 mg/L	MSG, PLP, and pyridoxine were shown to positively affect GABA production	[126]
L. plantarum BC114	Sichuan paocai (fermented vegetable)	MRS + 20 g/L MSG	3.45 g/L	*L. plantarum* BC114 highlighted the ability to produce GABA and reduce nitrates	[127]
L. plantarum LSI2- 1	Thailand fermented food	GYP + 3% MSG	22.94 g/L	Only the gadA as glutamate decarboxylase (GAD) was found in the genome	[128]
L. plantarum MNZ	fermented soybean	MRS	3.96 mM	6% glucose, 0.7% ammonium nitrate, pH 4.5 and temperature 37ºC.	[129]
Strain K255	kimchi	MRS+3% MSG	821.2 µg/mL	the K255 strain was incubated at 37° C for 18 h.	[130]
L. plantarum FBT215	kimchi	MRS modified (1%fructose; 2% tryptone, 50 mM MSG)	103.7 µg/mL	PLP is a major factor influencing GABA production	[105]
L. plantarum B-134	Makgeolli	MRS + 3% MSG	25 mM	optimum culture condition: 37°C, pH 5.7 without NaCl	[131]
L. plantarum N1-2	Nham	MRS + 5% MSG	0.13 mg/10g	pH of 5.7, without NaCl	[132]
L. plantarum Y7	kimchi	MRS modified (2% fructose, 2% peptone and 175 mM MSG)	4.9 µg/mL	culture conditions: 37 °C, pH 6.5, and 48 h.	[133]
L. plantarum L10-11	Plaa-som	MRS + 4% MSG	15.74 g/L	addition of NaCl by up to 7% (w/v) did not suppress GABA production	[134]

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L. plantarum FRT7	Paocai	MRS 3% MSG and 2 mmol/L of PLP	1158.6 mg/L	40 ◦C; pH of 7.0 for 48 h	[135]
L. plantarum HUC2W		MRS + 4% MSG	3.92 g/L	at 37 ◦C for 24 h	[136]

Abbreviations: MRS, de Man, Rogosa and Sharp medium; GI, gastrointestinal; CCARM, Culture Collection of Antimicrobial Resistant Microbes; CDM, chemical defined medium; HT-29/5FUR, human colon adenocarcinoma cell line (HT-29) resistant to 5-fluorouracil (5-FU); MSG, mono-sodic glutamate; TLC, thin layer chromatography; SM, synthetic medium (consisting of 100 g/L Yeast extract, 10 g/L dextrose, and 22.5 g/L MSG); PLP, pyridoxal 5′-phosphate; GYP, Glucose-yeast extract-peptone; GAD, glutamic decarboxylase.

The most commonly used culture medium is MRS (de Man, Rogosa and Sharp), a standard substrate designed to promote LAB growth [137]. Monosodium glutamate (MSG), as source of L-glutamine, is usually supplemented directly into MRS to enhance GABA synthesis from *L. plantarum* strains [117].

However, the optimal concentration of MSG depends on the bacterial strain. For example, Yogeswara et al. investigated the GABA production from *L. plantarum* FNCC 260 strain using a wide range of MSG concentrations. The results showed a maximum GABA production (1226 mg/L) by adding 100 mM of MSG to the MRS medium then incubated at 37 °C for 108 hours [126].

While in a other study, after 18 hours at 34°C, *L. plantarum* K74 produced 134.52 µg/mL of GABA in MRS broth containing 1% MSG, 212.27 µg/mL of GABA in MRS broth containing 2% MSG, and 234.63 µg/mL of GABA in MRS broth containing 3% MSG [130].

Gomaa et al. examined the effect of MSG and PLP on GABA production from *L. brevis* and *L. plantarum* strains, isolated from Egyptian dairy products. The culture medium used was the following composition: 50 g/L glucose; 25 g/L soya peptone; 0.01 g/L $MnSO_4C_4H_2O$ and 2 mL Tween 80. The results of the aforementioned study show that the amount of extracellular GABA produced is proportional to the amounts of MSG and PLP added. Co-culture of *L. brevis* and *L. plantarum* produced the highest amount of GABA, 160.57 mM and 224.69 mM, in the presence of 750 M MSG and 200 µM PLP respectively [138].

Park et al. have obtained high amounts of GABA (19.8 g/L) at 30°C from *L. plantarum* EJ2014 using the following culture medium: 100 g/L Yeast extract, 10 g/L dextrose, and 22.5 g/L (w/v) MSG [119].

In a study conducted by Shan et al *L. plantarum* NDC75017 produced 3.2 g/kg of GABA, at 30°C for 48 h, in skimmed milk with 80 mM MSG and 18 µM PLP [139].

Temperature and pH have been reported as the main environmental factors that can modulate gad gene expression [140].

Shin et al. showed that 40 °C and a pH of 4.5 were the best parameters for the expression of *gadB* gene encoding GAD from *L. plantarum* ATCC 14917 in *E. coli* BL21 (DE3) [141].

Variation in pH enhances activation of the GAD pathway since it is considered one of the mechanisms that preserve cell homeostasis [142]. Wu *et al.* evaluated performance of the GAD pathway in comparison with other acid resistance mechanisms and highlighted how the GAD system is an essential mechanism to maintain metabolic activity under intra- and extracellular acidity [114]. Therefore, the pH of the environment is crucial for the synthesis of GABA. However, it seems that this depends on the bacterial strain [141].

Zhang et al. tested how initial pH affects GABA production by *L. plantarum* BC114. The best concentration of GABA was detected at pH 5.5, obtaining double the amount of GABA yielded at pH 4.0 [127]. Similar results have been obtained in other studies.

Tajabadi et al. found that after 60 hours *L. plantarum* Taj-Apis362 produces the highest amount of GABA (7.15 mM; 0.74 g/L) at 36°C in modified MRS: 497.97 mM Glutamate, pH 5.31 [124].

While, Tanamool et al. found that the highest GABA production (15.74 g/L) by *L. plantarum* L10-11 cultured in MRS with 4% MSG at 30 °C was obtained within 48h, with a pH range of 5-6 [134].

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Very recently, Cai et al reported that *L. plantarum* FRT7 after 48 hours produced approximately 1.2 g/L in MRS supplemented with 3% MSG and 2 mmol/L of PLP at 40° C with an initial pH of 7.0 [135].

In a recent study conducted by Kim J et al, the optimal conditions for efficient GABA production by *L. plantarum* FBT215 in modified MRS broth containing 50 mM MSG were investigated. Therefore, the optimal culture temperature for GABA production (103.67 µg/ml) was 37°C and this efficiency was highest at pH 7.5 and 8.5 and decreased under acidic conditions [105].

Instead, Yogeswara et al. found that GABA production from *L. plantarum* FNCC 260 was greatly improved under acidic conditions (pH 3.8) in **Pigeon pea (*Cajanus cajan*) milk fermentation** [143]. This result is in line with a previous study by Yogeswara et al. where maximum GABA production from *L. plantarum* FNCC 260 in MRS was observed at pH 4.0 [126].

Regard the temperature, Yang et al. reported that GAD functionality is directly related to an increase in temperature until it reaches an optimum, after which GAD activity decreases until thermal inactivation [144]. Another study with *L. plantarum* showed an increase in GAD activity up to 40 °C, achieving optimal GABA production at 35 °C [139].

From the observation of the results of all the studies reported in this review, the optimal temperatures for maximum GABA production were in the range of 30-37°C.

According to available data, naturally occurring GABA in foods is usually low [66,145], therefore the food industry has shown great interest in GABA-enriched foods, through microbial fermentation.

Currently, *L. plantarum* is a LAB species commonly found in various fermented foods and beverages. Therefore, some food scientists have proposed some strains of *L. plantarum* as starter in single culture (Table 2) or in co-culture with other microbial species (Table 3) to enrich of GABA some traditional or innovative fermented foods, particularly from plant-based sources.

Table 2. GABA production by *Lactiplantibacillus plantarum* (previously *Lactobacillus plantarum*) in different fermented foods.

Microorganism	Isolation Source	Fermented food	GABA production	Comments	Refs
L. plantarum C48	cheese	buckwheat, amaranth, chickpea and quinoa flours	504 mg/kg in bread	Good organoleptic properties of bread enriched of GABA	[146]
L. plantarum DSM19463	cheese	grape must	8.9 g/kg in fermented grape must	In vitro potential anti-hypertensive effect and dermatological protection.	[147]
L. plantarum KB1253	pickles	tomato juice	41 mM	GABA-enriched fermented tomato juice	[148]
L. plantarum KCTC 3105	Unknown	soya milk	424.67 µg/g DW	Soya yogurt with high levels of GABA, produced using a co-culture of *L. acidophilus*, *L. plantarum* and *L. brevis* strains	[149]
L. plantarum NDC75017	fermented milk	12% skim milk + 80 mM MSG	314.56 mg/100 g	Good flavor and texture of fermented milk-based product	[139]
L. plantarum NTU102	cabbage pickles	8% skim milk + 1% (w/v) MSG	629 mg/L	together with GABA, production of ACEI was also found, suggesting a possible use of fermented products as potential functional food (hypertension regulation)	[150]
L. plantarum C48	cheese	wholemeal wheat flour	100 mg/K	low ACE inhibitory activity (15%) due to synthesis of ACEI	[151]

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L. plantarum GB01-21		cassava powder	80.5 g/L 2.68 g/L h (productivity)	two-step production with *Corynebacterium glutamicum* G01 (to produce glutamate) and *L. plantarum* GB01-21	[144]
L. plantarum Dad-13	FNCC	pigeon pea milk	5.6 g/L	The supplementation of sucrose, MSG, and whey isolate significantly increased GABA levels in fermented pigeon pea	[143]
L. plantarum NRRL B-59151		FOE and HFOE (oat)	GABA content: 7.35 mg/100 g in FOE and 8.49 mg/100 g in HFOE	Fermented oat demonstrated antidiabetic effects	[152] [153]
Lactobacillus plantarum HU-C2W		litchi juice	134 mg/100 mL	Fermentation condition: 37 °C for 40 h	[136]
L. plantarum DW12	fermented red seaweed	red seaweed+ 1% MSG	4 g/L	Fermentation at 30°C after 60 days. Substrate composition: red seaweed, cane sugar and potable water in a ratio of 3:1:10, pH 6	[154]
L. plantarum DW12	fermented red seaweed	red seaweed + 0.5% MSG	1284 mg/L	Fermentation at 30°C after 60 days. Substrate composition: red seaweed, cane sugar and potable water in a ratio of 3:1:10, pH 6	[155]
L. plantarum DW12	fermented red seaweed	MCW + 0.5% MSG	12.8 mg/100 mL	MCW supplemented with 0.5% MSG and 1% sugarcane, pH 6 after 72 h of fermentation	[156]

Abbreviations: DW, dry weight; MSG, mono-sodic glutamate; ACEI, angiotensin converting enzyme inhibitor; ACE, angiotensin converting enzyme; FNCC, Food and Nutrition Culture Collection; HFOE, fermented oat + honey; FOE, Fermented Oat; MCW, mature coconut water.

In a recent study [143], it has been proposed a drink prepared from germinated pigeon pea (*Cajanus cajan*) and fermented using probiotic *L. plantarum* Dad-13, isolated from dadih, fermented buffalo milk [157]. *C. cajan* commonly known as pigeon pea, red gram or gungo pea is an important grain legume crop, particularly in rain-fed agricultural regions in the semi-arid tropics, including Asia, Africa and the Caribbean [158].

Additional nutrients such as MSG 1%, whey 4%, sucrose 3% were added to pigeon pea extract and fermentation was carried out in a closed container at 30 ◦C for 48 h without shaking. Maximum GABA production (5.6 g/L) was obtained after 12 h of fermentation.

Wang et al. have shown that it is possible to increase the production of GABA in fermented lychee juice by ***L. plantarum*** HU-C2W [136]. Litchi (*Litchi chinensis* Sonn.) is a well-known tropical fruit originating from Asia [159]. After 40 hours at 37 °C, a GABA content of 134 mg/100 mL was observed [136].

In various studies, *L. plantarum* DW12, isolated by Ratanaburee et al. from a fermented red seaweed, has been successfully used as probiotic and starter culture to produce fermented foods and beverages due to its safety aspects and ability to produce GABA [118,154–156].

The results obtained in [154] reported that *L. plantarum* DW12 produce 4 g/L GABA in red seaweed fermentation (red seaweed-cane sugar-potable water = 3:1:10, w/w/v) at 30°C after 60 days.

The red seaweed *Gracilaria fisheri* is commonly found along the coast of south-east Asian countries and used as a fresh vegetable and as a dried product [160].

In another study conducted by Hayisama-Ae et al. a novel functional beverage was produced from red seaweed *Gracilaria fisheri* (known as Pom Nang seaweed in Thailand), using *L. plantarum* DW12 as starter culture [155]. Fermented red seaweed beverage was produced as follows: red seaweed, cane sugar and potable water in a ratio of 3:1:10 with addition of 0.5% of MSG and initial pH of 6.0. After 60 days the fermented red seaweed beverage (FSB) contained 1.28 g/L GABA.

A study conducted by Kantachote et al. aimed to add value to mature coconut water by using the probiotic *L. plantarum* DW12 for the production of GABA-enriched fermented beverages. Coconut water, with an initial pH of 5.0, was supplemented with 0.5% monosodium glutamate and 1% sugarcane and fermented from *L. plantarum* DW12. After 48 hours, the fermented product contained 128 µg/mL of GABA [156].

Coconut (*Cocos nucifera* L.) is an important fruit tree found in tropical regions and its fruit can be made into a variety of foods and beverages [161].

Zarei et al. investigated the potential of GABA production by a *L. plantarum* strain in whey protein beverage [162], building on previous research, in which this strain, isolated from traditional doogh (*yogurt, herbs and water*) from west region of Iran, have shown a high concentration of GABA production (170.492 ppm) in MRS broth [163]. The best conditions of the culture medium with the highest production of GABA were temperature 37°C, pH 5.19, glutamic acid 250 mM, and time 72 hours. The highest amount of GABA production (195.5 ppm) after 30 days of storage was observed in whey protein beverage containing banana concentrate and stored at 25°C.

L. plantarum NDC75017 (isolated from a traditional fermented dairy product from Inner Mongolia, China) was used as starter for fermentation at 36°of Skim Milk added addiction of 80 mM L-MSG and 18 µM PLP. Under these conditions, GABA production was about 310 mg/100 g [139].

Di Cagno et al. tested the potential of *L. plantarum* DSM19463 (formerly *L. plantarum* C48) for the production of a functional grape-based beverage [147]. Grape must, diluted to 1% (w/v) of total carbohydrates with the mixture of distilled water and fresh yeast extract, was supplemented with 18.4 mM L-glutamate and fermentation was allowed at 30°C for 96 h. *L. plantarum* DSM19463 synthesizes 4.83 mM of GABA, after 72 h at 30°C, in grape must with the addition of 18.4 mM L-glutamate [147].

In other study, the *L. plantarum* C48 has been used in sourdough fermentation [146].

The use of a blend of buckwheat, amaranth, chickpea and quinoa flours (ratio 1:1:5.3:1) subjected to sourdough fermentation by *L. plantarum* C48 allowed the manufacture of a bread enriched of GABA (504 mg/kg) [151]. Sourdough (120 g of flour and 280 g of tap water) started with *L. plantarum* C48 had concentrations of GABA of 12.65, 100.71, and 44.61 mg/kg for white wheat, wholemeal wheat, and rye flours, respectively [151].

In another recent study, *L. plantarum* VL1 was used for the production of Nem Chua (traditionally Vietnamese fermented meat product). Fresh pork without fat was minced and mixed with 5% salt, 20% sugar, and 1% sodium glutamate. *L. plantarum* VL1, was added to the mixture and after 72 hours of fermentation at 37°C the meat mixture (pH 4.59) contained 1.1 mg/g of GABA [164].

In a study conducted by Nakatani et al. *L. plantarum* KB1253, isolated from Japanese pickles, is used in GABA-enriched tomato juice production [148]. This strain produces 41.0 mM GABA from 46.8 mM glutamate in tomato juice (pH 4.0, 20°Bx) incubated for 24 h at 35°.

In other study conducted by Rezaei et al. the GABA-producing strain *L. plantarum* IBRC (10817) was used in the production of a probiotic beverage made from black grapes. After 21 days, the fermented beverage had a concentration of 117.33 mg/L GABA [165].

L. plantarum K16 isolated from kimchi has been used to valorize some agri-food by-products [166]. The agri-food by-product media (tomato, apple, orange, and green pepper) was enriched with extra 25 g/L of glucose, 12 g/L of yeast extract and 500 mM of MSG. Subsequently, the pH was adjusted to 5.5 with, and the media were inoculated with of *L. plantarum* K16 strain and incubated at 34 °C during 96 h [104]. *L. plantarum* K16 produced great amount of GABA reaching a concentration

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of 1166.81 mg/L, 1280.01 mg/L, 1626.52 mg/L and 1776.75 mg/L in apple, orange, green pepper, and tomato by-products, respectively [104].

In a study conducted by Hussin et al. [167], the effect of different carbohydrates was investigated on enhancing GABA production in yoghurt cultured using a mixture of UPMC90 and UPMC91, self-cloned LAB strains (*L. plantarum* Taj-Apis362, previously isolated from the stomach of honeybee *Apis dorsata* and engineered by Tajabadi et al. [124,168]). The glucose induced more GABA production (58.56 mg/100 g) compared to the inuline, FOS e GOS as prebiotics (34.19-40.51 mg/100 g), and the control sample with added PLP (48.01 mg/100 g) [167].

In other similar study conducted by Hussin et al., self-cloned and expressed *L. plantarum* Taj-Apis362 recombinant cells, UPMC90 and UPMC91 were used to improve the GABA production in yoghurt. Fermentation conditions at 39.0 ◦C, 7.25 h, and 11.5 mM glutamate concentration produced GABA-rich yogurt (29.96 mg/100 g) [169].

While many studies reported the use of single-strain LAB to generate GABA, only few reported the production of GABA by co-culturing different bacterial strains [170].

Co-culture fermentation is a novel technology for enhancing fermentation quality and promoting GABA yield. Further, coculture of GABA-producing strains is an efficient method for raising the GABA content.

Table 3 summarizes the results obtained from the use of *L. plantarum* in co-culture (co-fermentation or two-stage fermentation) with other microbial strains belonging to different species.

Table 3. GABA production by *Lactiplantibacillus plantarum* (previously *Lactobacillus plantarum*) in co-culture with other microbial species.

***L. plantarum* strains**	**cooperative species/strain**	**Food or culture medium**	**GABA production**	**Notes**	**Refs**
L. plantarum EJ2014	*B. subtilis* HA	pumpkin	1.47%	Two-step fermentation	[171]
L. plantarum K154	*B. subtilis* HA	turmeric (*Curcuma longa*) / roasted soybean meal mixture + 5% MSG	1.78 %	Two-step fermentation	[172]
L. plantarum K154	*B. subtilis* HA	defined medium fortified with glutamate and skim milk	4800 µg/mL	Two-step fermentation	[173]
L. plantarum K154	*Leuconostoc mesenteroides* SM	Water dropwort	100 mM	Two-step fermentation	[174]
L. plantarum BC114	*S. cerevisiae* SC125	mulberry beverage brewing	2.42 g/L	Co-fermentation	[74]
L. plantarum GB01-21	*C. glutamicum* G01	cassava powder	80.5 g/L	Two-step fermentation	[144]
L. plantarum Taj-Apis362	*S. thermophilus* and *L. delbrueckii* ssp. *bulgaricus*	Skim milk + 2% glucose and 11.5 mM MSG	59.0 mg/100 g	Co-fermentation	[169]
L. plantarum K154	*Ceriporia lacerata*	broth fortified with skim	15.53 mg/mL	Two-step fermentation	[122]

		milk and 2% MSG			
L. plantarum (KCTC 3105)	*Lactobacillus brevis* OPY-1 *L. acidophilus* KCCM 40265	Soya milk	424.67 μg/g	Co-fermentation	[149]
L. plantarum L10-11	*Lactococcus lactis* spp. *lactis* and *Lactococcus lactis* spp. *cremonis*	milk	11.3 mg/100 mL	Co-fermentation	[175]
L. plantarum JLSC2-6	*Levilactobacillus brevis* YSJ3	cauliflower stems	35.00 mg/L	Co-fermentation	[176]
L. plantarum MCM4	*Lactococcus lactis* subsp. *lactis*	whey-based formulate	365.6 mg/100 mL	Co-fermentation	[177]
L. plantarum DSM749	*L. brevis* NM101-1	PM	224.69 mM	Co-fermentation	[138]
L. plantarum C48	*Lactobacillus paracasei 15N, Streptococcus thermophilus DPPMAST1, Lactobacillus delbruecki subsp. bulgarigus DPPMALDb5*	Milk + 100 or mg/L of olive vegetation water phenolic extract	67 mg/L	Co-fermentation	[178]

* *Abbreviations*: MSG, mono-sodic glutamate; PM, production medium (50 g/L glucose; 25 g/L peptone; 0.01 g/L $MnSO_4 \cdot 4H_2O$; 2 mL Tween 80; 200 μM PLP); PLP, pyridoxal 5-phosphate.

In a study carried out by Lim et al., the co-fermentation of turmeric (*Curcuma longa*)/roasted soybean meal mixture, containing 5% MSG, was optimized to fortify it with bioactive compounds including GABA [172]. *Bacillus subtilis* HA was used for the first fermentation and *L. plantarum* K154 isolated from fermented kimchi was used for the second fermentation. The results showed that the amount of GABA increased from 0.01% before fermentation to 1.78% after second fermentation [123].

In a further study, a two-step fermentation of pumpkin (*Cucurbita moschata*) was performed using *B. subtilis* HA and *L. plantarum* EJ2014, with the aim of producing a novel food ingredient enriched with GABA [171]. *Bacillus subtilis* HA (KCCM 10775P) strain was isolated from cheonggukjang (traditional Korean fermented soybean) while *L. plantarum* EJ2014 (KCCM 11545P) was isolated from rice bran [179]. The co-fermented pumpkin contained 1.47% GABA. *Bacillus subtilis* HA was also used in a two step-fermentation with *L. plantarum* K154, obtaining a high level of GABA production (about 4800 μg/mL) in a defined medium fortified with glutamate and skim milk [173]. Instead, Yang et al. proposed a two-step method to produce GABA from cassava powder using *C. glutamicum* G01 and *L. plantarum* GB01-21 [144]. In this study, glutamic acid was first obtained from cassava powder by saccharification and simultaneous fermentation with *C. glutamicum* G01, followed by biotransformation of glutamic acid into GABA with resting cells of *L. plantarum* GB01-21. *C. glutamicum* G01 was isolated from soil and *L. plantarum* GB01-21 was obtained through multi-mutagenesis as described in our previous study [180]. After optimizing the reaction conditions (35°C, pH 7), the maximum concentration of GABA reached 80.5 g/L [144].

In other study, two self-cloned *L. plantarum* Taj-Apis362 strains possessing high intracellular GAD activity (UPMC90) and high extracellular GAD activity (UPMC91) and a wild-type *L. plantarum* Taj-Apis362 (UPMC1065) were co-cultured with starter culture (a mixture of *S. thermophilus* and *L. delbrueckii* ssp. *bulgaricus*) to produce GABA-rich yogurt [124].

The wild-type *L. plantarum* Taj-Apis362 (UPMC1065) was previously isolated from the stomach of honeybee *Apis dorsata* [168], and used as a host for GAD gene overexpression to produce UPMC90 and UPMC91 strains. After 7 h of fermentation at 39.0 °C, the starter co-culture in skim milk with 2% glucose and 11.5 mM glutamate produces 59.00 mg/100 g of GABA.

Water dropwort (*Oenanthe javanica* DC), a common aquatic perennial plant widely cultivated in most Southeast Asian countries, was co-fermented with *Leuconostoc mesenteroides* SM and *L. plantarum* K154 to produce a novel functional food ingredient enriched with GABA (100 mM) [174]. It is possible that, apart from the pH and acidity of the fermented broth, the low concentration of sugar remaining for the second fermentation and the presence of nitrogen sources, in particular MSG, stimulated *L. plantarum* K154 to use MSG as a nutrient and as a precursor for GABA production.

Woraratphoka et al. used a co-culture of *L. plantarum* L10-11, *Lactococcus lactis* spp. *lactis* and *L. lactis* spp. *cremonis* in fresh cheese production [175]. *L. plantarum* L10-11 which was isolated from Thai fermented fish (Plaa-som) while *Lactococcus lactis* spp. *lactis* and *L. lactis* spp. *cremonis* they were commercial strains (Lyofast MWO030, SACCO, Italy). After 18 h the fermented milk by single-L10-11 and co-L10-11 contained 1.21 and 11.30 mg/100 mL of GABA, respectively. Thus, this suggested that in the co-culture test, by transforming lactose into lactic acid, the commercial strains decreased the pH value, creating a favorable condition for the enzymatic activity (GAD) of *L. plantarum* L10-11 that catalyzes the conversion of glutamate to GABA. Therefore, co-fermentation by *L. plantarum* L10-11 with other LAB strains could possibly increase the rate of the GABA production [175].

In a previous study, it was reported that *L. plantarum* L10-11 was clearly involved in the conversion of MSG to GABA and the highest GABA production was obtained when the initial pH of MRS was in the range of 5.0-6.0 [134].

These data confirm that the optimal pH for GABA production by different LAB strains is mostly within the acidic pH range of 4-6. [3].

Zhang et al. evaluated the effects on GABA production by co-culture of *Levilactobacillus brevis* YSJ3 and *Lp. plantarum* JLSC2-6. The results indicate that co-culturing these two strains can improve GABA yield (35.00 ± 1.15 mg/L) in fermented cauliflower stems (*Brassica oleracea* L. var. *botrytis*) [176].

Functional milk beverages fortified with olive vegetation water phenolic extract (100 and 200 mg/l) was fermented at 40°C by *L. plantarum* C48, *L. paracasei* 15N, *Streptococcus thermophilus* DPPMAST1 and *L. delbruecki* subsp. *bulgarigu*s DPPMALDb5. The highest amount of GABA (67 mg/L) was detected after 30 days at 4°C in milk-based beverages enriched with 100 mg/L of OVWPE [178].

In other studies, co-cultures of *L. plantarum* and fungi for GABA production are evaluated.

Co-fermentation of *L. plantarum* K154 and fungus *Ceriporia lacerate* efficiently produced GABA (15.53 mg/mL) in a defined medium containing 3% glucose, 3% soybean flour, 0.15% MgSO4, and 5% rice bran for 7 days at 25°C. *C. lacerate* produced exopolysaccharides, protease, cellulose, and α-amylase, which served as nutrients for the growth of L. *plantarum* [122].

In a study conducted by Zhang et al., *S. cerevisiae* SC125 and *L. plantarum* BC114 were used in co-culture to ferment mulberry (*Morus alba* L.) and produce a novel beverage enriched of GABA [74]. *L. plantarum* BC114 and *S. cerevisiae* SC125 were inoculated in pasteurized mulberry substrate with 5 g/L L-glutamate and incubated at 30°C for 72 h.

Compared with single fermentations using *L. plantarum* BC114 and *S. cerevisiae* SC125, which resulted in poor GABA production (1.45 g/L and 1.03 g/L, respectively), the co-culture resulted in higher GABA production (2.42 g/L). *S. cerevisiae* SC125 predominated at the start of the co-culture mulberry fermentation, but as fermentation progressed and conditions became acidic and anaerobic, *L. plantarum* BC114 became predominant [74].

Therefore, co-cultures of fungi with GABA-producing strains belong to *L. plantarum* species may be a promising approach for the production of GABA-enriched foods.

8. Conclusions

In recent years, GABA-enriched foods have been significantly considered by researchers due to its important biological and functional properties.

Currently, GABA can be produced by a variety of methods, including chemical synthesis, plant enrichment, enzymatic methods, and microbial production. The use of microbial fermentation technology to produce GABA is considered effective as biological approach.

GABA producing LABs play an important role in the food industry, boasting a long and safe history of application and consumption in the context of fermented food products. Therefore, the production of GABA-fortified foods using beneficial LABs is an important strategy. *L. plantarum* is a LAB species generally associated with desirable properties in many fermented foods.

Therefore, fermentation by selected GABA-producing *L. plantarum* strains has been considered a promising possibility in order to increase the technological, nutritional, sensory, and functional properties of specific fermented foods.

The optimal conditions for the production of GABA extensively differs among the *L. plantarum* strains and is significantly affected by medium composition and culture conditions. Therefore, it is essential to optimize these conditions to improve the production of GABA also according to the production process adopted to obtain each specific fermented food. Considering that microbial fermentation is an important technology for increasing the GABA content of food, the selection of new GABA-producing strains belonging to *L. plantarum* species as will remain the focus of future research.

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