Chapter

# *Lactobacillus* Use for Plant Fermentation: New Ways for Plant-Based Product Valorization

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**Abstract**

Today, plant production is increasing, but most industrial processes generate a lot of waste and by-products for which, in the current context, it is a priority to recycle or valorize them. One of the cheapest valorization routes is fermentation, in particular lactic fermentation by *Lactobacillus* species, which produces lactic acid and other molecules of industrial interest such as bioactive compounds such as anthocyanin, organic acid, peptides, or phenol, which are widely found in the plant matrix, mainly in cereals, grass, fruits, and vegetables. Bioactive compounds may exert beneficial health effects, such as antioxidant, anti-inflammatory, antimicrobial, or prebiotic activities. In addition, lactic acid fermentation can improve existing products and lead to new applications in food, livestock feeding and biotechnology, such as the production of lactic acid, protein, or silage. This chapter reviews the use of *Lactobacillus* strains in the fermentation process of many plant bioresources or by-products through their different bioactivities, active molecules, and applications.

**Keywords:** *lactobacillus* genera, lactic acid fermentation, by-product valorization, bioactivities, health benefits

## 1. Introduction

The world's population of 7.6 billion people is still growing and is expected to reach 8.3 billion by 2025 and almost 10 billion by 2050 [1]. Concomitantly, the Earth's resources are depleting. According to the different scenarios, global food demand is expected to increase by 40–68% by 2050 [2]. Among food resources, plants are of particular interests, as the global production of plant-based products is constantly increasing while producing significant waste. In this context, recycling or revalorizing these by-products is a priority [1].

The main objectives of using plant by-products are to revalorize wastes, reduce pollution, and limit resource depletion. Fermentation is one of the least polluting methods. Plant by-products fermentation contributes to sustainable development; in fact, this type of valorization is part of some objectives of the United Nations 2030 Agenda, notably the third objective: good health and well-being and the twelfth objective: responsible consumption and production. The consumption of fermented plant by-products therefore allows responsible consumption. The fermentation of plant by-product leads to bioactivities related to human health such as antioxidant, anti-inflammatory, or antimicrobial activities that contribute to good health and well-being [3]. Plant-based foods are sources of many bioactive compounds such as fibers, vitamins, minerals, or phenolic compounds. These nutrients are necessary for the survival and growth of organisms [4]. In many countries, the health benefits of certain plant and their traditional use have been recognized for decades [5]. Since industries have been exploiting plant-based foods, many agro-industrial by-products that still contain valuable compounds have been generated. Many companies are now seeking to recycle waste from their fruit and vegetable activities in order to address environmental and economic issues. For example, cereal waste reached about 40,000–45,000 tons per year in Europe [6]. The by-products are mainly used for livestock feed or methanisation but have great potential to generate food or dietary supplements for human use [6, 7]. Another example concerns the waste from the citrus industry, which amounts to 50 million tons per year and is the most important waste from fruits exploitation. The management of by-products represents a real food waste problem and raises major issues [8]. Therefore, in recent years, there has been a growing interest in the valorization of plant by-products.

In China, for 9000 years, humans have empirically exploited the fermentation process for numerous applications [9]. Studied since the nineteenth century, lactic acid fermentation has been an essential process for food processing and preservation for many millennia [10]. Humans took advantage of it for their food, notably by developing bread, beer, wine, cheese, or vinegar. Subsequently, fermentation with lactic acid bacteria has been largely studied to improve the nutritional and functional properties of plants. Due to their richness in nutrients, water, and natural ferments, plants such as fruits and vegetables represent an optimal substrate for *Lactobacillus* [11]. Lactic acid bacteria constitute a diverse group of Gram-positive, catalase-negative bacteria producing lactic acid as the main end product. Many food products fermented by lactic acid bacteria are obtained with organisms belonging to the genus *Lactobacillus* [12]. With more than 200 species of *Lactobacillus* bacteria [11], this genus is certainly the main and most diverse group of lactic acid bacteria. A study published in 2020 re-evaluated the genetic relatedness and phylogeny of *Lactobacillus* species. Based on a polyphasic approach such as whole-genome comparison, core genome phylogeny, physiological criteria, and ecology of the organisms, the genus *Lactobacillus* was reclassified into 25 genera (2 preexisting genus and 23 new genera). This work showed the great and extensive diversity of the *Lactobacillaceae* family [13]. *Lactobacillus* species are commonly used in fermented food. Depending on the species, their enzymatic activities including amylase, lactate dehydrogenase, peptidase, proteinase, α- and β-glucosidases, decarboxylase, lactate dehydrogenase, peptidase, phenolic acid decarboxylase, phenol reductase, proteinase or tannase are very useful in food fermentation [14]. These enzymes can degrade the plant cell wall matrix, resulting in the release of many bioactive compounds, which may or may not be modified structurally by the action of other enzymes in the bacteria.

Today, several ecological and economic issues are at the heart of lactic fermentation research. The optimization of yield, cost, and energy consumption and the valorization of plant-derived products represent challenges for the industry [15]. To meet this demand, the use of new substrates and the genetic engineering of fermentation strains are being studied as potential solutions [11]. Moreover, it is now known that lactic fermentation increases the content of bioactive compounds. Indeed, this fermentation process is well known to strengthen the immune and antioxidant (AO) effect of medicinal plants by increasing the bioavailability of active compounds, but also through the production (or the bioconversion) of plant metabolites into new bioactive molecules [16]. To increase the bioactivities and organoleptic characteristics of fermented products, *Lactobacillus* converts metabolizable molecules with their enzymes, in particular *L. plantarum,* which is one of the most used *Lactobacillus* as a fermentation starter. This degradation increases the bioavailability of molecules and improves their absorption [17]. A fermentation starter is usually a consortium of bacteria that helps the fermentation process to start. Today, the use of starter cultures in food fermentation is one of the necessary ingredients for good production. In addition, LAB used as starter in the food industry provide safe product with good nutritional and organoleptic qualities. LAB are used as starter for many products, including fruit, vegetables, and cereal [18]. As illustrated in **Figure 1**, the production of biomolecules by lactic fermentation of plant by-products can induce other bioactivities. This chapter refers to antioxidant (AO), anti-inflammatory (AI), antimicrobial, prebiotic activities, and others. These can be used in human food and beverage, livestock feeding, or biotechnology mainly to produce lactic acid. Those activities and applications will be detailed in this chapter.

## 2. Bioactivities resulting from the fermentation of plant products or by-products by *Lactobacillus* genera

### 2.1 Antioxidant activity

Many *Lactobacillus* enzymes can generate compounds with strong AO activity from plant by-products. For example, β-galactosidase releases isoflavone and oleuropein aglycone while tannases generate propylgallate [16].

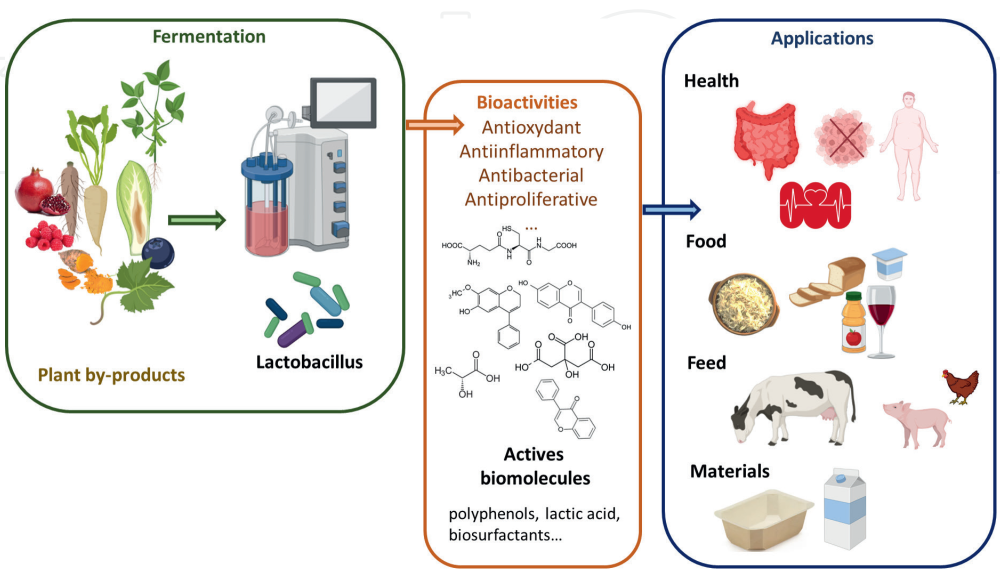


**Figure 1.**
*Summary of the biomolecules, bioactivities generated by the fermentation by* Lactobacillus *strains of plant products or by-products, and their application domains.*

Glycosylated polyphenols such as tannins, lignans, isoflavones, flavonols, and anthocyanins are widespread in plant products. Absorption in the intestine depends mainly on their degree of glycosylation. Some strains of *Lactobacillus,* such as *L. plantarum*, possess glycosidases that are crucial for the absorption of glycosylated polyphenols and consequently for the resulting AO activity [19]. In most cases, the AO activity is studied with classical biochemical antioxidant assays such as 2,2-diphenyl-1-picrylhydrazyl (DPPH), 2,2'-azino-bis (3-ethylbenzothiazoline-6-sulfonic acid) (ABTS), hydrolxyl or alkyl radical scavenging activities, the ferric-reducing antioxidant power (FRAP), superoxide dismutase (SOD) -like activity, β-carotene bleaching, and oxygen radical absorbance capacity (ORAC). In addition to *in vitro* biochemical tests, other studies have investigated the antioxidant capacity of fermented products with *in vitro* cell-based assays. Reference [16] demonstrated that the fermentation of *L. plantarum* increased the AO properties of a kiwi extract. They correlated this result with increased amounts of protocatechic and chlorogenic acid in the fermented products, which were less represented in the starting extract [20]. Gallic acid production was also observed with the fermentation of red chicory leaves by *L. plantarum* et *L. hilgardi* thanks to tannases [21]. In addition, co-fermentation by *L. gassieri* and *Bifidobacterium animalis* resulted in the release of caffeic acid and conjugated chlorogenic acid after fermentation of sunflower seeds through the action of cinnamoyl esterase. Tannins are also the product of biomass fermentation by *Lactobacillus.* Tannases hydrolyze the ester bond, and gallate decarboxylase converts gallic acid to pyrogallol; thus, *Lactobacillus* generates gallic acid, glucose, and pyrogallol [22].

Several studies have illustrated the fermentation of plants such as Indian chilli pepper, grape pomace, dandelion beverage, and cereal-based plant beverages by *Lactobacillus spp*., resulting in polyphenol compounds (caffeic acid, succinate, pyruvate, pyroglutamate) with AO capacity [23–25]. In [26], they evidenced that rice bran and wheat bran fermented with *L. plantarum* possessed AO capacity through their hydroxyl and oxygen radical scavenging activities. Furthermore, the purified fractions exerted reactive oxygen species (ROS) scavenging activity in HUVEC cells and decreased the senescence of the cultured cells, also conferring an antiaging activity to the fermented fractions. These activities were attributed to the acids and ketones [26]. Co-cultivation of *L. johnsonii* and *Bacillus coagulans* was undertaken in [27] to produce a soybean meal with improved AO properties. Interestingly, the co-cultivation resulted in a significant increase in total phenolic content [27]. Fruits are also an excellent matrix for fermentation due to their high content of dietary fiber, sugars, vitamins, minerals, and phenols. Furthermore, lactic fermentation preserves and improves food safety, nutritional value and preserves the organoleptic quality. In particular, when plants are fermented by *Lactobacillus* endophyte, it preserves of color, firmness, AO activity, growth of fermentation starters and inhibits pathogens in media. Many studies have been conducted on the lactic fermentation of polyphenol-rich berries and red fruits. *L. casei* has been studied for the fermentation of blueberry pulp [28]. In another example studied in [29], mulberry juice fermented in coculture by three different strains (*L. plantarum, L. acidophilus*, and *L. paracasei*) showed a higher AO capacity [29].

In reference [30], they investigated the fermentation of cherry silverberry fruits (*Elaeagnus multiflora Thunb*.) fermented with pure cultures of *L. plantarum* KCTC 33131 and *L. casei* KCTC 13086 alone or in mixed culture. In reference [31], they studied the fermentation by *L. plantarum* FNC 0027 of Jamaican cherry (*Muntingia calabura Linn.*), which induces the production of phenolic compounds and the inhibition of diabetic-related enzymes (α-glucosidase, α-amylase, and amyloglucosidase). They demonstrated the production of gallic acid, 5,7 dihydroxyflavone, and dihydrokaempferol [31].

The valorization of argan press cake was also carried out by lactic acid fermentation using a specifically isolated strain of *L. plantarum* Argan-L1. Argan press cake is a waste of oil production containing polyphenols and saponins. The authors demonstrated that sucrose from argan press cake was easily converted to lactic acid during the fermentation process. Furthermore, the fermented extract presented an increased AO capacity, but the total phenolic compound was slightly decreased [32].

*L. plantarum* KCCM 11613P isolated from Kimchi allowed the production of ginsenosides after fermentation of Korean red ginseng (*Panax ginseng*) [33]. In reference [34], it was shown that fermented soymilk products exhibited improved AO capacity associated with increased isoflavone aglycone content. In addition, fermented extracts inhibited the DNA oxidation induced by the Fenton reagent [34]. All these studies show the interest in using *Lactobacillus* to increase the antioxidant properties of fermented products. Moreover, this antioxidant activity is often associated with the anti-inflammatory activity of certain extracts. Fermentation of other plant matrices can induce antioxidant activity of the products, as shown in **Table 1**.

### 2.2 Anti-inflammatory activity

Vegetables, fruits, and plants (tomato, cucumber, pear, apple, mandarin, parsley, carrot, celery, onion, burdock, kale, spinach, aloe vera, civet, grape, jujube, cabbage, and perilla) fermented by *L. plantarum* offer interesting AI molecules [51]. These molecules include organic acids (OAs) such as lactic acid, 3-phennyl-lactate, indole-3-lactate, β-hydroxybutyrate, gamma-aminobutyric acid (GABA), and glycerol. When investigating the AI (and AO) capacity of these compounds, the parameters studied werethe levels of nitric oxide (NO), IL-6 (interleukins) and tumor-necrosis factor-alpha (TNF-alpha), and the DPPH test on RAW cells [52]. Another study showed the AI properties of a fermented plant extract (*Artemisia capillaris*) in RAW 264.7 cells, which stimulated NO and IL-10 secretion without cytotoxic effects [53]. Thus, the fermentation of *Aronia melanocarpa* extract by *L. plantarum* was investigated to produce GABA, polyphenol, and flavonoid compounds. The fermented extract was shown to exert AI effects inhibiting the production of proinflammatory cytokines in RAW 264.7 cells and modulating the immune response in mice [54]. Furthermore, several molecules derived from the fermentation of red fruit juices have been studied for their AI effects. For example, anthocyanins from these products are thought to produce the TNF-alpha and proinflammatory cytokines [23].

Fermented Asian products were highly investigated for their AI properties. For example, a specific strain of *L. plantarum* is involved in the fermentation of the traditional korean fermented vegetable food, the kimchi. It has been shown to secrete exopolysaccharides able to protect against rotavirus-induced diarrhea [55]. Turmeric, another plant originating from Asia, has been also extensively studied for its AI properties and particularly after fermentation. The development of turmeric extracts with potential health applications, particularly for inflammation, is increased.

The production of curcuminoid molecules, such as curcumin, has been enhanced by fermentation of turmeric (*Curcuma longa*) by *L. johnsonii*. The turmeric extracts showed AI and antiallergic effects in atopic dermatitis mice and induced a decrease in serum immunoglobulin E and proinflammatory cytokines in lipopolysaccharide-induced inflammation (LPS) [56]. Supplementation of turmeric extract fermented by *L. rhamnosus* (GG-ATCC 53103) and *Bifidobacterium animalis* (BB12) strains maintained bacterial growth of the gut microbiota in case of inflammation.

| **By-product used** | *Lactobacillus spp.* | **FP** | **Product generated** | **Bio activity** | **Remark** | **Reference** |
|---|---|---|---|---|---|---|
| Apple juice | *L. plantarum* | LF | PC | AO | | [35] |
| Apple juice | *Saccharomyces cerevisiae,* then *L. plantarum* | LF | PC, OA | AO | | [36] |
| Margosa (*Momordica charantia L.*) | *L. plantarum* NCU116 | LF | SCFA<br>LA<br>PC | AO | Juice's sterilization exerted adverse effects | [37] |
| Porcelain plant (*Graptopetalum paraguayense E. Walther)* | *L. plantarum* BCRC 10357 | LF | PC | AO | Assayed during the maturity of the leaves | [38] |
| Milled wheat | *L. plantarum+ Streptococcus thermophilus* | LF<br>Co | PC | AO, AM, PB | Anti-burning properties | [39] |
| Apple by-products | *L. plantarum* | LF | PC | AO, barrier integrity | Caco-2 | [40] |
| Mango | *L. plantarum + Saccharomyces cerevisiae* | SB<br>Co | Mango slurry, PC | AO | | [41] |
| Liquorice root | *L. plantarum* | SBF | PC | AO | | [42] |
| Jussara pulp (*Euterpe edulis*) | *Lactobacillus and Bifidobacterium* | LF<br>Co | OA: protocatechic acid | AO | Conversion of anthocyanins | [43] |
| Acerola | *L. acidophilus +Bifidobacterium longum* | BF | beverage | PB | ↗resistance of PB to gastrointestinal digestion | [44] |
| Cauliflower & white beans mix | L. plantarum 299 | SBF | Riboflavin, Folate, Vitamin B12, AA | | Nutritional value | [45] |
| Wheat germ | L. plantarum + L. rossiae | LF | Bread rich in PC, phytases | AO | ↘ anti-nutritional factor, ↗ protein digestibility | [46] |
| Date juice | *L. casei subsp. rhamnosus* | LF | LA | | Nitrogen source optimization | [47] |
| Date juice | *L. sp.* KCP01 | LF | LA | | Medium optimization | [48] |

| By-product used | *Lactobacillus spp.* | FP | Product generated | Bio activity | Remark | Reference |
|---|---|---|---|---|---|---|
| Solid carob | *L. rhamnosus* | BF | LA | Many diseases | Immobilization in alginate beads | [49] |
| Banana, papaya, pineapple, orange | *L. plantarum* | BF | LA | | Best LA's production for banana et pineapple | [50] |

*AI: Anti-inflammatory; AM: antimicrobial; AO: AO; BF: batch fermentation; Co: coculture; EPS: exopolysaccharides; FP: fermentation process; IL: interleukins; IM: immune-modulatory; LA: lactic acid; LF: liquid fermentation; NO: nitric oxide; OA: organic acids; PB: prebiotic effect; PC: phenolic compounds; SBF: solid batch fermentation; SCFA: short-chain fatty acid; and SF: solid fermentation.*

**Table 1.**
*Other studies that complement the in vitro examples cited in this chapter.*

It also reduced the inflammatory state by limiting the production of proinflammatory cytokines IL-8 [57]. Another study showed that the fermentation of turmeric by *L. fermentum* has increased the curcumin yield by 9.76%. The AI activity was demonstrated in RAW 264.7 cells by modifying the nitrite level, the expression of TNF-alpha and TLR-4, and the activation of the JNK pathway. These phenolic compounds also showed a protective effect against the activation of TLR-4 receptor cascade, TNF-alpha, and nitric oxide production. In addition, the extract limited the proinflammatory response and low-grade oxidative stress induced by LPS [58].

### 2.3 Antimicrobial activity

The molecules produced during the fermentation of plant biomasses by *Lactobacillus* can also exhibit antimicrobial activities. The production of antimicrobial molecules by *Lactobacillus* has already been described, including lactobrevin and lactobacillin [59]. For example, in [60], an interesting concept of valorization of okara by solid-state fermentation was presented with a coculture of the yeast *Yarrowia lipolytica* and *Lactobacullis casei*. Okara is an oleaginous by-product of plant milk production. The authors used fermentation to generate molecules with antimicrobial activity (up to 33% reduction of *Bacillus subtilis* development and a modest effect on *Aspergillus niger* one) [60].

In reference [61], a metabolic study on *Allium tuberosum* to produce a food additive with antimicrobial activity against poultry pathogens was conducted. Endophytic *Lactobacillus* have been isolated from Chinese chives. Among those *Lactobacillus* strains, *L. plantarum* can produce flavonols with antimicrobial activity [61]. In [62], fermentation of quinoa by the strain *L. plantarum* CDL 778 leads to a higher production of antifungal compounds. It was also observed that during the fermentation of sweet lemon juice (*Citrus limetta*), the antimicrobial activity against *Escherichia coli* and *Salmonella Typhimurium* was increased. These activities were correlated with the increase in lactic acid content and the decrease of citric acid, total phenolic compounds, and sugar content [63]. Moreover, fermentation of the red sorghum cereal allows the conversion of flavanones into eriodyctiol and naringenin, which have shown an interesting antimicrobial activity [22].

### 2.4 Prebiotic activity

Several studies have shown that fermented fruits and vegetables have prebiotic effects. The compounds produced by the fermentation of plants induce a modification of the intestinal microbiota. These fermented extracts offer great prospects. Studies highlighted their health potential for humans but also animals. Indeed, two fermented extracts obtained from algae and chicory, plantain, alfalfa, and broad leaf dock presented prebiotic and AO effects. This study was conducted on weaned lambs, and the results showed improved resistance to infection and survival for both extracts. Similar studies have shown the same effects for thyme and rosemary [64]. In reference [65], the prebiotic potential was determined, and the AI effect of chicory root and pulp compared with inulin, as a positive control, on the intestinal barrier on IPEC-J2 cells. These tests were performed with five fermented by-products (chicory roots, chicory and citrus pulp, rye bran, and soybean bark) by different *Lactobacillus spp.* An increase of *Lactobacillus* spp. was observed for all substrates except for chicory roots. The latter was very fermentable and produced a butyrate ratio similar to that of inulin, while chicory pulp had a higher ratio than inulin. For acetate, chicory and citrus pulp and soybean bark had a higher ratio than inulin. These short-chain fatty acids (SCFAs) derived from dietary fiber fermentation contribute to maintain intestinal health. Rye bran caused a significant stimulation of the growth of *Bifidobacterium spp.* Rye bran and soybean bark have a positive effect on the gut microbiota. Fermented chicory roots and pulp promote the upregulation of tiny junction genes and maintain the integrity of the gut barrier. Finally, fermented chicory pulp inhibits proinflammatory cytokines such as TNF-alpha and triggers the metabolic pathway that inhibits inflammatory cytokine production [65].

### 2.5 Other bioactivities related to medicine

Many bioactivities could result from the lactic fermentation of plant by-products. In reference [66], they associated the AO activity with potential hypoglycemic effects of *Diospyros lotus* fruit fermented by *L. plantarum* and *Microbacterium flavum*. They observed an inhibition of the α-glucosidase activity *in vitro*. In addition, the authors showed that catechinic, tannic, and ellagic acid levels were enhanced during fermentation [66]. Similarly, several studies were interested in the capacity of *Lactobacillus* fermented products to exert a positive effect in the prevention of obesity and associated metabolic diseases. In [67], cabbage-apple juice fermented by *L. plantarum* exerted anti-obesity and hypolipidemic effects *in vivo* in high-fat diet–fed rats was highlighted [67].

Moreover, soy products fermented with *Lactobacillus spp.* have interesting biomolecular contents and present antitumoral effects. Indeed, these fermented soybean extracts could inhibit, *in vitro,* the growth of several cancerous cell models: fibrosarcoma and adenocarcinoma of the breast. It also reduces the risk of breast cancer, significantly influencing survival, apoptosis, and tumor inhibition rates in mice. Clinical studies were also conducted to investigate the effects of fermented soybean extract on chemotherapy-induced immunosuppression. The results showed that the populations of immune cells with activity against tumor cells, the natural killer cells, are significantly increased [23]. Using cell-based experiments, other work has investigated putative health effects associated with AO activity. Indeed, the authors showed promising antiproliferative and apoptotic effects of the extracts on the HeLa cancer cell line. In another study, the authors showed that blueberries fermented by *L. plantarum* exhibited anticancer activities. Their results suggest that polyphenols, in high concentrations in blueberries, were metabolized during fermentation into active phenols such as catechol [68].

## 3. Applications

### 3.1 Food products

Product of the lactic fermentation, bread has been, for a longtime, an important foodstuff of the diet of many cultures. The bread fermentation process has often been optimized and revisited to better meet consumer needs or to address economic and social issues. The fermentation of wheat leaven by *L. plantarum* allows the conversion of ferulic acid into vinyl guaiacol, ethyl guaiacol, and dihydro ferulic acid. This conversion improves the quality of the final bread product [22].

Corn flour is another example of a bread raw material, and its application in bakery illustrates the potential of lactic fermentation. In addition to the different ingredients of wheat bread, maize meal improves the nutritional profile after being fermented with *L. plantarum* T6B10 and *Weissella onfuse* BAN8. Indeed, an increase in amino acid (AA) and protein content, AO activity, and inhibition of lipases and phytic acid were observed. This leads to an increase in dietary fiber, digestibility, and improves the texture, taste, and nutritional value of bread [69]. The same outcome was observed with the fermentation of brans from hullless barley, emmer and pigmented wheat varieties with the same *Lactobacillus* under the same conditions [70]. Another study highlighted the replacement of wheat flour substitute for breadmaking, a sourdough obtained from fermented djulis (*Chenopodium formosanum*) by *L. casei*. The bread produced contained higher levels of total phenolic and flavonoid compounds and increased hardness and chewiness compared with conventional bread. The addition of djulis sourdough also extended the shelf life by approximately 2 days [71].

A process to valorize semolina pasta with hemp flour, chickpea grains, and milling by-products by fermenting them with *L. plantarum* and *L. rossiae* has been proposed [72]. However, it is necessary to note that enzymatic pretreatment of the substrates must be carried out beforehand. This could affect the economic viability of the process. At a laboratory scale, they obtained extensive protein degradation and consequently digestibility, a 50% reduction in tannin concentration and also in phytic acid concentration [72]. *L. plantarum,* which has high proteolytic activities, was used for the fermentation of quinoa instead of wheat. Quinoa is an interesting cereal for celiac patients because it is gluten-free. The study revealed that quinoa is more easily fermented by lactic acid bacteria than wheat. These high proteolytic activities of the strain were evidenced by the increase of the total peptides and free AA contents from quinoa slurries compared with wheat slurries [62]. In reference [70], the potential use of oat extract from cereal processing with high protein content as an alternative to yoghurt was questioned. Fermentation of this by-product with *L. delbrüchii* subsp. *Bulgaricus* and *Streptococcus themophilus* followed by starch gelatinization by heating generated two kinds of gels with interesting rheological and organoleptic properties. Authors placed their studies in the context of plant-based products substituting dairy ones for health and environmental reasons. They discussed the consumer acceptance of these products but claimed that sensory descriptors such as soft, sweet, and smooth are highlighted by the sensory panel [73]. Another example of food products fermentation value is the fermentation of olive by *L. plantarum*. Kachouri et al. have shown that the phenolic content of olive oil increases after fermentation by this strain [74]. Other studies have shown that the fermentation of the common Spanish table olive improves preservation and the taste. Indeed, *L. plantarum* ferments olive brine, leading to a reduction in the oleuropein content of the olives [75–79]. In addition, wastewater from olive production, which is another olive coproduct, has been exploited in [80]. When fermented by *L. plantarum*, the content of phenolic compounds becomes more interesting. The antioxidant activity was tested by DPPH and ABTS assay. This coproduct has a 50% higher antioxidant activity after fermentation by *L. plantarum* [80].

In order to innovate in the food market, research is being carried out into the development of plant-based drinks rich in active compounds and with health benefits for consumers. Functional plant beverages fermented with *Lactobacillus* are being widely studied. Aqueous extracts of plants such as soy, pea, coconut, or rice represent alternatives to nondairy milk. Lactic acid fermentation of these beverages could improve the protein content, solubility, and availability of AA. Some strains of *Lactobacillus* are also responsible for the biosynthesis of vitamins during fermentation (vitamin K, vitamin B). Anti-nutritional compounds such as phytates are hydrolyzed during fermentation by some phytase-producing strains, which improves the digestibility and mineral content of the final product [81]. However, optimizing flavors and nutritional quality remains a challenge today because the latter are often criticized for their low nutritional quality and bland taste caused by their short shelf life. A color change has been observed by Do and Fan in fruit or carrot juices fermented by *Lactobacillus* strains, indicating that carotenoids are modified to cis-carotenoid isomers responsible for color change during fermentation by *Lactobacillus* [82]. Rheological studies have also been performed. Indeed, in [83], the effects of different *Lactobacillus* species on volatile and nonvolatile flavor compounds in juices fermentation were studied. The main objective of this research was to identify the marker metabolites generated by different species of *Lactobacillus* strains, which contribute to the flavor and reveal the roles of various *Lactobacillus* species in the formation of flavor compounds. The main markers were 2.3 butanedione, hexenal, acetic acid, formic acid as volatile compounds and lactic acid, malic acid, citric acid as nonvolatile compounds [83].

In another application for the beverage sector, one of the main ideas is to provide fermented products with prebiotic effects from a different matrix of vegetable juice as raw material. Consumers' demand for non-dairy prebiotic foods is constantly increasing due to drawbacks related to dairy foods such as allergy, lactose intolerance, as well as lifestyle change or religious beliefs. In this context, reference [71] presents a development of a functional drink based on soy and quinoa (*Chenopodium quinoa Willd*) obtained by fermentation by *Lactobacillus casei* LC-1. This drink presents a prebiotic effect stimulating the gut microbiota and reducing the following bacterial populations: *Clostridium spp, Bacteroides spp, Enterobacteria, and Enterococcus spp* [84]. Cabbage juice and fresh cabbage, fermented by *Lactobacillus*, are also being studied for the development of probiotic products. When mixed with other vegetables (carrots, onion, cucumber), white and red cabbage fermented with *L. plantarum, L. casei , L. acidophilus,* or *L. delbrueckii* shows a good fermentation profile and potential as a functional probiotic drink as demonstrated by Hyunah et al. [85–88]. Dunkley and Hekmat evaluated the sensory properties and worked to assess the growth and viability of *L. rhamnosus* GR-1 in carrot juice, carrot apple juice, carrot orange juice, and carrot beetroot juice over 72 h of fermentation and 30 days of refrigerated storage at 4°C. The conclusion was that carrot, carrot apple, carrot orange, and carrot beetroot juice fermented with *L. rhamnosus* GR-1 proved to be a satisfactory alternative to dairy-based prebiotic products. All juices achieved viable counts above the minimum counts required to be classified as prebiotic. The results of sensory evaluation also indicated a market potential for prebiotic vegetable juice. The development of prebiotic vegetable juice using *L. rhamnosus* GR-1 as a probiotic agent will provide consumers a viable non-dairy alternative that can provide many health benefits [89]. Co- or triculture can be used to enhance activities. Bergamot juice was fermented by three *Lactobacillus* (*L. plantarum* 107 subsp *plantarum* PTCC 1896, *L. plantarum* AF1, *L. plantarum* LP3) in triculture. This combination resulted in a higher AO activity. Bergamot juice fermented could also be used as a functional drink [90].

Other by-products are recycled, especially in the brewery sector. One study aimed to produce a polyphenol-rich beverage from brewers' spent grain. Fermentation by *L. plantarum* ATCC 8014 was realized, followed by tests on phenolic compound content and AO activity. Phenol content and AO have increased during fermentation. The beverage was more concentrated in phenolic compounds than before fermentation, and its bioactive compounds were more stable [91]. More recently, coffee cherry pulp has been used in infusion to obtain an AO drink called cascara. To improve the AO activity of this beverage, it was fermented by endophytic *L. casei* [92]. A turmeric-based functional drink was also obtained by co-fermentation with *Enterococcus faecium, Lactococcus lactis subsp. Lacti, and L. plantarum*. The AO capacity was measured by titration of total phenolic compounds, and the prebiotic effect was also highlighted by *in vitro* and *in vivo* tests.

Kombucha is a sweet infusion of green tea leaves usually fermented with Kombu, a fungus. One study shows that replacing Kombu with *L. casei* and *L. plantarum*, which are derived from kefir, enhances the production of glucuronic acid, leading to greater antimicrobial and antioxidant activities [93]. Another study showed that a mixture of LAB from kefir and kombucha (*L. casei, L. plantarum*, *L. acidophilus. L. casei,* and *L. plantarum*) increases the glucuronic acid concentration, antimicrobial and antioxidant activities and allows the use of Kombucha as a health drink [94]. Hou et al. demonstrated the link between antimicrobial activities of kombucha with polyphenols and LAB, especially against *Escherichia coli, Salmonella tiphy, Vibrio cholerae,* and *Shigella dysenteriae* [95]. Green tea used in Kombucha may have activity when fermented by *L. plantarum*. Indeed, fermented extract derived from *Camellia sinensis* is able to mitigate ethanol-induced liver damage. *In vitro* and *in vivo* tests on hepatic cells (HepG2,) and murin model exposed to fermented green tea extract show after exposure of ethanol a better viability and an increase of hepatic alcohol dehydrogenase [96].

### 3.2 Livestock feeding

The products of plant fermentation by *Lactobacillus* strains can be used in many fields ranging from livestock feeding, such as ruminant by decreasing gas production [97]. *Lactobacillus* strains can also be used for silage preparation. Silages are grass or other green fodder that is compacted and stored under airtight conditions, typically in a silo, for use as livestock feeding in the winter. Many studies focus on using *Lactobacillus* strains to improve the quality of the silage. In reference [98], the effect of *L. brevis* and *L. parafarraginis* used as inoculants and the microbial communities of corn stover silage were studied. After 20 days, the two *Lactobacillus* strains were predominant, and a reduction in lactic acid content coupled with an increase in acetic acid and 1.2-propanediol contents was observed. An improvement in the silage quality and reproducibility of the ensiling process were observed [98]. Recently in [99], the effect of *L. plantarum* addition on the nutritive value of dwarf elephant grass (*Pennisetum purpureum* cv Mott) silage was presented. The aim was to examine the effects of different *L. plantarum* addition on the physical quality, pH, and nutritional value (dry matter, organic matter, crude protein, crude fiber). After incubation, a good silage quality (fresh and acidic odor, good texture, and no fungi) and a pH around 4 were observed. *L. plantarum* addition accelerates ensilage fermentation [99]. In [100], an increase in silage quality by adding waste molasses to *L. plantarum* MTD1 was observed. In the same context, the addition of cellulase was studied to evaluate the effects on the chemical composition, bacterial communities, stability of mixed silage made with high-moisture amaranth and rice straw fermented by *L. plantarum*.

Cellulases increased the abundance of *Lactobacillus* bacteria and reduced the abundance of other lactic acid bacteria. It decreased pH, acetic acid content, ammonia nitrogen content and increased lactic acid concentration after 7 days of ensiling [101]. In conclusion, silage treated with both *Lactobacillus* bacteria and cellulase showed the best silage quality. Optimizing the digestibility of feeds and thus increasing their nutritional value are a challenge for the livestock feeding industry. In another study, the fermentation product of a mixture of ginger and turmeric extract by *Lactobacillus* spp. was supplemented to chickens. Biological analyses of AO enzymes and analysis of gut microbiota and lymphoid organs showed a prebiotic effect, an AO effect, and an improvement in resistance to bacterial infections [102].

### 3.3 Lactic acid production from plant biomass

The use of low-cost by-products is of primary interest as it reduces production costs compared with the use of complex culture media made with pure and refined products. Consequently, many by-products have been tested in the last few years, in association with screening of the best microbial strains, the best fermentation process, and the best conditions to make them work together [103]. Lactic acid is one of the most widely used organic acids for a long time in various industries, such as food, cosmetics, pharmaceutical, and textile industries, and flavor, conservation, AO, and antimicrobial activity [104]. In the last decade, it has also become an essential platform molecule in the biomaterials sector to produce poly-lactic acid (PLA), a bio-based polymer. This new interest has led to an explosion in worldwide demand. One of the characteristics of polylactic acid is its thermal resistance, a critical parameter for manufacturing thermoformed materials (packaging, film, etc.). *Lactobacillus* have been traditionally used for lactic acid production [105, 106]. When using large-scale fermentation bioprocesses, the biomass feedstock must be carefully selected as it accounts for almost half of the biopolymers production costs [105]. To address this production cost issue, scientists and industrials have been focused on lignocellulosic biomass as a fermentation substrate for lactic acid production. Nevertheless, in order to be easily usable, saccharification pretreatments are needed to break down the cellulose into fermentable carbohydrates. Moreover, *Lactobacillus* are classified as either homofermentative or heterofermentative. *L. delbrueckii* is a homofermentative strain commonly used for the production of lactic acid [107]. Homofermentative strains of *Lactobacillus* cannot use pentose carbohydrates from hemicellulose, but heterofermentative ones, such as *L. brevis*, can use these carbohydrates through the phosphoketolase pathway [106].

In reference [105], the fermentation of 11 different carbohydrates from seaweed or plant biomass as a carbon source to produce L-lactic acid with seven different *Lactobacillus* species was investigated. A comparative analysis of the expected yield of lactic acid production revealed that seaweeds provided comparable production rates to lignocellulosic biomasses [105]. In another study, beet molasse was used to produce lactic acid using *L. delbrueckii* IFO 3202 during batch and continuous fermentation, dilution rate of 0.5 $h^{-1}$ was determined to be the best one and allowed to reach a maximum productivity of 11 g $L^{-1}$ $h^{-1}$. Authors have demonstrated the importance of medium supplementation by yeast extract, as Lactobacilli are tedious microorganisms that require many substrates and substances to grow [108]. Nevertheless, it is estimated that the addition of yeast extract can contribute up to 30% of the cost of producing lactic acid [109]. Zhang & Vadlani studied the production of D-lactic acid by a homofermentative strain, *L. delbrueckii* ATCC 9649, through a sequential hydrolysis and fermentation process (SHF) and a simultaneous saccharification and fermentation process (SSF). In this work, first, the saccharification of pulp and corn stover was done, and then carbohydrates generated from hydrolysis were used by *L. delbrueckii* and converted to D-lactic acid with high purity (99.8 %). The authors highlighted that the SHF process, compared with the SSF process, avoids substrate inhibition and increases the productivity and the yield of D-lactic acid [107]. The same researchers' team has then engineered a strain of *L. plantarum*, introducing gene encoding isomerase and xylulokinase, for the overproduction of D-lactic acid from corn stover and soybean meal extract. In this work, the authors optimized the culture medium through response surface methodology using saccharified corn stover as carbon source and soybean meal extract as a nitrogen source to substitute YE in the medium to produce high purity of D-lactic acid (99%). A maximum productivity of 0.82 g $L^{-1}$ $h^{-1}$ of D-lactic acid was obtained in the optimized medium, 10% higher than with YE as the main nitrogen source [106].

Saccharification and fermentation could be performed at the same time (simultaneous saccharification and fermentation) and have been used for instance by Tu et al. for LA production. With *L. plantarum*, they obtained up to 65.6 g $L^{-1}$ of lactic acid with a cellulose conversion of 69% [110]. Using inulin from chicory, in [111] they obtained a better performance by simultaneous saccharification and fermentation to produce D-lactic acid with *L. bulgaricus*. In their process, they obtained an optically pure molecule (99.9%), which could be interesting for further chemical processes. Productivity is also high with 123 g $L^{-1}$ starting from 120 g $L^{-1}$ of inulin treated by inulinase. The enzymatic treatment yielded inulin, which was used instead of glucose in MRS medium for fermentation [110, 111].

In another example, lactic acid production from fermented orange peels was evaluated by ion-exchange chromatography. The solid fermentations were in mono or coculture, with *L. casei* 2246, *L. plantarum* 285, and *L. paracasei* 4186. This study showed that fermentation resulted in higher lactic acid production with the monoculture *L. casei* 2246 and the coculture *L. casei* 2246 with *L. plantarum* 285. Glucose can also be converted to lactic acid by symbiotic relationship between different lactic acid bacteria. *L. helveticus* is an AA-producing strain (alanine, serine, aspartate, glutamate, aromatic AA, and histidine), whereas *L. delbrueckii* is a lactic-acid-producing strain but produces little of these AAs necessary for its growth. Thus, this co-fermentation optimized the lactic acid yield [104]. Before industrialization of such a process, scale-up has to be demonstrated and downstream processes (purification) to be implemented and considered. However, another technology could also be used for lactic acid production by microorganisms. Indeed, solid-state fermentation was used with cassava bagasse as substrate and *L. delbruechii* as microorganism [103, 112].

### 3.4 Other applications of active ingredients produced from fermented plant extracts

Another biotechnology application is the production of proteins, peptides, or AA such as GABA. Indeed, plant by-products are sources of different proteins, which can be hydrolyzed during fermentation by *Lactobacillus* species. These microorganisms, especially *L. plantarum,* have developed a proteolytic system to satisfy their nitrogen requirements. The proteolytic activities and protein hydrolysis patterns are very different from one strain to another. The resulting peptides displayed different biological functions such as angiotensin-converting enzyme inhibition, mineral binding, antidiabetic, satiating, immunomodulating, opioid, AO, or antimicrobial activities [12]. The *L. plantarum* LP-9 strain was used to coproduce GABA and lactic acid from agri-residues such as wheat bran, rice bran, corn bran. The results were compared with the use of cassava (starchy food crop), and the production yields were significant and comparable to this control condition [113]. Co-fermentation of Ginseng root and leaf extract always by *L. plantarum* EJ2014 and *B. subtilis,* also showed GABA production [114]. The fermentation of Kimchi by *L. brevis* BJ20 allows the conversion of glutamic acid into GABA. This process is particularly interesting because GABA has an AO activity demonstrated during the study of DPPH scavenging, superoxide scavenging, and xanthine oxidase inhibition tests [115]. Biotechnology also allows production of cosmetic or pharmaceutical products or surfactants. Biosurfactants production was investigated using *L. paracasei* on enzymatically hydrolyzed vineyard pruning waste. This study presented the complete process for this waste valorization using acid hydrolysis, delignification, and enzymatic hydrolysis steps. Authors have demonstrated the impact of the carbon source extraction process on the biosurfactant composition produced by the strain *L. paracasei* A20 [116].

## 4. Limitations and future challenges

Faced with environmental and societal problems such as pollution, global warming, and overpopulation, crop yields are increasingly challenging to sustain. Moreover, while demand is increasing in developed countries, poor populations are struggling to feed themselves, and undernutrition is high in these countries. This is why the food and agriculture industry must find solutions to meet the needs of all. Among these, better use of plant resources and better exploitation of their by-products are two solutions of interest. In addition, consumers are looking for more natural and healthy products, and industrials are looking for economically viable bio-based solutions. Fruit and vegetable waste and cereal by-products are likely to be reused because of their quantity and richness in nutrients and bacterial strains suitable for lactic fermentation.

When lactic acid bacteria ferment the nutrients in them, the functional and nutritional properties increase, representing significant opportunities for the agri-food, biotechnology, medical, nutraceutical, and cosmetic industries. As presented in this chapter, the fermentation of plant products by *Lactobacillus* allows the production of numerous bioactive molecules for the development of many applications. Nevertheless, to meet the demand, lactic acid fermentation by *Lactobacillus* requires optimization. First of all, the use of plant by-products requires a crucial design of the fermentation process according to the raw material (solid, liquid, semiliquid fermentations). This design could lead to the development and emergence of new processes that should be able to meet industrial viability, economic returns, and consumer needs. Therefore, much work is still needed on these processes to increase the commercialization of new bio-based products from plant by-products. On the other hand, *Lactobacillus* strains are fastidious bacteria in their nutritional requirements and are not necessarily well adapted metabolically for growth from any substrate, and the use of GMOs is a very limiting criterion for many applications (food, cosmetics, etc.). The growth parameters and enzymatic activities of *Lactobacillus* strains have a major impact on applications, particularly when the fermentation substrate is complex. It is therefore necessary to work on the culture conditions and metabolic adaptation of these strains in order to maximize the enzymatic activities and production rates of the molecules of interest. Therefore, many constraints exist, such as the lack of scientific data and hindsight, the control of culture conditions, and the separation and purification processes to recover bioactive compounds. Further efforts are urgently needed to overcome these problems. Nevertheless, one of the advantages of production with *Lactobacillus* is its ability to produce several types of molecules simultaneously, typically lactic acid and other molecules (derived or transformed from the substrate), which makes the fermentation process industrially interesting. Such multiproduct strategies should be promoted in the near future up to industrial scale.

## 5. Conclusion

Lactic acid fermentation is an ancestral process performed by numerous bacterial strains. Fermentation conditions, substrates, and potential additives represent challenges and constraints for yield optimization, process stabilization, and standardization. Indeed, lactic fermentation by *Lactobacillus* allows the production of many molecules of interest. When these bacteria ferment plant products, they induce biochemical conversions and the production of phenolic compounds, organic acids, and vitamins through their enzymatic activities. This review highlights the different applications related to the production of these compounds. The latter have bioactivities such as AO, AI, prebiotic, antimicrobial, and many others.

In addition, they are of growing interest to the food industry for their ability to increase nutritional value but also for their use as preservatives and modifiers of organoleptic properties. The different studies reviewed here are looking for alternatives to meet environmental and social consumer demand. In order to reduce production costs and the carbon footprint of the process, genetic engineering and the revalorization of plant by-products appear to be interesting avenues of research to improve the yield of compounds of interest. However, there is still a lack of scientific data on the control of fermentation by *Lactobacillus.* Further studies are needed to identify the biochemical reactions and metabolism of *Lactobacillus* involved in the production of bioactive compounds. In addition, studies are needed to further investigate the mechanisms involved in the bioactivities of interest.

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## Acronyms and abbreviations

| | |
|---|---|
| AA | Amino acids |
| ABTS | Acid 2,2'-azino-bis(3-éthylbenzothiazoline-6-sulphonique) |
| AI | Anti inflammatory |
| AM | Anti-microbial |
| AO | Antioxidant |
| BF | Batch fermentation |
| Co | Coculture |
| DNA | Deoxyribonucleic acid |
| DPPH | 2,2-DiPhenyl-1-PicrylHydrazyl |
| EPS | Exopolysaccharides |
| FP | Fermentation process |
| FRAP | Ferric reducing antioxydant power |
| GABA | Gamma-aminobutyric acid |
| IL-6, Il-10 | Interleukins |
| IM | Immuno-modulatory |
| LA | Lactic acid |
| LF | Liquid fermentation |

| | |
|---|---|
| LPS | Lipopolysaccharide |
| NO | Nitric oxide |
| OA | Organic acids |
| ORAC | Oxygen radical absorbance capacity |
| PC | Phenolic compounds |
| PB | Prebiotic effect |
| ROS | Reactive oxygen species |
| SBF | Solid batch fermentation |
| SF | Solid fermentation |
| SFCA | Short-chain fatty acid |
| TNF-alpha | Tumor-necrosis factor-alpha |

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