

# Characterization, High-Density Fermentation, and Production of Lactobacilli

Subjects: [Food Science & Technology](#)

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*Lactobacilli* have been widely concerned for decades. Bacteria of the genus *Lactobacillus* have been commonly employed in fermented food to improve the appearance, smell, and taste of food or prolong its shelf-life. They comprise 261 species (by March 2020) that are highly diverse at the phenotypic, ecological, and genotypic levels. Some *Lactobacilli* strains have been documented to be essential probiotics, which are defined as a group of living microorganisms that are beneficial to the health of the host when ingested in sufficiency. The viability and stability of *Lactobacilli* in the food industry and gastrointestinal environment are critical challenges at the industrial scale. The new production equipment and technology of DVS starter of *Lactobacilli* strains will have the potential for large-scale application, for example, developing low-temperature spray drying, freezing granulation drying, and spray freeze-drying.

Lactobacilli strains

probiotics

characterization

performance improvement

production of DVS starter

## 1. Introduction

*Lactobacilli* are Gram-positive rod, non-spore-forming, catalase-negative bacteria that commonly colonize the human intestine and have essential physiological functions in the human body [1][2]. Microscopically, these bacteria represent non-motile, thin rods that differ from long to short. Sometimes, they are present in coryneform, bent morphology, or chains. *Lactobacilli* comprise 261 species (by March 2020) that are highly diverse at the phenotypic, ecological, and genotypic levels [3]. Moreover, *Lactobacilli* have been documented to be important probiotics, defined as a group of living microorganisms that are beneficial to the host's health when ingested in sufficiency [4].

*Lactobacilli* may be added as starters, which are used to ferment and produce specific changes in the chemical composition and sensory properties of foods [5]. It can produce amylase, protease, dehydrogenase, decarboxylase,  $\beta$ -glucosidase, and peptidase during the fermentation, thereby can be widely used in the food industry for the production of yogurt [6], cheese [7], sourdough [8], sausages [9], cucumber pickles [10], olives [11], sauerkraut [12], and so on. However, there is some diversity in the *Lactobacilli* used in fermented food, depending on the food matrix. One example is *Lactobacillus plantarum*, which is used as a starter culture in meat and wine (malolactic) fermentation [5], whereas *L. bulgaricus* can be found as the primary starter culture in yogurt fermentation [13].

## 2. Screening out *Lactobacilli* Strains

*Lactobacilli* used in the fermented food industry are diverse and many. Due to their excellent fermentation performance, they are extensively used to ferment food based on various raw materials, including milk, meat, cereals, fruits, vegetables, and seafood. Their commercial products, including probiotics, have ample market space [14]. So, screening out one or several new strains with excellent fermentation performance and potential probiotic properties is very meaningful work. High-throughput screening technology is a method for the quick selection of certain strains of *Lactobacilli* species with outstanding performance (such as extracellular polysaccharides, bacteriocin, gamma amino acid, butyric acid, short-chain fatty acid, etc.) [15]. These *Lactobacilli* strains can be traditionally isolated from a wide range of sources, such as human and animal mucosal membranes, plants or material of plant origin, and fermented food.

Researchers constructed a phylogenetic tree containing 64 *Lactobacilli* species based on the related *Lactobacilli* 16S rRNA gene sequence derived from National Center for Biotechnology Information (<https://www.ncbi.nlm.nih.gov/>). It shows that the *Lactobacilli* species used in the food industry are not clustered in a particular branch but are almost evenly distributed in all branches of the *Lactobacilli* phylogenetic tree. Based on this, the other species in this genus may also have potential use value in the field of food, livestock breeding, and medicine. Given that *Lactobacilli* have strain specificity, the traditionally safe *Lactobacilli* strains cannot ensure the safety of all strains in the species. Thus, the identification and detection of *Lactobacilli* are of significance.

Generally, microorganisms always contain desirable and undesirable characteristics. A qualified candidate for use in the food industry initially requires a desirable characterization, especially safety. For *Lactobacilli* strains, researchers expect to select strains with probiotic properties. These characteristics of new *Lactobacilli* strains need to be evaluated by in vitro and in vivo experiments to understand their potential probiotic properties and industrial uses.

## 3. Identification and Safety Assessment of *Lactobacilli* Strains

The safety status of *Lactobacilli* used in food production has become the focus of the attention of manufacturers and government departments. Although European Qualified Presumption of Safety regulations have identified microorganisms that can be safely used in food [16], some safety aspects must be evaluated before the newly screened cultures are applied to fermented food. For a newly screened *Lactobacilli* strain, its inherent characteristics need to be tested in vitro. First, researchers need to identify the isolate to make sure it is what researchers want and safe, and it can preliminarily predict whether the strains of this genus can be fully put into production [17].

The identification methods of *Lactobacilli* use phenotypic methods and molecular identification methods. In contrast to phenotypic approaches, molecular identification and characterization tools can distinguish even between closely related groups of species, which are indistinguishable based on phenotype, which is far more consistent, quick,

trustworthy, and reproducible [18][19]. The most commonly employed molecular techniques for the identification of *Lactobacilli* can be divided into two groups: species-specific identification techniques (including amplified ribosomal DNA restriction analysis (ARDRA) and 16S and 23S rRNA sequencing) and strain-specific identification techniques (including ribotyping, restriction enzyme analysis (REA) with pulsed-field gel electrophoresis (PFGE), genetic probes/DNA dot blot, multiplex PCR using specific primers, randomly amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), PCR-denaturing gradient gel electrophoresis (DGGE), and fluorescent in situ hybridization (FISH)) [20][21][22][23][24][25][26][27][28][29][30][31][32][33][34]. Taxonomy and phylogeny of the genus *Lactobacillus* have been recognized as rather complicated, because of a great number of species with a diverse group of species [3]. It is clear that for reliable species determination within this genus, a polyphasic approach based primarily on one or more molecular methods is required. Additionally, the International Committee on Systematic Bacteriology has acknowledged polyphasic taxonomy as a trustworthy method for describing species and revising the current nomenclature of specific bacterial groupings. In a recent study, Zheng et al. [3] proposed reclassification of the genus *Lactobacillus* into 25 genera including the emended genus *Lactobacillus*, which includes host-adapted organisms that have been referred to as the *Lactobacillus* delbrueckii group, *Paralactobacillus* and 23 novel genera including *Holzapfelia*, *Amylolactobacillus*, *Bombilactobacillus*, *Companilactobacillus*, *Lapidilactobacillus*, *Agri lactobacillus*, *Schleiferilactobacillus*, *Loigolactobacillus*, *Lacticaseibacillus*, *Latilactobacillus*, *Dellaglioia*, *Liquorilactobacillus*, *Ligilactobacillus*, *Lactiplantibacillus*, *Furfurilactobacillus*, *Paucilactobacillus*, *Limosilactobacillus*, *Fructilactobacillus*, *Acetilactobacillus*, *Apilactobacillus*, *Levilactobacillus*, *Secundilactobacillus*, and *Lentilactobacillus*. This reclassification reflects the phylogenetic position of the micro-organisms and groups *Lactobacilli* into robust clades with shared ecological and metabolic properties that can anticipate the addition of new species shortly. Then, the relevant antibiotic susceptibility is usually determined and evaluated according to the protocol provided by the European Food Safety Agency (EFSA) [35]. Microdilution broth tests on test tubes, disk diffusion [36], and commercial ready-to-use kits [37] have been used to determine the physical sensitivity of known antibiotics to newly screened strains. Hemolytic activity was also investigated [38]. The production of various enzymes should also be evaluated. Maybe they are the cause of pathogenicity. Strains should be tested for known human toxins (e.g., cytolyisin) by appropriate in vitro analysis. Detecting the toxicity of pathogenic genes and metabolites is also conducted; several *Lactobacilli* can decarboxylate and reduce amino acids in food to produce biogenic amines, which can cause poisoning symptoms if they accumulate in excess amounts in the body [39]. These in vitro experimental analyses are simple and rapid in determining the safety of a newly screened strain and avoid the use of harmful strains. For example, a hemolytic and toxin-producing strain can easily be excluded from further analysis [38]. The false negative strains created by in vitro experimental research are concerning. Therefore, further in vivo experiments are needed, including animal models and clinical applications [11][40].

## 4. Potential Probiotic Functionalities of Lactobacilli Strains

Some *Lactobacilli* have been reported as strains with high probiotic potential and support efforts to improve probiotic quality, such as *L. salivarius* strains BCRC14759 and BCRC 12574, with the highest exopolysaccharide production [41], *L. johnsonii* ZLJ010, with better adaptation to the gut environment and its probiotic functionalities

[42], and *L. helveticus* D75 and D76 that can inhibit the growth of pathogens and pathobionts [43]. However, *Lactobacilli* strains in the probiotic market are still limited, and *Lactobacilli* strains with potential probiotic properties should be explored. An important aspect is to evaluate the selected *Lactobacilli* in vitro and find their probiotic potential. Some in vitro probiotic performance evaluations of the strains include survival under stress (low pH, high bile salt, high osmotic pressure, high oxygen, oxidation, starvation, etc.), adhesion ability, and antibacterial, antioxidation, cholesterol-lowering, and anticancer activities.

As probiotics, *Lactobacilli* colonizing the intestine to reach  $1 \times 10^6$  CFU is necessary for its probiotic effect [44]. *Lactobacilli* can survive in the robust acid environment in the gastric juice and high bile salt concentration in the small intestine, which are two criteria for screening good probiotic *Lactobacilli* strains. The acid and bile salt tolerance of *Lactobacilli* strains use the rate of viable bacteria incubated in various acid pH environments as an indicator in in vitro assays. Additionally, many studies conducted artificially simulated gastric juice tolerance and animal model tests of probiotic *Lactobacilli* [14][45][46]. The survival rate was used as an index to evaluate probiotic *Lactobacilli*'s acid and bile salt tolerance.

Adhesion is another of the essential characteristics of probiotic bacteria that contributes to the colonization of probiotics in the gastrointestinal tract [47]. The ability of the bacteria to stick with hydrocarbons determines the extent of adhesion to the epithelial cells in the gastrointestinal tract, known as cell surface hydrophobicity [48]. The direct method of cell surface hydrophobicity of bacteria is to determine the change of absorbance of the supernatant of bacterial cell solution at 600 nm after treatment with hydrocarbons such as n-hexadecane and toluene. More precisely, the adhesion of *Lactobacilli* strains to mucin has also been determined [49]. Moreover, commercial kits for determining these mucins have been reported and can be used for high-throughput screening [50].

Intestinal epithelial cell (IEC) lines are often presumed to better represent conditions in the tissues of the GIT. Several studies have been conducted using human epithelial cell lines (such as HT-29, HT-29MTX, and Caco-2) to screen the adhesion of probiotic strains [47]. Additionally, other studies have focused on the self-aggregation of probiotics [51], which is also related to adhesion.

*Lactobacilli* strains can secrete lactic acid and other organic acids, lowering the environment's pH and thereby inhibiting other microorganisms' growth [52]. Additionally, *Lactobacilli* strains produce medicinal probiotic metabolites and bacteriocin BACs, often used as biological preservatives in the food industry, arousing people's attention [53]. These metabolites have antagonistic activity against bacteria genetically similar to producing bacteria, which are immune to their own BACs. BACs have also been considered biologically active molecules with potential activities for human health, such as use as antiviral and anticancer drugs. BACs are extracellular antimicrobial peptides synthesized by ribosomes. They have extensive antibacterial activity and are a safe alternative to antibiotics. As a result, the shelf life of naturally fermented foods has increased. Therefore, screening high-yield BAC probiotic *Lactobacilli* strains from naturally fermented food should be an option. Researchers have also studied the production and characterization of BACs by different probiotics [12]. Additionally, the combined culture of different probiotics may produce new antibacterial products [54][55].

Some reports show that *Lactobacilli* strains have antioxidant activity and can be used as antioxidants in food, stabilizing food's color, flavor, and taste [56]. Additionally, *Lactobacilli* strains can reduce the oxidative stress injury of Caco-2 cells and improve the antioxidant capacity under oxidative stress. Firstly, the tolerance of *Lactobacilli* strains to hydrogen peroxide was studied [57]. The antioxidant capacity of *Lactobacilli* strains was evaluated by measuring the hydroxyl radical scavenging capacity of cell-free extracts of these strains. These strains can produce metabolites such as superoxide dismutase, glutathione, and extracellular polysaccharide to inhibit oxidation.

## 5. Fermentation Performance of Lactobacilli Strains

As a lactic acid starter, *Lactobacilli* strains should be tolerant to harsh conditions, such as temperature changes, osmotic pressure (high fat and protein concentration in milk and meat and high salt in kimchi), and lactic acid accumulation. These characteristics can ensure the rapid adaptation and growth of microorganisms to bring good physical properties and taste to the products. Due to different food components, some of them are used for specific food manufacturing, such as yogurt and cheese (*L. delbrueckii*), fermented vegetables (*L. plantarum* and *L. pentosus*), and fermented meat (*L. pentosus*).

The diversity of lactic acid food produced by *Lactobacilli* strains requires that the fermentation characteristics of these strains are different [58]. For example, *Lactobacilli* strains used in meat processing should be able to improve the flavor of end products without producing biogenic amines, because these compounds are produced by the deacidification of free amino acids and have toxic effects on human intestines. Studies have revealed that *Lactobacilli* strains with protein hydrolytic activity [59], which belong to homogeneous fermentation, can significantly reduce the biogenic amines of fermented sausage. The production of bacteriocin by *Lactobacilli* strains, for example, is another feature of evaluating the development of meat products by *Lactobacilli* strains. It can inhibit the growth of pathogenic bacteria and increase the shelf life of products. As mentioned above, the antibacterial activity of *Lactobacilli* strains was screened to resist various pathogens evaluating the production of nisin against *Listeria monocytogenes*, *Clostridium perfringens*, *Bacillus cereus*, and *Staphylococcus aureus* [52][60][61][62].

*Lactobacilli* strains produce large amounts of lactic acid, a non-volatile, odorless compound that contributes to the aroma of the product [63]. Therefore, the production of another fermentation performance flavor molecule was evaluated by gas chromatography–mass spectrometry. The main aroma components include aldehydes, organic acids, higher alcohols, esters, carboxylic acids, and ketones [64][65]. *Lactobacilli* strains convert precursor molecules into aromatic compounds by secreting various extracellular enzymes [59][66][67]. In a protein-rich environment, proteolytic enzymes play a major role in forming aromatic molecules from the amino acids released by complex proteins. For example, milk is rich in casein, and *Lactobacilli* strains used in yogurt and cheese convert these precursor molecules into flavor substances. Lipid degradation also plays a vital role in the aroma formation of fermented meat and dairy products [68].

## 6. Health Functions of Lactobacilli Strains

From the functional characteristics, the existence of *Lactobacilli* strains in the intestinal microbiota is related to the host's health status [69][70]. Clinical research showed that the reduction or increase in the proportion of this genus in the human body would produce health problems, such as irritable bowel syndrome [71], human immunodeficiency virus [72], obesity [73], type 2 diabetes [74], etc. Several strains with probiotic properties of specific metabolites have been successfully included in various functional foods. Although the mechanism of their role is uncertain, the health-promoting effect of these strains is related to the strains themselves and their active metabolic substances (such as extracellular polysaccharide, bacteriocin, polypeptide, short-chain fatty acid, etc.). Several meta-analyses and systematic research [75][76][77][78][79][80] support the health effects of probiotic *Lactobacilli* strains and specific metabolites produced by *Lactobacilli* strains in treatment cases, including acute rotavirus diarrhea in children, antibiotic-related diarrhea in children, *Helicobacter pylori* infection, allergic rhinitis, high blood pressure, hyperlipidemia, and other diseases. Additionally, based on its excellent physiological characteristics and probiotic function, *Lactobacillus* has become an important direction in the field of probiotic function. Given the specificity of the *Lactobacilli* strains, the new strains may have potential unique functional characteristics.

## 7. Performance Development and Improvement of Lactobacilli Strains

As mentioned above, numerous species of *Lactobacilli* are used in food production, including improving traditional food and developing new products. On the one hand, *Lactobacilli* strains can enhance the quality of fermented food and, on the other hand, prolong the storage period of food as a preservative. Therefore, the excellent characteristics of *Lactobacilli* strains are the key to their application in the food industry. However, *Lactobacilli* strains have specificity themselves. Different strains of the same species show significant differences; therefore, new characteristics can be found [81]. Thus, scholars are committed to screening new *Lactobacilli* strains.

On the one hand, the growth of naturally screened *Lactobacilli* strains is limited by physical and chemical factors, such as pH [82][83], oxygen [84][85], osmotic stress [86], temperature [83], carbohydrate substrates [87], and other factors [88][89]. On the other hand, the yields of beneficial metabolites of naturally screened *Lactobacilli* strains, such as lactic acid [90],  $\gamma$ -aminobutyric acid [91][92], extracellular polysaccharide [92], and bacteriocin [93] are relatively low and cannot meet the requirements of industrial production. Therefore, reasonable breeding strategies are used to improve the performance of *Lactobacilli* strains with potential application in the food industry.

One method is mutagenesis breeding. Mutation breeding of *Lactobacilli* strains can change the genetic structure and function of *Lactobacilli* strains, and then screen mutants to obtain the required high-yield and high-quality strains [94]. It is the most basic modern breeding method. The breeding speed is fast, the cost is low, the time is short, and the method is simple, mainly including physical, chemical, and biological mutagens. Chemical mutagenesis primarily uses nitrosoguanidine, diethyl sulfate, and other chemicals. These chemicals are harmful to the human body. Thus, they are not widely used in the food industry. A limited number of studies focused on the biological mutagenesis of *Lactobacilli* strains, mainly involving transposon mutations [95][96]. Physical mutagenesis of *Lactobacilli* strains commonly uses ultraviolet [97] or microwave radiation [98]. Given the possible tolerance of traditional radiation technology of *Lactobacilli* strains, new mutation technologies, such as heavy ion beam

irradiation and plasma mutation breeding, have recently appeared [99][100][101]. The operation of traditional mutation breeding is simple, and the experimental conditions are not high; the mutation is random, and the workload is enormous despite the introduction of high-throughput screening technology in the mutation process [99][102][103].

Another method is metabolic engineering, a continuation, and upgrade of gene engineering technology. This method can directionally change the functional characteristics of *Lactobacilli* strains and compensate for the shortcomings of classical mutagenesis screening [104][105][106][107][108]. The metabolic strategies of *Lactobacilli* mainly focus on the changes in pyruvate metabolism to produce essential fermentation end products, such as sweeteners, spices, aromatic compounds, and complex biosynthetic pathways, leading to the production of extracellular polysaccharides and vitamins [109]. Currently, the most commonly used methods for metabolic engineering of *Lactobacilli* include whole-genome amplification [110], genome shuffling [111][112], and genome editing (plasmid-based homologous recombination, Red/RecET-mediated double-stranded DNA recombination, and single-stranded DNA recombination) [113][114]. However, the safety of these methods for metabolic engineering to change the metabolic characteristics of *Lactobacilli* is worth considering and is not accepted by the European Union [115].

## 8. Role of *Lactobacilli* Strains in Food Production

The primary role of *Lactobacilli* strains in dairy processing (such as yogurt, dahi, kefir, koumiss, and cheese) is not only to improve the nutritional value but also to produce lactic acid, butyric acid, a variety of amino acids, and vitamins and other metabolites, resulting in a unique food flavor. Additionally, these strains use dairy products as a carrier to promote human health due to their probiotic effect [116]. The application of *Lactobacilli* strains to meat products can improve the appearance of meat products, promote the improvement of taste, inhibit the growth of spoilage bacteria, reduce the generation of nitrite and greatly improve the overall quality of meat products [117].

In turn, fermented foods as a carrier play a role in transporting and storing these excellent strains. On the one hand, these strains were found in traditional fermented foods, which characterized their excellent properties. On the other hand, these strains were intensively inoculated into conventional fermented food to improve product control. Fermented fruits can be produced by natural fermentation of the surface flora spontaneously formed (such as *Lactobacilli* and *Pediococcus* spp.) or inoculated with fermentation starter (such as *L. plantarum*, *L. rhamnosus*, and *L. acidophilus*). Food nutritionists are developing a new generation of fermented fruit products with special biological and unique sensory characteristics [5][118][119]. Fermented vegetable products can positively impact human health because they are rich in substances beneficial to human beings (such as dietary fiber, minerals, antioxidants, and vitamins). The principle is to use *Lactobacilli* strains attached to vegetables and several artificially selected excellent strains to carry out a series of microbial fermentations and finally obtain the finished pickle. The *Lactobacilli* contained in kimchi can promote human gastrointestinal peristalsis, reduce fat, and enhance immunity [10][65].

The fermentation of probiotic strains with excellent performance has attracted people's attention. The screened new strains are often used in the development of new products. In recent years, several *Lactobacilli* strains have

been widely used in various functional foods due to their unique physiological efficacy and flavor, such as active *Lactobacilli* drinks and solid drinks [64][120]. With the deepening of relevant research, *Lactobacilli* will be used in human health conditioning treatments as a probiotic functional food to a greater extent, and the application direction will be more extensive.

*Lactobacilli* can also be applied to preserving food, such as meat, fruit, vegetables, seafood, etc. These *Lactobacilli* strains are used as biological preservatives due to the following manifestations: (1) produce organic acids, such as lactic acid and acetic acid, to inhibit the growth and reproduction of most spoilage bacteria; (2) H<sub>2</sub>O<sub>2</sub> production activates the catalase thiocyanate system in milk; (3) produce small proteins or peptides similar to bacteriocin, etc., [121][122].

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