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Lactobacillus use for plant fermentation: new ways for plant-based product valorization

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Abstract

Today plant production increases, but most industrial processes generate a lot of waste and by-products for which, in the actual context, it is a priority to re-cycle or valorize. One of the cheapest ways of valorization is fermentation, especially lactic fermentation by *Lactobacillus* species, which produces lactic acid and other molecules of industrial interest such as bioactive compounds like anthocyanin, organic acid, peptides or phenol, widely found in plant matrix mostly in cereals, grass, fruits and vegetables. Bioactive compounds can exert health benefits like antioxidant, anti-inflammatory, antimicrobial or prebiotic activities. Moreover, lactic fermentation can improve existing products and lead to new applications in food, livestock feeding, and biotechnology as lactic acid, proteins or silage production. This chapter reviews the use of *Lactobacillus* strains in the fermentation process of many plant bioresources or plant 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 continues to grow, forecasted to reach 8.3 billion in 2025 and nearly 10 billion by 2050 [1]. Concomitantly, the Earth's resources are depleting. Depending on the different scenarios, global food demand is expected to increase by 40% to 68% by 2050 [2]. Among food resources, plants are at the center of particular interests, with the global production of plant-based products constantly increasing while at the same time producing significant waste. In this context, it's a priority to re-cycle or revalue those by-products [1].

The main objectives of using plant by-products is to revalorize wastes, to reduce pollution and to limit resource depletion. Fermentation represents one of the least polluting methods. Plants by-products fermentation contribute to sustainable development, in fact, this type of valorization intervenes in some goals of the United Nations 2030 Agenda, including the third objective: good health and well-being and the twelfth objective: the responsible consumption and production. Consumption of fermented plant by-products therefore allows responsible consumption. Fermentation of plant by-product leads to bioactivities linked to human health like antioxidant, anti-inflammatory, or antimicrobial activities which are involved in good health and well-being [3]. Plant-based foods are sources of numerous bioactive compounds such as fibers, vitamins, minerals or phenolic compounds. These nutrients are required for organism survival and growth [4]. In many countries, certain plants' health benefits and traditional use have been recognized for decades [5]. Since industries exploit plant-based foods, many agro-industrial by-products that still contain valuable compounds are generated. Many companies are now seeking to re-cycle wastes from their fruit and vegetable activities to address environmental and economic issues. For example, cereal waste reached about 40 000 to 45 000 tons per year in Europe [6]. By-products are mostly used for livestock feeding or methanization 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 represents the most important waste from fruits exploitation. The by-products management represents a real problem of food waste and raise major issues [8] Consequently, in recent years, there is an increasing interest in plant by-products valorization.

In China dating back 9000 years, humans empirically exploited the fermentation process for numerous applications **[9]**. Studied since the 19th 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. Then, fermentation using lactic acid bacteria has been largely studied to improve plants' nutritional and functional properties. 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. Numerous lactic acid bacteria-fermented food products are obtained with organisms belonging to *Lactobacillus* genera **[12]**. With more than 200 species of *Lactobacillus* bacteria **[11]**, this genus is certainly the main and most diverse lactic acid bacteria group. 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 pre-existing genus and 23 new genera). This work showed the wide 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, leading to the liberation of many bioactive compounds, which can be modified structurally or not by the action of other enzymes in the bacteria.

Today, several ecological and economic issues are at the heart of the research surrounding lactic fermentation. The optimization of yield, cost and energy consumption, as well as 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 studied as they represent 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 by 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 the metabolizable molecules thanks to their enzymes, in particular *L. plantarum,* which is one of the most used *Lactobacillus* as a fermentation starter. This degradation increases molecules' bioavailability 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 food industry provide safe product with good nutritional and organoleptic qualities. LAB are used as starter for many products, including fruit, vegetables and cereal products **[18].** As illustrated in figure 1, the production of biomolecules by lactic fermentation of plant by-products can induce other bio-activities. 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.

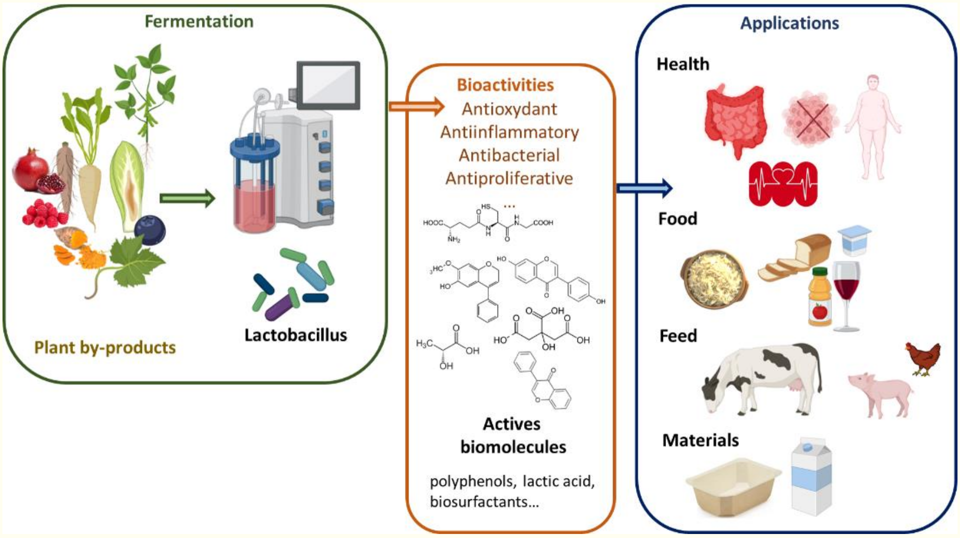

Figure 1: Summary of the biomolecules, bioactivities generated by the fermentation by *Lactobacillus* strains of plant products or by-products and their application domains.

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].

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, thus, the resulting AO activity [19]. In most cases, the AO activity is studied with conventional biochemical antioxidant tests 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 biochemical *in vitro* tests, other studies investigated the antioxidant capacity of fermented products with *in vitro* cell-based assays. In reference [16] demonstrated that the fermentation of *L. plantarum* increased the AO properties of a kiwi extract. They correlated this result with the increased protocatechic and chlorogenic acid amounts in the fermented products, less represented in the starting extract [20]. The production of gallic acid was also observed with the fermentation of red chicory leaves by *L. plantarum* et *L. hilgardi* thanks to tannases [21]. Moreover, co-fermentation by *L. gassieri* and *Bifidobacterium animalis* allowed the release of caffeic acid and conjugated chlorogenic acid after fermentation of sunflower seeds by 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 as Indian chilli pepper, grape pomace, dandelion beverage and cereal-based plant beverages by *Lactobacillus spp*., allowing the obtention of 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 thanks to their hydroxyl and oxygen radical scavenging activities. Furthermore, purified fractions exerted reactive oxygen species (ROS) scavenging activity in HUVEC cells and decreased the senescence of the cultured cells, also conferring to the fermented fractions an antiaging activity. These activities were attributed to the acids and ketones [26]. Co-cultivation of *L. johnsonii* and *Bacillus coagulans* was undertaken in [27] to yield an soybean meal with enhanced AO properties. Interestingly, co-cultivation induced a significant increase in total phenolic content [27]. Fruits are also an excellent matrix for fermentation thanks to their high levels of dietary fiber, sugars, vitamins, minerals and phenols. Furthermore, lactic fermentation preserves and improves food safety, the nutritional value and preserves the organoleptic quality. Especially, when plants are fermented by endophyte *Lactobacillus*, it allows preservation of color, firmness, AO activity, growth’s fermentation starters and inhibits pathogens in mediums. Numerous studies have been conducted on the lactic fermentation of berries and red fruits rich in polyphenols. *L. casei* was studied for the fermentation of blueberry pulp [28]. In another example studied in [29], the mulberry juice fermented in co-culture 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 by pure cultures of *L. plantarum* KCTC 33131 and *L. casei* KCTC 13086 alone or in mixed culture [30]. In reference [31] they studied the fermentation by *L. plantarum* FNC 0027 of Jamaican cherry (*Muntingia calabura Linn.*), which induce the production of phenolic compounds and the inhibition of diabetic-related enzymes (α-glucosidase, α-amylase and amyloglucosidase). They evidenced that gallic acid, 5,7 dihydroxyflavone and dihydrokaempferol were produced [31].

Valorization of argan press cake were also carried-out by lactic acid fermentation using a specifically isolated strain of *L. plantarum* Argan-L1. Argan press cake is a waste from oil production containing polyphenols and saponins. The authors demonstrated that the saccharose from argan press cake was easily converted to lactic acid during the fermentation process. Moreover, the fermented extract presented an enhanced 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] evidenced that fermented soymilk products showed a better AO capacity associated with increased isoflavone aglycone contents. Moreover, the 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 some extracts. The fermentation of other vegetable matrices can induce an antioxidant activity of the products, as shown in the 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 [35]. These molecules include organic acids (OA) such as lactic acid, 3-phennyl-lactate, indole-3-lactate, β-hydroxybutyrate, gamma-aminobutyric acid (GABA) and glycerol. When studying the AI capacity (and the AO capacity) of these compounds, the parameters studied are nitric oxide (NO), IL-6 (interleukins) and tumor-necrosis factor-alpha (TNF-alpha) levels and the DPPH test on RAW cells [36]. Another study showed the AI properties of fermented plant extract (*Artemisia capillaris*) in RAW 264.7 cells, which stimulated NO and IL-10 secretion without cytotoxic effects [37]. Thus, the fermentation of *Aronia melanocarpa* extract by *L. plantarum* was investigated to produce GABA, polyphenol and flavonoid compounds. The fermented extract was evidenced to exert AI effects inhibiting the production of proinflammatory cytokines in RAW 264.7 cells and modulating the immune response in mice [38]. 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 believed to produce the TNF-alpha and proinflammatory cytokines [23].

Fermented Asian products were highly investigated for their AI properties. Thus, a specific strain of *L. plantarum* is implicated in the fermentation of the traditional Korean fermented vegetable food, the kimchi. It secreted exopolysaccharides able to protect against rotavirus-induced diarrhea [39]. Turmeric, another plant from Asia was also the subject of numerous studies 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 was enhanced by the 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) [40]. Supplementation of turmeric extract fermented by *L. rhamnosus* (GG-ATCC 53103) and *Bifidobacterium animalis* (BB12) strains, have allowed the maintenance of gut microbiota's bacterial growth in case of inflammation. It also reduced the inflammatory state by limiting the production of proinflammatory cytokines IL-8 [41]. Another study showed that the fermentation of turmeric by *L. fermentum* have 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 TLR-4 receptor cascade activation, TNF-alpha and nitric oxide production. In addition, the extract limited the proinflammatory response and low-grade oxidative stress induced by LPS [42].

2.3. Antimicrobial activity

The molecules produced during the fermentation of plant biomasses by *Lactobacillus* can also present antimicrobial activities. The production of antimicrobial molecules by *Lactobacillus* has already been described, including lactobrevin and lactobacillin [43]. For example, in [44] an interesting concept of valorization of okara's by solid state fermentation was presented with a co-culture of the yeast *Yarrowia lipolytica* and *Lactobacullis casei*. Okara's 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)[44].

In reference [45], a metabolic study on *Allium tuberosum* to produce a food additive with antimicrobial activity against pathogens poultry was conducted. Endophytic *Lactobacillus* have been isolated from Chinese chives. Among those *Lactobacillus* strains, *L. plantarum* can produce flavonols exerting antimicrobial activity [45]. In [46], fermentation of quinoa by the strain *L. plantarum* CDL 778 leads to a higher production of antifungal compounds was shown. 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 of lactic acid content and the decrease of citric acid, total phenolic compounds and sugars contents [47]. Moreover, fermentation of the red sorghum cereal allows the conversion of flavanones into eriodyctiol and naringenin, which displayed an interesting antimicrobial activity [22].

2.4. Prebiotic activity

Several studies showed that fermented fruits and vegetables harbor prebiotic effects. Compounds produced by fermentation from 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 an improvement of their resistance to infection and their survival, for both extracts. Similar studies showed these same effects for thyme and rosemary [48]. In reference [49], the prebiotic potential was determined and the AI effect of chicory root and pulp compared to inulin, as a positive control, on the intestinal barrier on IPEC-J2 cells. Those tests were realized 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 inulin, while chicory pulp had a higher ratio than inulin. For acetate, chicory and citrus pulp, soybean bark had a higher ratio than inulin. Those short-chain fatty acids (SCFA) derived from dietary fiber fermentation contribute to maintain intestinal health. Rye bran caused an important stimulation on *Bifidobacterium spp.* Growth. Rye bran and soybean bark have a positive effect on the intestinal microbiota. Fermented chicory roots and pulp promote up-regulation of tiny junction genes and maintain the integrity of the intestinal barrier. Finally, fermented chicory pulp inhibited proinflammatory cytokines such as TNF-alpha and triggered the metabolic pathway that inhibits inflammatory cytokine production. [49].

2.5. Other bioactivities related to medicine

Numerous bioactivities could result from the lactic fermentation of plant by-products. In reference [50], 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 [50]. In the same way, 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 [51], cabbage-apple juice fermented by *L. plantarum* exerted anti-obesity and hypolipidemic effects *in vivo* in high fat diet-fed rats was highlighted [51].

Moreover, soy fermented products by *Lactobacillus spp.* Have interesting biomolecule contents and present anti-tumoral 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. 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 works investigated putative other 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, authors have shown that the fermented blueberries by *L. plantarum* displayed anticancer activities. Their results suggest that polyphenols, in high concentrations in blueberries, were metabolized during fermentation into active phenols such as catechol [52].

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 was often optimized and revisited to better meet the needs of consumers or to face 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 allows the improvement of the final bread product quality [22].

Corn flour is another example of bread raw material, and its application in the bakery illustrates the potential of lactic fermentation. In addition to different wheat bread ingredients, maize milling improves the nutritional profile after being fermented by *L. plantarum* T6B10 and *Weissella 8onfuse BAN8*. Indeed, an increase in amino acids (AA) and proteins contents, AO activity, and lipase and phytic acid inhibition have been observed. It leads to increase dietary fiber, digestibility, and it improves the texture, taste and nutritional value of bread [53]. The same outcome was observed with the fermentation of brans from hull-less barley, emmer and pigmented wheat varieties with the same *Lactobacillus* in the same conditions [54]. Another study highlighted wheat flour substitute to make bread, a sourdough obtained from fermented djulis (*Chenopodium formosanum*) by *L. casei*. The produced bread contained higher levels of total phenolic and flavonoid compounds and increased hardness and chewiness compared to classical bread. The addition of djulis sourdough also extended the shelf life by approximately two days [55].

A process to valorize semolina pasta with hemp flour, chickpea grains and milling by-products by fermenting them with *L. plantarum* and *L. rossiae* was proposed [56]. However, it is necessary to note that enzymatic pre-treatment of the substrates must be carried out beforehand. This could affect the economic viability of the process. In a laboratory scale, they obtained extensive protein degradation and consequently digestibility, reduction of 50% of tannins concentration and also of phytic acid concentration [56]. *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 this lactic acid bacteria than wheat. Those high proteolytic activities of the strain were highlighted by the increase of the total peptides and free AA contents from quinoa slurries compared to wheat slurries [46]. In reference [54], the potential use of oat extract resulting from cereal processing and displaying high protein content as yoghurt alternatives 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 such products but claimed that sensory descriptors like soft, sweet and smooth are highlighted by the sensory panel [57]. 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[58]. 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 [59–63]. In addition, wastewater from olive production, which is another olive co-product, has been exploited in [64]. When fermented by *L. plantarum*, the content of phenolic compounds becomes more interesting. The antioxidant activity was tested by DPPH and ABTS assay. This co-product has a 50% higher antioxidant activity after fermentation by *L. plantarum*.[64].

In order to innovate in the food market, research is being conducted into the development of plant beverages rich in active compounds and with health benefits for consumers. Functional plant beverages fermented by *Lactobacillus* are widely studied. Water extracts of plants such as soy, pea, coconut or rice represent non-dairy milk alternatives. Lactic fermentation of these beverages could improve protein content, solubility and AA's availability. Some *Lactobacillus* strains are also responsible for vitamins biosynthesis during fermentation (vitamin K, vitamin B). Anti-nutrient compounds such as phytates are hydrolyzed during fermentation by some phytase-producing strains, which improve the digestibility and mineral content of the final product [65]. 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 fermented fruit or carrot juices by *Lactobacillus* strains, indicating that carotenoids are modified in cis carotenoid isomers responsible for color change during fermentation by *Lactobacillus* [66]. Rheological studies have also been performed. Indeed, in [67], 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 clear the marker metabolites generated by different species of *Lactobacillus* strains, which contribute to the flavor and reveal the roles of diverse species of *Lactobacillus* 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 [67].

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 that context, the reference [55] 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* [68]. Cabbage juice and fresh cabbage, fermented by *Lactobacillus*, are also being studied for the development of probiotic products. Mixed with other vegetables (carrots, onion, cucumber), white and red cabbage fermented with *L. plantarum, L. casei* , *L. acidophilus* or *L. delbrueckii* have a good fermentation profile and a potential as a functional probiotic drink as demonstrated by Hyunah et al. [69–72]. 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 beet 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 beet juice fermented with *L. rhamnosus* GR-1 proved to be a satisfactory alternative to dairy-based prebiotic products. All juices achieved viable counts greater than the required minimum counts to be classified as prebiotic. Sensory evaluation results also indicated a market potential for prebiotic vegetable juice. Developing prebiotic vegetable juice using *L. rhamnosus* GR-1 as a probiotic agent will give consumers a viable non-dairy alternative which can provide many health benefits [73]. Co or triculture can be used to improve activities as bergamot juice has been fermented by 3 *Lactobacillus* (*L. plantarum* 107 subsp *plantarum* PTCC 1896, *L. plantarum* AF1, *L. plantarum* LP3) in tri culture. This combination allowed a higher AO activity. Bergamot juice fermented could also be used as a functional drink [74].

Other by-products are re-cycled, especially in the brewery sector. A study aimed to produce a beverage rich in polyphenol 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 phenol compounds than before the fermentation, and its bioactive compounds were more stable [75]. 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 has been fermented by endophytic *L. casei* [76]. A turmeric-based functional drink was also obtained by co-fermentation with *Enterococcus faecium, Lactococcus lactis subsp. lacti and L. plantarum*. The measurement of the AO capacity was done 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 glucuronic acid production, leading to greater antimicrobial and antioxidant activities [77]. 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 [78]. Hou et al. have demonstrated the link between antimicrobial activities of kombucha with polyphenols and LAB, especially against *Escherichia coli, Salmonella tiphy, Vibrio cholerae,* and *Shigella dysenteriae* [79]. Green tea used in Kombucha may have activity when it's fermented by *L. plantarum*. Indeed, fermented extract derivated 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 [80].

3.2. Livestock feeding

The products of the fermentation of plants by *Lactobacillus* strains can be used in many fields ranging from livestock feeding, such as ruminant by decreasing gas production [81]. *Lactobacillus* strains can also be used for silage preparation. Silages are grass or other green fodders compacted and stored in airtight conditions, typically in a silo, to be used as livestock feeding in the winter. Many studies focus on using *Lactobacillus* strains to improve the quality of the silage. In reference [82], the effect of *L. brevis* and *L. parafarraginis* used as inoculants and microbial communities of corn stover silage was studied. After 20 days, the 2 *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 of the silage quality and a reproducibility ensiling process were observed [82]. Recently in [83], 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 quality of silage (fresh and acidic odor, good texture and no fungi) and a pH around 4 was observed. *L. plantarum* addition accelerates ensilage fermentation [83]. In [84], an increase in silage quality thanks to the addition of 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 [85]. In conclusion, the silage treated with both *Lactobacillus* bacteria and cellulase showed the best silage quality. Optimizing the digestibility of feeds and thus increasing their nutritional value is a challenge for the livestock feeding industry. In another study, the fermentation product of an extract of ginger and turmeric mixture by *Lactobacillus* spp. was supplemented to chickens. Biological analyses of AO enzymes and analysis of gut microbiota and lymphoid organs, showed a prebiotic effect, AO effect and improvement of resistance to bacterial infections [86].

3.3. Lactic acid production from plant biomass

The use of low-cost by-products is of primary interest since it allows the production costs to be lowered compared to 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 [87]. Lactic acid is one of the most widely used organic acids for a long time in various industries, such as the food, cosmetics, pharmaceutical, and textile industries, and flavor, conservation, AO and antimicrobial activity [88]. 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 [89,90]. When using large-scale fermentation bioprocesses, the biomass feedstock must be carefully selected as it accounts for almost half of the production costs of biopolymers [89]. To address this production cost issue, scientists and industrials have focused on lignocellulosic biomass as a fermentation substrate for lactic acid production. Nevertheless, to be easily usable, saccharification pre-treatments are necessary to break down 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 [91]. Homofermentative strains of *Lactobacillus* cannot use pentose carbohydrates from hemicellulose, but heterofermentative ones, such as *L. brevis* can use these carbohydrates by taking the phosphoketolase pathway [90].

In reference [89], 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. Comparative analysis of the expected yield of lactic acid production revealed that seaweeds allowed production rates comparable to lignocellulosic biomasses [89]. 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 as the best one and allows to reach a maximum productivity of 11 g L^{-1} h^{-1}. Authors demonstrated the importance of medium supplementation by yeast extract, as Lactobacilli are tedious microorganisms that require many substrates and substances to grow [92]. Nevertheless, it is estimated that the addition of yeast extract can contribute up to 30% of the cost of producing lactic acid [93]. Zhang & Vadlani have 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 to the SSF process, avoids substrate inhibition and increases the productivity and the yield of D-lactic acid [91]. Same researchers' team have 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, authors have 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 [90].

Saccharification and fermentation could be performed at the same time (simultaneous saccharification and fermentation) and was used for instance by Tu et al for LA production. With *L. plantarum*, they obtained up to 65.6 g/L of lactic acid with a conversion of cellulose of 69% [94]. By using inulin from chicory, in [95] they obtained a best performance by simultaneous saccharification and fermentation to produce D-lactic acid with *L. bulgaricus*. In their process, they obtained a molecule optically pure (99.9%) which could be interesting for further chemical processes. The productivity is also high with 123 gL^{-1} starting from 120 gL^{-1} of inulin treated by inulinase. The enzymatic treatment yielded inulin used instead of glucose in MRS medium for fermentation [94,95].

In another example, the lactic acid production from fermented orange peels was evaluated by ion-exchange chromatography. The solid fermentations are in mono or co-culture, with *L. casei* 2246, *L. plantarum* 285 and *L. paracasei* 4186. This study showed that fermentation allows higher lactic acid production with the monoculture *L. casei* 2246 and the co-culture *L. casei* 2246 with *L. plantarum* 285. Glucose could 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 [88]. Before industrialization of such a process, scale-up has to be demonstrated and down-stream 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 [87,96].

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

Another biotechnology application is the production of proteins, peptides, or AA like GABA. Indeed, plant by-products are sources of different proteins which could be hydrolyzed during fermentation by *Lactobacillus* species. These microorganisms, especially *L. plantarum,* have developed a proteolytic system to fulfil their nitrogen requirement. The proteolytic activities and protein hydrolysis patterns differ widely 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 strain *L. plantarum* LP-9 of was used to co-produce GABA and lactic acid from agro-residues such as wheat bran, rice bran, corn bran. Results were compared to the use of cassava (starchy food crop), and production yields were significant and comparable to this control condition [97]. Co-fermentation of Ginseng root and leaf extract always by a *L. plantarum* EJ2014 and *B. subtilis,* showed also a production of GABA [98]. 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 [99]. 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 [100].

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

By-product used	*Lactobacillus spp.*	FP	Product generated	Bio-activity	Remark	Reference
Apple juice	*L. plantarum*	LF	PC	AO		[101]
Apple juice	*Saccharomyces cerevisiae,* then *L. plantarum*	LF	PC, OA	AO		[102]
Margosa (*Momordica charantia L.*)	*L. plantarum* NCU116	LF	SCFA LA PC	AO	Juice's sterilization exerted adverse effects	[103]
Porcelain plant (*Graptopetalum paraguayense E. Walther)*	*L. plantarum* BCRC 10357	LF	PC	AO	Assayed during the maturity of the leaves	[104]
Milled wheat	*L. plantarum+ Streptococcus thermophilus*	LF Co	PC	AO, AM, PB	Anti-burning properties	[105]
Apple by-products	*L. plantarum*	LF	PC	AO, barrier integrity	Caco-2	[106]
Mango	*L. plantarum + Saccharomyces cerevisiae*	SB Co	Mango slurry, PC	AO		[107]
Liquorice root	*L. plantarum*	SBF	PC	AO		[108]
Jussara pulp (*Euterpe edulis*)	*Lactobacillus and Bifidobacterium*	LF Co	OA: protocatechic acid	AO	Conversion of anthocyanins	[109]
Acerola	*L. acidophilus +Bifidobacterium longum*	BF	beverage	PB	↗resistance of PB to gastrointestinal digestion	[110]
Cauliflower & white beans mix	L. plantarum 299	SBF	Riboflavin, Folate, Vitamin B12, AA		Nutritional value	[111]
Wheat germ	L. plantarum + L. rossiae	LF	Bread rich in PC, phytases	AO	↘ anti-nutritional factor, ↗ protein digestibility	[112]
Date juice	*L. casei subsp. rhamnosus*	LF	LA		Nitrogen source optimisation	[113]
Date juice	*L. sp.* KCP01	LF	LA		Medium optimisation	[114]
Solid carob	*L. rhamnosus*	BF	LA	Many diseases	Immobilization in alginate beads	[115]
Banana, papaya, pineapple, orange	*L. plantarum*	BF	LA		Best LA's production for banana et pineapple	[116]

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

4. Limitations and future challenges

Faced with ecological 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 struggle to feed themselves, and there is much undernutrition in these countries. This is why the food and agriculture industry have to find solutions to provide for the needs of all. Among these, a better use of plant resources and a better exploitation of their by-products appear to be two solutions of interest. In addition, consumers are looking for more natural products with health benefits and industrials are looking for economically viable bio-based solutions. Fruit and vegetable wastes and by-products from cereals are potential for revalorization because of their quantity and richness in nutrients and bacterial strains suitable for lactic fermentation.

When lactic acid bacteria ferment the nutrients that compose them, the functional and nutritional properties increase, representing significant opportunities for the agri-food, biotechnology, medical, nutraceutical and cosmetic industries. As it was 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. Firstly, the use of plant by-products requires a crucial design of the fermentation process depending on the raw material (solid, liquid, semi-liquid fermentations). This design could lead to the development and the emergence of new processes which should be able to meet the industrial viability, economic yields and consumer's needs. Consequently, an important work is still needed on these processes to increase the commercialization of new bio-based products from plant by-products. In another hand, *Lactobacillus* strains are fastidious bacteria in their nutritional requirements and are not necessary well metabolically adapted for their growth from any substrates, and the use of GMOs is a very limiting criteria for many applications (food, cosmetics, etc.). The growth parameters and enzymatic activities of *Lactobacillus* strains have an important impact on the applications and particularly when the fermentation substrate is complex. Therefore, it is necessary to work on the culture conditions and metabolic adaptation of these strains to maximize the enzymatic activities and the production rates of the molecules of interest. Consequently, many constraints exist, such as the lack of scientific data and hindsight, the control of the culture conditions and the separation and purification processes to recover the bioactive compounds. More 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 multi-products strategies have to 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 thanks to their enzymatic activities. This review highlights the different applications related to the production of these compounds. The latter possess bioactivities such as AO, AI, prebiotic, antimicrobial, and many others.

Moreover, they represent a growing interest for the food industry for their capacity to increase the nutritional value but also for their use as preservative and modifier of organoleptic properties. The various studies reviewed here are looking for alternatives to meet consumer's demand for environmental and societal issues. To reduce production costs and the carbon footprint of the process, genetic engineering and the revalorization of plant by-products appear as interesting avenues of research to improve the yield of compounds of interest. However, many scientific data are still missing for the mastery of fermentation by *Lactobacillus*. More studies are necessary to identify the biochemical reactions and metabolism of *Lactobacillus* involved in producing bioactive compounds. Furthermore, studies need to be conducted to investigate further the mechanisms involved in the bioactivities of interest.

Acronyms and Abbreviations

AA: Amino acids
ABTS : Acide 2,2'-azino-bis(3-éthylbenzothiazoline-6-sulphonique)
AI: Anti inflammatory
AM: Anti-microbial
AO: Antioxidant
BF: Batch fermentation
Co: Co-culture
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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