Lactic acid production – producing microorganisms and substrates sources-state of art

Elahe Abedi *, Seyed Mohammad Bagher Hashemi

Department of Food Science and Technology, College of Agriculture, Fasa University, Fasa, Iran

A R T I C L E   I N F O
Keywords:
Biotechnology
Microbiology
Lactic acid
Fermentation
Microorganisms
Agricultural waste
Industrial waste

A B S T R A C T
Lactic acid is an organic compound produced via fermentation by different microorganisms that are able to use different carbohydrate sources. Lactic acid bacteria are the main bacteria used to produce lactic acid and among these, Lactobacillus spp. have been showing interesting fermentation capacities. The use of Bacillus spp. revealed good possibilities to reduce the fermentative costs. Interestingly, lactic acid high productivity was achieved by Corynebacterium glutamicum and E. coli, mainly after engineering genetic modification. Fungi, like Rhizopus spp. can metabolize different renewable carbon resources, with advantageously amylolytic properties to produce lactic acid. Additionally, yeasts can tolerate environmental restrictions (for example acidic conditions), being the wild-type low lactic acid producers that have been improved by genetic manipulation. Microalgae and cyanobacteria, as photosynthetic microorganisms can be an alternative lactic acid producer without carbohydrate feed costs. For lactic acid production, it is necessary to have substrates in the fermentation medium. Different carbohydrate sources can be used, from plant waste as molasses, starchy, lignocellulosic materials as agricultural and forestry residues. Dairy waste also can be used by the addition of supplementary components with a nitrogen source.

1. Introduction

Lactic acid as an organic acid is authorized by the U.S. Food and Drug Administration as GRAS (generally regarded as safe). It provides leading roles in the food and non-food industry. i) It is utilized in the food industry including beverage industry (as food preservative, fermentation agent, acidulant, flavour enhancer, and decontaminant), antioxidant, probiotic activity, cryoprotectant, viscosity modifier, ii) chemical industry mainly mosquito repellent, descaling agents, pH regulator, neutralizers, green solvent, cleaning agents, metal complexing agents, substitution of synthetic plastics derived from petro-chemically compounds and environmentally friendly alternative due to production of poly-lactic acid as biodegradable polymers for commercial uses such as fibers and films, production of propylene glycol, lactate esters, acrylic acid, propylene oxide, propanoic acid, acetaldehyde, 2,3-pentanedione, and dilactide; iii) cosmetic industry as moisturizers, skin-lightening agents, skin rejuvenating agents, anti-acne agents, humectants, anti-tartar agents; iv) medicine and pharmaceuticals industry as a building-block molecule, dialysis solution, mineral preparations, tableting, prostheses, surgical sutures, controlled drug delivery system, immune-stimulant and manufacture of hygiene and esthetic products [1, 2]. Lactic acid is commonly sold as an 88% solution. The price varies with the application (e.g., food, pharmaceuticals, and PLA) and also depends on the price of commodity starch and sugar feedstocks used for fermentation. A range of around $3.0-$4.0/kg was reported in 2019 (https://www.pharmacompas.com). Upon annual growth of 16.2%, the global lactic acid market increased from 1,220.0 kilotons in 2016 to 1,960.1 kilotons in 2025. This should display USD 9.8 billion in the global market. Market studies mention that the major growth will be for medicines and cosmetics in the Latin America and the Asia Pacific region [2].

The direct conversion of complex compounds to lactic acid can be categorized mainly into four groups. a) The lactic acid producing fungi such as Rhizopus oryzae. b) amylolytic lactobacilli namely Lb. amylovorus, Lb. manihotivorans, Lb. amylophilus etc. c) The simultaneously degradation of substrate further treat with enzymes. d) glycolysis pathway in E. coli, K. lactis and S. cerevisiae [3, 4] (Figure 1).

The fermentation capacity by several LAB has been studied in order to produce LA. Plenty of lactic acid bacteria have amylase activity were originated from various plant and animal. Main obstructions lactic acid bacteria is that they require complex nutrients and slightly lower fermentation temperatures (~45 °C) than other microorganisms, which lead to increased costs and contamination risk and are also poor
productivity due to the amylase production in the initial step, causing a long lag phase. Otherwise they require partially hydrolyzed substrates. Certain fungi including *Rhizopus* sp. can generate high content of lactic acid. They also specify with advantages compared with the bacterial process such as i) the consumption of a chemically defined medium (including inorganic nitrogen sources), which can facilitate product separation and purification, ii) consume both complex carbohydrates and pentose sugars iii) high product concentrations of pure L-lactic acid owing to metabolize high amount of glucose which is preferred for poly-lactide manufacture. For instance, fungal species of *R. oryzae* 2062 and *R. arrhizus* 36017 produce lactic acid in a single-stage simultaneous saccharification and fermentation process. In contrast, homofermentative lactic acid bacteria have highly more efficiencies than the fungi to convert sugars to lactic acid because production other byproducts such as ethanol and fumaric acid by *R. oryzae*-based process. Some researcher tried to enhance lactic acid production using a mutant of *R. oryzae* with declined alcohol dehydrogenase activity under oxygen limiting conditions. This strain generated almost 10-fold more lactic acid production when compared to the parent strain [3, 4].

Figure 1. Pathways of lactic acid production from agro-industrial residues. Number on arrow catalyzed by enzyme and other reaction. 1: Exo β1,4 Glucanase, 2: β-Glucosidase, 3: lactose phosphotransferase system (Lac-PTS), 4: permease, 5: Amylase, 6: β-galactosidase, 7: ATP→ADP, 8: galactose-1-phosphate uridylyltransferase, 9: phosphoglucosutase, 10: NAD→NADH, 11: ATP→ADP, 12: ATP→ADP, 13: Phosphoenolpyruvate carboxylase, 14: ATP→ADP, 15: ATP→ADP, 16: NAD⁺→NADH, 17: arabinose isomerase, 18: ribulokinase and ATP→ADP, 19: xylose reductase and xylitol dehydrogenase, 20: ATP→ADP, 21: ribulose 5-phosphate 3-epimerase, 22: D-lactic acid Dehydrogenase, 23: Pyruvate-fomarate lyase, 24: Pta, 25: Pyruvate dehydratase complex, 26: Aldehyde dehydrogenase, 27: Acetate kinase, 28: 4 ADP→4ATP, 2 NAD⁺→2NADH, 29: 2NADH→2NAD⁺, 30: ADP→ ATP, 31: NADH→ NAD⁺, 32: NADH→ NAD⁺, 33: 2ADP→ATP, NAD⁺→NADH, 34: Lactate dehydrogenase, NADH→NAD⁺, 35: Acetaldehyde dehydrogenase, 36: Pyruvate decarboxylase. A route: D-tagatose 6-phosphate pathway. B route: Pentose phosphoketolase (PK) pathway: for Hetero lactic acid metabolism. C route: Embden-Meyerhof-Parnas (EMP) pathway: for Homo lactic acid metabolism. D route: Glycolysis pathway in *E. coli, K. lactis* and *S. cerevisiae*. 

2
by engineering genetic modification [5]. Moreover, \textit{Saccharomyces cerevisiae} is one of the more promising organisms that reveal high tolerance to low pH-values. Interestingly, good LA productivities were achieved by genetically modified \textit{Candida} spp [5].

Relatively to substrate sources, worldwide there is a lot of interesting agro-industrial waste or sub-products with a lower value, which can be fermented by several organisms. Molasses, juices waste, starchy biomass, agricultural residues, and forestry residues that is rich in mono and disaccharides, which in some cases need to be hydrolysed by pectinases to enhance the LA production. To use dairy wastes as a substrate, mainly whey, it is necessary to use an enriched mediums, due to insufficient proteolytic enzyme activity [5, 6, 7, 8]. In this paper, different bacterial groups that capable of producing lactic acid at different rates and under different conditions were discussed.

In this paper, different bacterial groups that capable of producing lactic acid at different rates and under different conditions were discussed. Moreover, chemical and physical pretreatment of substrates were explained.

2. LA producing microorganisms

2.1. Bacteria

2.1.1. Lactic acid bacteria

Lactic acid bacteria (LAB) are gram-positive microorganisms known as the main safe industrial-scale producers of lactic acid (LA). LA is produced by glycolysis pathway under anaerobic conditions, and this compound can be produced from hexoses and pentoses LAB metabolism pathways, as indicated in Figure 1. LA production yield and productivity depends on pH (3.5–9.6), temperature (5–45 °C), nutrients presence (such as amino acids, peptides, nucleotides and vitamins) and the LAB strain producers used (so far have been used strains belonging to the \textit{Leuconostoc}, \textit{Lactococcus}, \textit{Lactobacillus}, \textit{Pediococcus}, \textit{Enterococcus}, \textit{Streptococcus}, \textit{Vagococcus}, \textit{Aerococcus}, \textit{Carnobacterium}, \textit{Tetragenococcus}, \textit{Oenococcus} and \textit{Weissella}) [5, 6, 7, 8]. However, LAB species including \textit{Lactobacillus}, \textit{Lactococcus}, \textit{Leuconostoc}, \textit{Streptococcus}, and \textit{Pediococcus} are also used as starter cultures in industrial food fermentations. Among LAB strains, \textit{Lactobacillus} strains have great commercial importance due to high acid tolerance, high yield, and productivity, and can be engineered for the selective production of L/D-lactic acid [5]. However, there are some disadvantages when using the LAB for commercial LA production, such as the high requirement of complex nutrients (with increasing production costs) and the low fermentation temperature (that could result in contamination risks and prevention of simultaneous saccharification of starch or cellulosic biomass and conversion to sugars by amylases enzymes and fermentation of sugars and lignocellulosic biomass) [9, 10]. However, the alkaliphilic LAB that includes \textit{Marinilactibacillus}, \textit{Halolactibacillus}, and \textit{Alkalibacterium} spp. and other various strains from LAB genera, such as \textit{Microbacterium} spp., \textit{Enterococcus} spp., \textit{Alkalibacterium} spp., \textit{Exiguobacterium} spp., \textit{Oceanobacillus} spp. and \textit{Bacillus} spp., can produce LA at high pH-values (7.0–11.5), resulting in a contamination minimization during the fermentation process [9, 10, 11, 12]. For example, \textit{Exiguobacterium} is a genus of bacilli, being the alkaliphilic \textit{Exiguobacterium} sp. strain 8-11-1 used to produce optically pure L-lactate, in nonsterile fed-batch fermentation with productivity of 8.15 g/L/h under glucose concentration of 80 g/L and using NaOH as a neutralizing agent [9].

Since the complex nutritional requirements of the LAB complicate industrial processes and enhance cost, genetic engineering methods by gene manipulation with plasmid transformation could improve the fermentation efficiency of LA production. Some microorganisms, such as \textit{Corynebacterium glutamicum} (section 1.3), \textit{Escherichia coli} (section 1.4) and yeasts lack activities for pyruvate-formate lyase and lactate dehydrogenase (LDH), and these genes can be inserted through gene sources of L/-D-LDH from LAB, bovine and fungi, to express the D(-)-LDH gene from LAB, producing D(-)-lactate in minimal medium with >99.9% optical purity.

Glucose fermentation by homofermentative LAB needs somewhat acidic to neutral pH. However, low pH, has an inhibitory impact on cellular metabolism, in turn lactic acid production. The large number of LAB cannot grow lower than pH 4. In order to maintain cell survival two solutions are used: i) lime is routinely introduced to the fermentors to keep a neutral pH, which cause to produce calcium lactate (>90% of the lactic acid). Subsequent fermentation, the broth containing calcium lactate would be acidified with sulfuric acid to generate lactic acid. High sulfuric acid consumption leads to form high content of insoluble calcium sulfate as gypsum compared to the amount of lactic acid produced, waste disposal concerns, further corrosion problems and a significant cost factor in the product recovery step of commercial operations. Ideally, microbial fermentation would take place in medium with a pH at or lower than the pKₐ of lactic acid (the pKₐ of lactic acid is 3.78), permitting direct purification of the acid form. ii) Metabolic engineering has been applied to modify for variants of Lactobacillus sp. with improved tolerance to the acidified medium generated during fermentation. Improved strains has been achieved after UV and nitrosoguanidine treatment, which they are capable to produce lactic acid at rates and yields like to those of the traditional, neutral-pH lactic acid processes. In order to maximize resistance to the acidic conditions inducing by lactic acid production, enzymes namely trehalose 6-phosphate phosphatase from \textit{Propionibacterium freudenreichii} has been expressed in \textit{Lb. lactis}, leading to 5- to 10-fold greater survivability at pH 3.0. Similarity, the enzymes in histidine decarboxylation pathway from \textit{Streptococcus thermophilus} was expressed in \textit{Lb. lactis}, making survival at pH levels as low as 3 in which the host cells were easily dying [1]. There are two fermentative LAB pathways:

A) The homofermentative LAB

LAB possesses the aldolase enzyme and can convert glucose almost exclusively into LA. The homofermentative LAB usually uses hexose and pentose sugars via the Embden-Meyerhof (by using glycolysis pathway and pentose phosphate pathway). Homofermentative LAB produces two LA molecules as a major end-product per mole of consumed glucose, with a theoretical yield of 1 g/g and experimental yields among being this related to the type of the carbon source used [11]. For LA commercial production (more than 100 g/L of lactic acid) only homofermentative LAB is available due to the high yield (near maximal theoretical value), productivity and a high optical purity of lactic acid (>99%). Homofermentative LAB includes \textit{Streptococcus}, \textit{Lactococcus}, \textit{Enterococcus}, \textit{Pediococcus}, and some \textit{Lactobacillus}, as shown in Table 1. Homofermentative \textit{Lactobacillus} spp. includes mainly \textit{Lb. delbrueckii} subsp. \textit{bulgaricus}, \textit{Lb. acidophilus}, \textit{Streptococcus salivarius} subsp. \textit{thermophilus}, and \textit{Lb. helveticus}. Abdel-Rahman et al. [13, 14] reported that \textit{Enterococcus mundtii} CU 25 and engineered \textit{Lactobacillus plantarum} could also metabolize homofermentative pentoses to LA.

B) The heterofermentative LAB

LAB can metabolize glucose into LA, acetic acid (AA), formate, ethanol, diacetyl, acetoin, and carbon dioxide (\textit{CO}_2 gas detection is a diagnostic test for heterofermentative from homofermentative fermentation) [14]. The heterofermentative LAB can use the phosphogluconate pathway (with a theoretical yield of 0.5 g/g) and phosphoketolase pathway (with a theoretical yield of 0.6 g/g), when metabolizing hexose and pentose sugars, respectively [13, 14].

The utilization of heterofermentative LAB as dairy starter cultures are not common due to \textit{CO}_2 release and simultaneous production of LA and other organic acids, considered as defects which induce several problems in the products, including bloated packaging and cracks in dairy products and hard cheeses, respectively. Heterofermentative LAB includes mainly \textit{Oenococcus}, \textit{Leuconostoc}, and some \textit{Lactobacillus} spp., and the main
Table 1. Compilation of organisms studied for lactic acid (LA) production, with respective LA concentration, yield, productivity, substrate source and reference.

| Organism Lactic acid | Yield g/g | Productivity g/(L/h) | Source | Reference |
|----------------------|-----------|----------------------|--------|-----------|
| **Homo and Heterofermentative LAB** | | | | |
| Lb. delbrueckii NCIMB 8130 | 90.0 | 0.97 | 3.8 | Molasses | [125] |
| Lb. delbrueckii sp. delbrueckii ATCC 9649 | 58 | 0.48 | | Glucose | [13, 14] |
| Lb. delbrueckii sp. lactis ATCC 8000 | 83 | 0.83 | | Glucose | [13, 14] |
| Lb. delbrueckii sp. lactis DSM 20073 | 82 | 0.82 | | Glucose | [13, 14] |
| Lb. delbrueckii mutant DP3 | 77 | 0.64 | | Glucose | [13, 14] |
| Lb. delbrueckii mutant DP3, 19 | 68 | 0.57 | | Glucose | [13, 14] |
| Lb. delbrueckii sp. bulgaricus AU | 20 | 0.45 | | Whey permeate | [13, 14] |
| Lb. delbrueckii sp. bulgaricus 5085 | 16 | 0.38 | | Whey permeate | [13, 14] |
| Lb. delbrueckii sp. bulgaricus 5085 | 7.9 | 0.18 | | Whey permeate | [13, 14] |
| Lb. delbrueckii sp. bulgaricus ATCC 11842 | 15 | 0.41 | 4 | Whey permeate | [13, 14] |
| Lb. delbrueckii sp. bulgaricus ATCC 11842 | - | - | - | Sorghum | [13, 14] |
| Lb. delbrueckii sp. lactis 447 | 55 | 0.85 | | Lignocellulose hydrolysate | [13, 14] |
| Lb. delbrueckii sp. bulgaricus 5085 | 7.9 | 0.18 | | Whey permeate | [13, 14] |
| Lb. delbrueckii sp. bulgaricus 5085 | 16 | 0.38 | | Whey permeate | [13, 14] |
| Lb. delbrueckii sp. bulgaricus CRL 870 | 12 | - | - | Skim milk | [13, 14] |
| Lb. delbrueckii sp. bulgaricus 5085 | 106 | 0.82 | | Hydrolysate wheat flour | [13, 14] |
| Lb. delbrueckii IFO 3534 | 24 | 0.48 | | Hydrolysate newspaper | [13, 14] |
| Lb. delbrueckii sp. bulgaricus CBS 743.84 | 53 | 0.53 | | Hydrolysate pure cellulose | [13, 14] |
| Lb. delbrueckii sp. bulgaricus CNRZ 369 | 35 | 0.85 | | Glucose | [13, 14] |
| Lb. delbrueckii sp. bulgaricus CNRZ 369 | 32 | 1.6 | | Cellulose | [13, 14] |
| Lb. delbrueckii sp. delbrueckii ATCC 9649 | 87 | 0.87 | | Glucose | [13, 14] |
| Lb. delbrueckii sp. delbrueckii ATCC 9649 | 94 | 0.94 | | Fructose + glucose | [13, 14] |
| Lb. delbrueckii sp. delbrueckii ATCC 9649 | 85 | 0.85 | | Sucrose | [13, 14] |
| Lb. delbrueckii sp. bulgaricus ATCC 11842 | 58 | 0.85 | | Glucose | [13, 14] |
| Lb. delbrueckii sp. bulgaricus ATCC 11842 | 40 | 0.75 | | Lactose | [13, 14] |
| Lb. delbrueckii sp. bulgaricus ATCC 11842 | 18 | 0.11 | | Hydrolysate of wheat flour | [13, 14] |
| Lb. delbrueckii sp. bulgaricus ATCC 11842 | 26 | 0.18 | | Hydrolysate wheat flour | [13, 14] |
| Lb. delbrueckii sp. lactis ATCC 12315 | 100 | 1.0 | | Hydrolysate potato | [13, 14] |
| Lb. delbrueckii IFO 3534 | 93 | 0.78 | | Hydrolysate potato waste | [13, 14] |
| Lb. delbrueckii sp. delbrueckii ATCC 9649 | 83 | 0.83 | | Glucose | [13, 14] |
| Lb. delbrueckii sp. delbrueckii ATCC 9649 | 55 | 0.55 | | Glucose | [13, 14] |
| Lb. delbrueckii MIX several strains | 85 | 0.87 | | Hydrolysate maize + barley | [13, 14] |
| Lb. delbrueckii sp. bulgaricus ATCC 11842 | 71 | 0.73 | | Hydrolysate maize + barley | [13, 14] |
| Lb. delbrueckii sp. bulgaricus ATCC 11842 | 90 | 0.9 | | Glucose | [13, 14] |
| Lb. delbrueckii sp. bulgaricus ATCC 11842 | 75 | 0.75 | | Glucose | [13, 14] |
| Lb. delbrueckii sp. bulgaricus | 44 | 0.95 | | Whey | [13, 14] |
| Lb. delbrueckii sp. bulgaricus | 13 | 0.28 | | Whey | [13, 14] |
| Lb. delbrueckii sp. bulgaricus ATCC 11842 | 50 | 1.0 | | Whey | [13, 14] |
| Lb. delbrueckii sp. bulgaricus Ch H 2217 | 9.5 | 0.19 | | Whey | [13, 14] |
| Lb. delbrueckii sp. bulgaricus NRRL B-548 | 115 | 0.86 | | Whey | [13, 14] |
| Lb. delbrueckii sp. bulgaricus ATCC 55163 | 45 | 0.90 | | Lactose | [13, 14] |
| Lb. delbrueckii sp. bulgaricus ATCC 11842 | 50 | 0.64 | | Whey | [13, 14] |
| Lb. delbrueckii sp. bulgaricus CNRZ 369 | - | - | - | Sorghum | [13, 14] |
| Lb. delbrueckii sp. bulgaricus NRRL B-548 | 52 | 0.58 | | Cellulose | [13, 14] |
| Lb. delbrueckii | 35.4 | 0.35 | 0.75 | Alfalfa fibers | [157] |
| Lb. delbrueckii NCIM 2025 | 81.9 | 0.94 | 1.36 | Cassava bagasse | [164] |
| Lb. delbrueckii subsp. delbrueckii IFO 3202 | 28.0 | 0.28 | 0.78 | Defatted rice bran | [13, 14] |
| Lb. delbrueckii mutant Uc-3 | 67.0 | 0.83 | 0.93 | Sugarcane bagasse waste | [174] |
| Lb. delbrueckii sp. lactis DSM 20073 | 9.9 | 0.83 | | Glucose | [24] |
| Lb. delbrueckii sp. delbrueckii ATCC 9649 | 0.82 | 1.6 | | Wheat | [13, 14] |
| Lb. delbrueckii sp. bulgaricus ATCC 11842 | 0.11 | 0.56 | | Wheat | [13, 14] |
| Lb. delbrueckii NCIM 2025 | 1.36 | | | Cassava bagasse | [164] |

(continued on next page)
| Organism | Lactic acid | Yield | Productivity | Source | Reference |
|----------|-------------|-------|---------------|--------|-----------|
| Homo and Heterofermentative LAB | | | | | |
| Lb. delbrueckii ZU-52 | 0.92 | 0.93–5.75 | Corn cob residue | [206] |
| Lb. delbrueckii subsp.delbrueckii Mutant Uc-3 | 0.83 | 0.93 | Sugarcane bagasse | [207] |
| Lb. delbrueckii UFV H2B20 | 108.0 | 1.57–3.7 | Orange waste enzymatic hydrolysates | [216] |
| Lb. delbrueckii subsp. bulgaricus ATCC 15009 | 49 | 1.1 | Cheese whey | [219] |
| Lb. delbrueckii ATCC 10863 | 68.0 | 0.76 | Cheese whey | [218] |
| Lb. delbrueckii ATCC 7469 | 28 | 0.93 | Glucose | [218] |
| Lb. delbrueckii DSM 20024 | 22 | 0.74 | Glucose | [218] |
| Lb. delbrueckii ATCC 7469 | 24 | 0.80 | Lignocellulose hydrolysate | [218] |
| Lb. delbrueckii ATCC 7469 | 18 | 0.40 | Molasses | [218] |
| Lb. delbrueckii ATCC 7469 | 30 | 0.71 | Whey permeate | [219] |
| Lb. delbrueckii ATCC 10863 | 30 | 0.71 | Whey permeate | [219] |
| Lb. delbrueckii ATCC 7469 | 30 | 0.71 | Whey permeate | [219] |
| Lb. delbrueckii ATCC 7469 | 14 | 0.71 | Fructose | [218] |
| Lb. delbrueckii ATCC 7469 | 16 | 0.81 | Glucose + fructose | [218] |
| Lb. delbrueckii ATCC 7469 | 15 | 0.73 | Sucrose | [218] |
| Lb. delbrueckii ATCC 10863 | 17 | 0.86 | Glucose | [218] |
| Lb. delbrueckii ATCC 10863 | 14 | 0.71 | Fructose | [218] |
| Lb. delbrueckii ATCC 10863 | 16 | 0.81 | Glucose + fructose | [218] |
| Lb. delbrueckii ATCC 10863 | 15 | 0.73 | Sucrose | [218] |

(continued on next page)
| Organism                | Lactic acid | Yield | Productivity | Source                  | Reference |
|-------------------------|-------------|-------|--------------|-------------------------|-----------|
| Homo and Heterofermentative LAB |             |       |              |                         |           |
| **Lb. rhamnosus ATCC 10863** | 16          | 0.81  |              | Hydrolysate molasses    | [13, 14]  |
| **Lb. rhamnosus ATCC 10863** | 58          | 0.95  |              | Glucose                 | [176]     |
| **Lb. rhamnosus ATCC 10863** | 29          | 1.00  |              | Hydrolysate wood        | [13, 14]  |
| **Lb. rhamnosus ATCC 11443** | 53          | 0.66  |              | Glucose                 |           |
| **Lb. rhamnosus ATCC 7469** | 34          | 1.1   |              | Glucose                 |           |
| **Lb. rhamnosus ATCC 9595 (CECT288)** | 32.5       | 0.88  | 5.41         | Apple pomace            | [13, 14]  |
| **Lb. rhamnosus ATCC 7469** | 42.0        | 0.38  | 0.87         | Cellulosic bioludge     | [13, 14]  |
| **Lb. rhamnosus ATCC 7469** | 73.0        | 0.97  | 2.9          | Paper sludge            |           |
| **Lb. rhamnosus ATCC 10863** | 67          | 0.84  | 2.5          | Glucose                 | [13, 14]  |
| **Lb.rhamnosus IFO 3863** | 0.53 – 0.77 | 2.90 – 13.15 | Glucose |       | [221]     |
| **Lb. rhamnosus ATCC 9595 (CECT288)** | 0.36 – 0.88 | 0.82 – 5.41 | Glucose |       |           |
| **Lb. rhamnosus ATCC 7469** | 0.97        | 2.9   |              | Paper sludge            | [175]     |
| **Lb. rhamnosus and Lb. brevis (mixed culture)** | 20.95 | 0.70 | 0.58         | Corn stover             | [122]     |
| **Lb. rhamnosus ATCC 7469** | 18.58       | 0.73  |              | Liquid distillery stillage | [222]   |
| **Lb. rhamnosus LA-04-1** | 82          | 0.81  | 3.73         | White rice bran hydrolysate | [222] |
| **Lb. rhamnosus ATCC 7469** | 34.7        | 0.81  | 0.66         | Liquid distillery stillage | [222]     |
| **Lb. rhamnosus ATCC 7469** | 42.2        | 0.99  | 1.22         | Liquid distillery stillage | [222]     |
| **Lb. rhamnosus** | Date juice  |       |              |                         | [133]     |
| **Lb.rhamnosus** | Glucose      |       |              |                         | [224]     |
| **Lb. rhamnosus ATCC 7469** | 73.2 – 179  | 0.81  | 0.76         | Recycled paper sludge   | [225]     |
| **Lb. rhamnosus ATCC 10863** | 60          |       |              | Softwood pre-hydrolysate and paper mill sludge | [226] |
| **Lb. rhamnosus** | 41.65       | 0.83  | 0.87         | Cassava wastewater      | [227]     |
| **L. rhamnosus ATCC 7469** | 97.1        | 1.80  |              | Bread stillage          | [200]     |
| **Lb.rhamnosus HGU09F5-27** | 157.22     | 8.77  |              | Yam tuber starch        | [228]     |
| **Lb. rhamnosus 6003** | 45.5        |       |              | Food waste              |           |
| **Lb. rhamnosus** | 22.40       | 76.9  | 1.22         | Solid carob waste       | [229]     |
| **Lb. rhamnosus PCM 489** | 27.5        |       |              | Cheese industry – whey  | [231]     |
| **Lb. rhamnosus B103** | 143.7       |       |              | Dairy industry waste    | [232]     |
| **L. rhamnosus ATCC 7469** | 58.01       | 1.19  |              | Brewer's spent grain    | [233]     |
| **Lb. bulgaricus NRRL B-548** | 38.7        | 0.90  | 3.5          | Lactose, glucose, and galactose | [234] |
| **Lb. bulgaricus ATCC 8001, PTCC 1332** | 24.6        | 0.81  |              | Cheese whey             | [235]     |
| **Lb. bulgaricus CGMCC 1.6970** | 70.70–113.18 | 1.47–2.36 | Cheese whey powder | [236] |
| **Lb. bulgaricus** | 19.5        | 1.22  |              | Cheese whey             | [182]     |
| **Lb. bulgaricus & K. marxianus (mixed culture)** | 16.2        | 0.41  | 10.5         | Cheese whey             | [13, 14]  |
| **Lb. casei NRRL B-441** | 82.0        | 0.91  | 5.6          | Glucose                 | [13, 14]  |
| **Lb. casei NRRL B-441** | 120         | 0.67  |              | Hydrolysate barley flour | [13, 14]  |
| **Lb. casei SU No 22** | 16          | 0.32  |              | Whey                    | [13, 14]  |
| **Lb. casei SU No 22** | 20          | 0.39  |              | Deproteinised whey      | [13, 14]  |
| **Lb. casei NRRL B-441** | 112         | 0.68  |              | Liquefied barley starch + glucoamylase | [13, 14]  |
| **Lb. casei NRRL B-441** | 162         | 0.87  |              | Liquefied barley starch + glucoamylase + alpha-amylase | [13, 14]  |
| **Lb. casei** | 36          | 0.26  |              | Barley flour            | [13, 14]  |
| **Lb. casei L100** | 50          | 0.83  |              | Corn starch             | [13, 14]  |
| **Lb. casei Shiram** | 94          | 0.92  | 2.61         | Mixed food waste bakery waste | [237] |
| **Lb. casei CICC 6056** | 55.1        | 0.835 | 0.574        | Sophora flavescens residues | [238] |
| **Lb. casei** | 21.3        | 0.63  |              | Sugarcane bagasse       | [239]     |
| **Lb. casei SU No 22** | 45          | 0.45  | 2.0          | Whey                    | [13, 14]  |

(continued on next page)
| Organism | Lactic acid<br>g/L | Yield<br>g/g | Productivity<br>g/(L/h) | Source | Reference |
|----------|----------------------|------------|-----------------------|--------|-----------|
| Lb. casei | 22 | 0.44 | Whey | [13, 14] |
| Lb. casei NRRL B-441 | 80 | 0.89 | Glucose | [13, 14] |
| Lb. casei | - | 0.10 | 0.13 | Banana wastes | [168] |
| Lb. casei | 39.1–63.3 | 0.51–0.91 | Food waste (mango, orange, green peas and) | [240] |
| Lb. casei subsp. rhamnosus NRRL-B445 and Lc. lactis subsp. lactis ATCC19435 | 60.3 | - | 3.20 | Date juice | [133] |
| Lb. casei ATCC 10863 | 44 | 0.44 | 1.22 | Ram horn hydrolysate | [241] |
| Lb. casei NRRL B-441 | 96.0 | 0.93 | 2.2 | Cheese whey | [182] |
| Lb. casei SU No. 22 and Lb. lactis WS 1042 (mixed culture) | 22.5 | 0.48 | 0.93 | Cheese whey | [13, 14] |
| Lb. casei | 33.73 | | | Whey | [15, 14, 243] |
| Lb. casei | -130 | Reuse of anaerobic digestion effluent | | | [244] |
| L. casei | Yucca | | | | [164] |
| Lb. casei M-15 | Molasses | | | | [129] |
| L. lactis ATCC 4797 | 12.5–24.3 | Casein whey permeate | | | [245] |
| L. lactis | Molasses | | | | [246] |
| L. lactis | Pineapples syrup | | | | [246] |
| L. lactis WS 1042 | 11 | 0.22 | Whey | [15, 14, 243] |
| L. lactis sp. lactis 2432 | 8.3 | 0.21 | Whey permeate | | |
| L. lactis sp. cremoris 2487 | 37 | 0.88 | 4.6 | Whey permeate | |
| L. lactis sp. lactis 5085 | 37 | 0.88 | Whey permeate | | |
| L. lactis WS 1042 | 15 | 0.30 | Deproteinised whey | | |
| L. lactis sp. lactis 2432 | 9.0 | 0.20 | Whey permeate | | |
| L. lactis sp. cremoris SBT 1306 | 80 | 1.5 | Lactose | | |
| L. lactis sp. lactis ATCC 19435 | 96 | 0.76 | Hydrolysate wheat flour | | |
| L. lactis sp. lactis AS211 | 95 | 0.77 | Hydrolysate wheat flour | | |
| L. lactis sp. lactis NRRL B-4449 | 6.6 | 0.16 | Waste paper | | |
| L. lactis IO-I JCM 7638 | 23 | 0.45 | Xylose | | |
| L. lactis sp. lactis 2432 | 28 | 0.70 | Xylose + glucose | | |
| L. lactis sp. lactis ATCC 13673 | 36 | 1.0 | Glucose | | |
| L. lactis sp. lactis ATCC 19435 | 13 | 0.42 | Xylose | | |
| L. lactis sp. lactis 4.9 | 0.86 | Glucose | | |
| L. lactis sp. lactis 3.2 | 0.70 | Maltose | | |
| L. lactis sp. lactis NRRL B-4449 | 6.6 | 0.66 | Glucose | | |
| L. lactis sp. lactis 2.8 | 0.28 | Galactose | | |
| L. lactis sp. lactis 5.8 | 0.58 | Mannose | | |
| L. lactis sp. lactis 1.8 | 0.18 | Xylose | | |
| L. lactis sp. lactis NRRL B-4449 | 0.16 | Hydrolysate cellulose + glucose + mannose + xylose + galactose | | |
| L. lactis IFO 12007 + Aspergillus awamori IFO 4033 | 25 | 0.50 | Potato starch | | [13, 14] |
| L. lactis IFO 101 JCM 7638 | 24 | 0.96 | Glucose | | |
| L. lactis sp. lactis AS211 | 107 | 0.91 | Hydrolysate wheat flour | | |
| L. lactis sp. lactis ATCC 19435 | 106 | 0.88 | Hydrolysate wheat flour | | |
| L. lactis sp. lactis ATCC 19435 | 90 | 0.98 | Hydrolysate wheat flour | | |
| L. lactis sp. lactis ATCC 19435 | 75 | 1.0 | Un hydrolysate wheat flour + glucose | | |
| L. lactis 53 | 53 | Hydrolysate wheat flour | | |
| L. lactis 65.1 | 39 | 0.75 | Glucose | | |
| L. lactis IFO 12007 | 25 | 0.50 | Potato starch | | |
| L. lactis sp. lactis ATCC 19435 | 65 | 1.5 | Glucose | | |
| L. lactis sp. lactis ATCC 19435 | 0.3 | 0.3 | Glucose | | |
| L. lactis IO-I JCM 7638 | 45 | 0.90 | Glucose | | |
Table 1 (continued)

| Organism                     | Lactic acid | Yield | Productivity | Source                      | Reference |
|------------------------------|-------------|-------|--------------|-----------------------------|-----------|
|                              | g/L         | g/g   | g/(L/h)      | Source                      | Reference |
| Homo and Heterofermentative LAB |             |       |              |                             |           |
| L. lactis ATCC19435           | 5.4         | 0.92  |              | Glucose                     | [149]     |
| L. lactis sp. lactis ATCC 19435 | 5.1         | 1.0   |              | Maltose                     | [15, 14]  |
| L. lactis sp. lactis biovar diacetylactis CNRZ 2125 | 38          | 0.73  |              | Lactose + citrate           |           |
| L. lactis BME5-18 M           | 0.97        | 2.2   |              | Glucose                     | [83]      |
| L. lactis IO-1               | 4.5         |       | 0.76         | Wheat                       | [15, 14]  |
| L. lactis sp. lactis         | 10.9        | 0.36  | 0.17         | Sugar cane baggage          | [165]     |
| L. lactis IO-12007            | 0.76        | 0.6   |              | Cassava                     | [248]     |
| L. lactis sp. lactis AS211    | 0.77        | 1.7   |              | Wheat                       | [15, 14]  |
| L. lactis ATCC19435           | 92.5        | 0.68  | 0.5          | Artichoke hydrolysate       | [249]     |
| L. lactis IL 1403/pciSaA      | 15.6        | 0.89  | 1.57         | Soluble starch              | [13, 14]  |
| L. lactis IO-1               | 10.9        | 0.36  | 0.17         | Sugar cane baggage          | [165]     |
| Lb. lactis sp. lactis IFO 12007 | 90.0       | 0.76  | 1.6          |                             | [248]     |
| L. lactis NCIM 2368           | 17.01–72.24 |       |              | Glucose                     | [250]     |
| Lb. plantarum NRRL B-787     | 17          | 0.42  |              | Solid waste                 | [13, 14]  |
| Lb. plantarum NRRL B-788     | 19          | 0.46  |              | Solid waste                 | [13, 14]  |
| Lb. plantarum NRRL B-813     | 18          | 0.43  |              | Solid waste                 | [13, 14]  |
| Lb. plantarum NRRL B-531     | 18          | 0.43  |              | Solid waste                 | [13, 14]  |
| Lb. plantarum                | 17          | 0.70  |              | Corn syrup                  | [13, 14]  |
| Engineered Lb. plantarum NCIMB 8826 (GMO) | 73.2–141.9 | 0.9–0.93 | 2.95 | Glucose and xylose | [251]     |
| Lb. plantarum NRRL B-787     | 17          | 0.42  |              | Solid waste                 | [13, 14]  |
| Lb. plantarum NRRL B-788     | 19          | 0.46  |              | Solid waste                 | [13, 14]  |
| Lb. plantarum NRRL B-813     | 18          | 0.43  |              | Solid waste                 | [13, 14]  |
| Lb. plantarum NRRL B-531     | 18          | 0.43  |              | Solid waste                 | [13, 14]  |
| Lb. plantarum                 | 17          | 0.70  |              | Corn syrup                  | [13, 14]  |
| Lb. plantarum NRRL B-787     | 5.4         | 0.54  |              | Glucose                     | [13, 14]  |
| Lb. plantarum NRRL B-788     | 3.7         | 0.37  |              | Galactose                   |           |
| Lb. plantarum NRRL B-531     | 5.7         | 0.57  |              | Mannose                     |           |
| Lb. plantarum NRRL B-787     | 3.7         | 0.37  |              | Galactose                   |           |
| Lb. plantarum NRRL B-788     | 5.7         | 0.57  |              | Mannose                     |           |
| Lb. plantarum NRRL B-813     | 4.9         | 0.49  |              | Hydrolysate cellulose: glucose, mannose, xylose, galactose | [13, 14]  |
| Lb. plantarum USA 422         | 6.0         | 0.60  |              | Glucose                     |           |
| Lb. plantarum USDA 422        | 4.9         | 0.49  |              | Galactose                   |           |
| Lb. plantarum USDA 422        | 4.9         | 0.46  |              | Hydrolysate cellulose: glucose, mannose, xylose, galactose | [13, 14]  |
| Lb. plantarum USDA 422        | 7.3         | 0.73  |              | Glucose                     |           |
| Lb. plantarum USDA 422        | 4.7         | 0.47  |              | Galactose                   |           |
| Lb. plantarum USDA 422        | 8.3         | 0.83  |              | Mannose                     |           |
| Lb. plantarum USDA 422        | 8.3         | 0.43  |              | Hydrolysate cellulose: glucose, mannose, xylose, galactose | [13, 14]  |
| Lb. plantarum USDA 422        | 5.2         | 0.52  |              | Glucose                     |           |
| Lb. plantarum USDA 422        | 3.1         | 0.31  |              | Galactose                   |           |
| Lb. plantarum USDA 422        | 6.2         | 0.62  |              | Mannose                     |           |
| Lb. plantarum USDA 422        | 1.3         | 0.13  |              | Xylose                      |           |
| Lb. plantarum USDA 422        | 46.4        | 0.46  | 0.64         | Alfalfa fibers              | [252]     |
| Lb. paracasei (NBRC 15889)    | ~100        |       |              | Brown rice polish           | [161]     |
| Lb. paracasei                 | 139.71      |       |              |                             |           |
| Lb. paracasei                 | ~125        |       |              |                             |           |
| Lb. paracasei                 | 160.97      |       |              |                             |           |
| Lb. paracasei                 | 137.67      |       |              |                             |           |

(continued on next page)
| Organism                      | Lactic acid g/L | Yield g/g | Productivity g/(L/h) | Source                        | Reference          |
|-------------------------------|-----------------|-----------|---------------------|-------------------------------|--------------------|
| Homo and Heterofermentative LAB |                 |           |                     |                               |                    |
| *Lb. plantarum* (JCM 1149)    | ~115            | -         |                     |                               | [13, 14]           |
| *Lb. plantarum* A6            | 8.41            | 0.98      | -                   | Muskel processing wastes      | [13, 14]           |
| *Lb. plantarum* ATCC 21028    | 41.0            | 0.97      | 1.0                 | Synthetic lactose medium       | [13, 14]           |
| *Lb. plantarum* NCIMB 8826    | 73.2            | 0.85      | 3.86                | Corn starch                    | [253]              |
| *Lb. plantarum* Bamboo        |                 |           |                     |                               | [254]              |
| *Lb. plantarum* A6            | 86.6            | 0.89      | 4.54                |                               | [255]              |
| *Lb. plantarum* ∆ldhL1        | 73.2            | 0.85      | 3.86                |                               | [255]              |
| *Lb. plantarum* ΔldhL1/pCU-CelA | 38.6           | 0.82      | 3.78                |                               | [253]              |
| *Lb. plantarum* ΔldhL1-xpk1:tkt | 41.2           | 0.89      | 4.54                |                               | [255]              |
| *Lb. plantarum* ∆ldhL1-xpk1:tkt-Δxpk2/pCU-PxylAB | 57.5           | 0.81      | 2.61                |                               | [256]              |
| *Lb. amylovorus* ATCC 33620   | 4.2             | 0.1       |                    | Potato                         | [140]              |
| *Lb. amylophilus* GV6         | 76.2            | 0.70      | 0.8                 |                               | [146]              |
| *Lb. amylovorus* ATCC 33622   | 93              | 0.52      |                    | Hydrolysate barley flour       | [13, 14]           |
| *Lb. amylophilus* ATCC 49845  | 21              | 0.95      |                    | Glucose                        | [13, 14]           |
| *Lb. amylovorus* ATCC 33620   | 4.8             | 0.48      |                    | Cassava starch                 | [259]              |
| *Lb. amylovorus* ATCC 33622   | 45              | 0.82      |                    | Raw corn starch                | [260]              |
| *Lb. amylovorus* NRRL B-4542  | 114             | 0.63      |                    | Barley flour + gluco amylase   | [146]              |
| *Lb. amylophilus* ATCC 49845  | -               | -         |                    | Glucose                        | [13, 14]           |
| *Lb. amylophilus* ATCC 49845  | 30              | 0.60      |                    | Starch                         | [146]              |
| *Lb. amylophilus* GV6         | 27.3            | 0.3       |                    | Barley                         | [261]              |
| *Lb. amylophilus* BCRC 14055  | 21.62           | 0.98      | 0.31                | Starch                         | [261]              |
| *Lb. amylophilus*             |                 |           |                     | Corn                           | [146]              |
| *Lb. amylophilus*             |                 |           |                     | Potato                          | [146]              |
| *Lb. amylophilus*             |                 |           |                     | Wheat (bran or flour)           | [143]              |
| *Lb. zeae* ATCC 393           | 21              | 0.71      |                    | Glucose                        | [13, 14]           |
| *Lb. zeae* ATCC 393           | 37              | 0.98      | 5.0                 | Glucose                        | [13, 14]           |
| *Lb. salivarius* sp. salivarius ATCC 11742 | 28           | 0.92      |                    | Glucose                        | [13, 14]           |
| *Str. thermophilus*           | 18              | 0.50      |                    | Whey permeate                  |                    |
| *Str. thermophilus*           | 15              | 0.35      |                    | Whey permeate                  |                    |
| *Str. thermophilus*           | 19              | 0.47      |                    | Whey permeate                  |                    |
| *Str. thermophilus* CRIL 807  | 8.5             |           |                     | Skim milk                      | [262]              |
| *Str. thermophilus*           | 40              |           |                     | Lactose                        |                    |
| *Str. thermophilus*           | 24.18–39.71     | 0.55–0.80 |                     | Magazine and office paper      | [154]              |
| *Lb. casei* ATCC 25600        | 24.0            | 0.5       |                    | Cellulose                      |                    |
| *Lb. casei* ATCC 25600        | 23.1            | 0.51      | 0.48                | Cardboard waste                | [154]              |
| *Lb. casei* ATCC 25600        | 39              | 0.98      | 2.6                 |                               | [13, 14]           |
| *Lb. casei* ATCC 25600        | 91.6–97.1       | 0.91–0.96 | 2.08–2.7            | Curcuma longa waste (food waste) | [263]          |
| *Lb. casei* subsp. torques    | 57.0            | 0.97      | 2.8                 |                               | [264]              |
| *Lb. casei* subsp. Torques ATCC 25600 | 36.6           | 0.46      | 1.02                | Hydrodictyon reticulum         | [199]              |
| *Lb. casei* sp. torques ATCC 25600 | 23.4          | 0.51      | 0.49                | Waste cardboard                | [154]              |
| *Lb. kefir*                   | 9.8             | 0.20      |                    | Paneer whey                    | [13, 14]           |
| *Lb. acidophilus* R           | 8.6             | 0.17      |                    | Paneer whey                    | [13, 14]           |
| Organism | Lactic acid | Yield | Productivity | Source | Reference |
|----------|-------------|--------|--------------|--------|-----------|
| Homo and Heterofermentative LAB | | | | | |
| Lb. acidophilus CRL 640 | 14 | 0.45 | | Skim milk | [13, 14] |
| E. faecium | 27 | 0.91 | | Alfalfa | [13, 14] |
| E. faecalis RKY1 | 144.0 | 0.96 | 3.66-6.20 | Glucose | [136, 265] |
| E. faecium No. 78 | 3.04 | | | Sago | [266] |
| E. faecalis RKY1 | 0.93-1.04 | 0.5-4.8 | | Corn, wheat, tapioca, potato | [136, 267] |
| Lb. acidophilus | | | | | |
| E. faecalis RKY1 | 36.3 | 0.57 | 1.96 | Liquefied sago starch | [270] |
| E. faecalis RKY1 | 95.7 | 0.93 | 1.0-4.8 | Corn, wheat, tapioca, potato | [136, 267] |
| E. faecalis RKY1 | 1.7 | | | Wood | [268] |
| E. faecalis RKY1 | 55.3 | 0.99 | | | [269] |
| E. faecalis RKY1 | 93.0 | 0.93 | | | [140] |
| E. faecalis RKY1 | 92-94 | | 6.03-6.2 | | [136] |
| E. faecalis RKY1 | 48.0 | 0.92 | 4.0 | Wood hydrolyzate | [271] |
| E. durans BP130 | 28.8 | 0.85 | 0.24 | | [12] |
| E. mundtii QU 25 | 67.2-129 | 0.78-0.90 | 0.76-1.2 | Glucose/xylose mixture | [272] |
| E. faecium strain FW26 | 33.3 | 0.84 | | Banana peels and food wastes mixture | [273] |
| Ped. acidilacti | 13 | 0.51 | | Hydrolysate cod + corn syrup | [236] |
| Engineered Pediococcus acidilactici | 87.8-104.5 | 1.22-1.45 | | | [236] |
| Lb. plantarum NRRL B-4496, Lb. acidophilus NRRL B-4495, and L. reuteri B-14171 | | | | Egg white hydrolysates | [274] |
| Lb. manihotivorans LMG18011 | 48.7 | 0.098 | 0.76 | Food wastes | [162] |
| Lb. pentosus NRRL B-227 | 21 | 0.51 | | Solid waste | [13, 14] |
| Lb. pentosus NRRL B-473 | 18 | 0.43 | | Solid waste | [13, 14] |
| Lb. pentosus | 6.9 | 0.69 | | Glucose | [274] |
| Lb. pentosus | 5.9 | 0.59 | | Xylose | [274] |
| Lb. pentosus | 7.4 | 0.74 | | Glucose + xylose | [274] |
| Lb. pentosus | 1.4 | 0.14 | | Hydrolysate wood | [274] |
| Lb. pentosus | 0.43 | | | Hydrolysate cellulose: glucose + xylose + mannose + galactose | [274] |
| Lb. pentosus ATCC 8041 | 21.8 | 0.77 | 0.84 | Vine-trimming wastes | [163] |
| Lb. sakei KTU05-06, Pediococcus acidilactici + KTU05-7 + P. pentosaceus KTU05-9 | 40.0-93.0 | 0.62-1.45 | 0.83-1.94 | Wheat bran | [275] |
| Lb. pentosus ATCC-8041 | 23.0 | 0.93 | 0.45 | Nannochloropsis salina | [110] |
| Lb. pentosus CHCC 2355 | 0.88 | | | Wheat straw | [158] |
| Lb. pentosus ATCC 8041 | 0.65-0.77 | 0.1-0.9 | | Vine-trimming wastes/Corn Stover | [152, 158] |
| Lb. pentosus | | | | | |
| Lb. paracasei LA1 | 23.4 | 0.72 | 0.23 | Wastewater sludge | [176] |
| Lb. paracasei LA104 | 37.11 | 0.46 | 1.03 | Hydrodictyon reticulum | [199] |
| Lb. paracasei No. 8 | 81.5 | 2.7 | | Sweet sorghum | [13, 14] |
| Lb. paracasei No. 8 | 84.5 | 2.4 | | Rye | [13, 14] |
| Lb. paracasei No. 8 | 106.0 | 3.5 | | Sweet sorghum | [13, 14] |
| Lb. paracasei NCBI001-M2 | 223.7 | 5.53 | | Glucose | [279] |
| Lb.paracasei | 169.9 | 1.42 | | Molasses enriched potato stillage | [280] |
| L. paracasei DSM 23505 | 123.7 | 0.91 | | Chicory flour | [281] |
| L. paracasei A-22 | 80.10 | 0.97 | 1.48 | Agro-industrial waste such as sunflower seed hull, brewers’ spent grain, and sugar beet pulp | [282] |
| L. paracasei subsp. paracasei CHB2121 | 192 | 0.96 | 3.99 | Glucose | [283] |
| L. paracasei KTTC13169 | 92.5 | 0.9 | 8.12 | Artichoke tuber extract | [284] |
| Lb. sp. RY2 | 129.0 | 2.9 | | Rice | [140] |
| Organism | Lactic acid g/L | Yield g/g | Productivity g/(L/h) | Source | Reference |
|----------|----------------|-----------|----------------------|--------|-----------|
| Homo and Heterofermentative LAB | | | | | |
| Lb. sp. RKY2 | 3.1 | | | Rice and wheat bran | [140] |
| Lb. sp. strains A28a | –52.4 | 0.07 | 0.27 | Mixed food waste | [285] |
| Lb. sp. strains A59 | 0.14 | 0.53 | | Mixed food waste | |
| Lb. sp. strains A211 | 0.14 | 0.37 | | Mixed food waste | |
| Lb. brevis ATCC 14869 | 12.5 | 0.57 | 0.56 | Glucose, xylose or a glucose/xylose mixture | [286] |
| Lb. rhamnosus + L. brevis (mixed culture) | 14.8 | 0.73 | 0.4 | Glucose/xylose mixture | [287] |
| Lb. brevis | 15 | 0.22 | | Cottonseed cake, wheat straw, sugarcane bagasse | [288] |
| L. brevis and Lb. plantarum | –15–35 | 0.52–0.8 | | Lignocellulosic biomass | [289] |
| Lb. brevis CHCC 2097 and Lb. pentosus CHCC 2355 | 7.1 | 0.95 | | Wheat straw | [158] |
| Exiguobacterium sp. strain 8-11-1 | – | – | 8.15 | | [296] |
| Lb. bifermens DSM 20003 | 0.83 | 1.17 | | Wheat straw | [296] |
| Halolactibacillus halophilus JCM 21694 | 65.8 | 0.83 | 1.1 | Sucrose | [291] |
| Lb. sp. G-02 and Aspergillus niger SL-09 (mixed culture) | 120.5 | 0.95 | 3.3 | Artichoke tubers | [91] |
| Sporolactobacillus sp. strain CASD | 207 | 0.93 | 3.8 | Peanut meal and glucose | [28] |
| Sporolactobacillus bulinus YBS1-5 | 107.2 | 0.85 | 1.19 | Corn cob residues & cottonseed meal | [292] |
| Sporolactobacillus bulinus YBS1-5 | 87.3–99.5 | 0.65–0.89 | 0.81–1.94 | Wheat bran | [292] |
| Sporolactobacillus sp. strain CASD | 82.8 | 0.94 | 1.72 | Glucose | [40] |
| Sporolactobacillus bulinus | 93.4 | 1.37 | | Glucose | [294] |
| Sporolactobacillus bulinus YBS1-5 | 70.5 | 0.65 | | Corn stover | [295] |
| Sporolactobacillus laevolacticus DSM442 | 144.4 | 4.13 | | Cottong seed | [296] |
| Lb. sp. G-02 | 141.5 | 0.94 | 4.7 | Artichoke tubers | [297] |
| Lb. sp. RKY2 | 94.06 | 0.98 | 1.06 | Cheese whey | [184] |
| Lb. TY50 | 36.29 | ND | | Kitchen waste | [298] |
| Lb. sp. | 23.21 | | | Food waste + cu^3+ | [301] |
| Lactobacillus sp. B2 | 19.5L | 0.81 | | Crustacean waste | [299] |
| Lb. paracasei ATCC 334 | 1.2 | 1 | | Chlorella | [300] |
| Lb. lactis subsp. lactis NBRC 12007 | 0.8 | | | | [301] |
| Lb. reuteri JCM 1112 | 1.02–4.29 | | | Glucose-sucrose | |
| Lactococcus lactis JCM 7638 | | | | Glucose-sucrose | |
| Lb. gasseri NCIMB 11718 | 8.42–18.7 | | | Glucose-sucrose | |
| Lb. plantarum NCIMB 8826 | | | | Glucose-sucrose | |
| Lb. paracasei ATCC 334 | 8.01–12.3 | 5.17–7.03 | 7.77–9.60 | | |
| Lb. paracasei 7B | 52.61 | 0.96 | 1.25–3.23 | Wood lignocellulosic hydrolysate | [302] |
| Lb. paracasei br 601 | 21.19 | | | | |
| Lb. plantarum A1 | 41.91 | | | | |
| Lb. plantarum K1 | 25.22 | | | | |
| Lb. plantarum N14-2 | 36.95 | | | | |
| Lb. fermentum h602 | 31.11 | | | | |
| Lb. fermentum ATCC 14931 | 12.99 | | | | |
| Lb. fermentum E1 | 5.91 | | | | |
| Lb. brevis ATCC 8287 | 39.15 | | | | |
| B. coagulans T10-2 | 13.44 | | | | |
| B. coagulans T5-1 | 4.43 | | | | |
| W. paramesenteroides H1-6 | 18.49 | | | | |

(continued on next page)
Table 1 (continued)

| Organism | Lactic acid g/L | Yield g/g | Productivity g/(L/h) | Source | Reference |
|----------|-----------------|-----------|----------------------|--------|-----------|
| Homo and Heterofermentative LAB | | | | | |
| **Lb. points** (32%), **Lb. frumenti** (10%), **Lb. amylovorus** (8%), **Lb. acidophilus** (8%), and **B. bifidobacterium** (mixed culture) | 10–20 | | | Acidogenic fermentation of fruit and vegetable wastes | [301] |
| **Lb. plantarum** + **Lb. buchneri** + **Lb. rhamnosus** | 30.4–127.9 | | | **Maize and amaranth** | [304] |
| **Lb. plantarum** + **Lb. paracasei** | 30.4–127.9 | | | **Maize and amaranth** | [304] |
| **Lb. manihotivorans** LMG18011 | 48.7 | 1.11 | | **Starch and food waste** | [162] |
| **Lb. rhamnosus** & **B. coagulans** | 112.5 | 0.88 | 2.74 | **Cassava bagasse** | [305] |
| **Lb. delbrueckii spp. bulgaricus** | 19.46 | 0.396 | 0.405 | | |
| **P. acidilactici** KTU05-7 | 24.54 | 0.499 | 0.511 | | |
| **P. pentosaceus** KTU05-8 | 21.45 | 0.396 | 0.447 | | |
| **P. pentosaceus** KTU05-9 | 25.49 | 0.519 | 0.531 | | |
| **P. pentosaceus** KTU05-10 | 22.82 | 0.464 | 0.475 | | |
| **P. acidilactici** | 97.3 | 0.95 | | **Corn stover** | [306] |
| **P. acidilactici** ZP26 | 77.66 | 1.06 | | **Corn stover** | [307] |
| **Pediococcus acidilactici** (DSM, 20284) | –125 | | | **Brown rice polish** | [161] |
| **Pediococcus pentosaceus** (ATCC 25745) | –65 | | | | |
| **Lb. buchneri** NRRL B-30929 | 13.35 | | | **Elephant grass** | [308] |
| **E. casseliflavus/Lb. casei** (mixed culture) | 95 | 0.63 | 0.49 | **Glucose/xylose mixture** | [309] |
| **Actinobacillus succinogenes** | 183.4 | 0.97 | 1.53 | **Glucose** | [310] |
| **Pediococcus acidilactici** TM14 and **Weissella paramesenteroides TA15** | | | | **Food waste composting** | [311] |
| **Weissella sp. S26/Weissella sp. AD83** | 13.2 | | | **Xylose** | [312] |
| **Enterobacter aerogenes** ATCC 29007 | 46.02 | 0.41 | | **Mannitol** | [313] |
| **Thermoanaerobacterium aestuarium** LA1002-G40 | 78.5 | 0.85 | 1.63 | **Mixed bakery waste** | [314] |
| **Lb. sanfranciscensis** MR29 | 2.85 | 0.057 | | **Wheat straw biomass** | [315] |
| **Lb. rassic G14** | 0.96 | 0.0192 | | | |
| **Lb. frumenti** H10 | 1.90 | 0.038 | | | |
| **Lb. rassic M2** | 1.54 | 0.0308 | | | |
| **Lb. rassic W19** | 2.94 | 0.058 | | | |
| **Lb. sanfranciscensis** MW15 | 4.56 | 0.0988 | | | |
| **Lb. helveticus DSM 20075** | 2.03 | 0.0406 | | | |
| **Lb. delbrueckii subsp. bulgaricus** MI | 4.74 | 0.0948 | | | |
| **Lb. delbrueckii subsp. bulgaricus** DSM 20081 | 4.81 | 0.0962 | | | |
| **Leuconostoc mesenteroides** NRRL B 512 | 60.2 | 1.25 | | **Sugarcane juice** | [316] |
| **B. coagulans** LA1507 and **Lactobacillus rhamnosus** LA-04-1 (Mixed culture) | 118 | 1.84 | | **Sweet sorghum juice** | [317] |
| **Engineered Pediococcus acidilactici** | 130.8 | 1.82 | | **Wheat straw** | [318] |
| **Streptococcus sp. (indigenous consortium)** | 50–69 | 1.27–2.93 | | **Highly viscous food waste** | [319] |
| **Streptococcus sp.** | 66.5 | 0.33 | 3.38 | **Mixed food waste** | [320] |
| **Bifidobacterium longum** | 0.51 | | | **Cheese whey** | [321, 322] |

**Bacillus strains**

| B. coagulans | | | | | |
|---|---|---|---|---|---|
| B. coagulans | 20.1 | 0.60 | 0.93 | | **Sucrose** | [4] |
| B. coagulans 36D1 | 80 | 0.80 | 0.30 | | **Cellulose** | [151] |
| B. coagulans strains 36D1 | 92.0 | 0.77 | 0.96 | | **Paper sludge** | [20] |
| B. coagulans strains P4–102B | 91.7 | 0.78 | 0.82 | | **Paper sludge** | [20] |
| B. coagulans SIM-7 DSM 14043 | 0.96 | 9.9 | | **Glucose** | [24] |
| B. coagulans DSM 2314 | 0.27 | | | **Wheat straw** | [323] |
| B. coagulans strain 36D1 | 103.6 | 0.93 | 0.71 | | **Glucose** | [151] |
| B. coagulans strain 36D1 | 102.3 | 0.86 | 0.71 | | **Xylose** | |
| B. coagulans NBRC 12583 | 2 | | | **Sludge hydrolyzate** | [324] |
| **Alkaliphilic Bacillihic** | | | | | |
| B. coagulans strain IPE22 | 46.12 | | | **Wheat straw** | [33] |
| B. coagulans C106 | 83.6–215.7 | 4.7–5.5 | | **Xylose** | [325] |
| B. coagulans NBRC12583 | | | | | **Kitchen refuse** | [27] |

(continued on next page)
Table 1 (continued)

| Organism | Lactic acid g/L | Yield g/g | Productivity g/(L/h) | Source | Reference |
|----------|-----------------|-----------|----------------------|--------|-----------|
| **Bacillus strains** | | | | | |
| B. coagulans | 60.7 | 0.71 | 2.68 | Municipal solid wastes | [112] |
| B. coagulans DSM2314 | 58.7–70.4 | 0.83–0.73 | 1.14–1.81 | Sugarcane bagasse | [326] |
| B. coagulans | 79.4–93.7 | | | Glucose, xylose and cellobiose | [327] |
| B. coagulans BCS13002 | 11.75 | | | Gelatinized corn starch | [328] |
| B. coagulans | 0.26 | | | Corn starch | |
| B. coagulans | 99.1 | | | Glucose | [329] |
| B. coagulans | 145 | | | Glucose | [330] |
| B. coagulans | 110 | 0.86 | 1.29 | Cassava bagasse | [304] |
| B. coagulans | 29.7–33.7 | 0.92 | | Lignocellulosic hydrolysate | [331] |
| B. coagulans J112 | 0.97 | | | Oil palm empty fruit bunch hydrolysate | [332] |
| B. coagulans WCP 10-4 | 210 | 0.955 | 3.5 | Glucose or corn starch | [333] |
| B. coagulans C106 | 83.6 | 0.983 | 7.5 | Xylose | [334] |
| B. coagulans strain IPE22 | 38.73 | 0.813 | 0.39–0.65 | Pretreated wheat straw | [335] |
| B. coagulans | 0.94 | 0.33 | | Glucose/Cane molasses | [336] |
| B. coagulans strain AD | 1.4 | 3.69 | | Corn stover hydrolysate | [337] |
| B. coagulans strain IPE 22 | 7.52–56.13 | 0.13–0.94 | 0.31–2.77 | Single sugar (glucose, xylose, arabinose) | [338] |
| B. coagulans C106 | 49.15–51.47 | 0.82–0.86 | 2.05–3.08 | Mixed sugar (glucose + xylose + arabinose) | [339] |
| B. coagulans | 50.48–53.51 | 0.89–0.92 | 2.97–3.16 | Corn cob hydrolysate | |
| B. coagulans L-LA 1507 | 78–97.5 | 0.325–0.406 | 1.25–3.25 | Corn stover | [340] |
| B. coagulans AT107 | 98.8 | 0.80–0.92 | 1.25–3.15 | Alfalfa green juices and clover green juice | [341] |
| B. coagulans | 79.1 | 0.76 | | Lignocellulosic corn cob residue | [342] |
| B. coagulans | 92.5 | 0.578 | 2.01 | Dilute ethyldiamine pre-treated rice straw | [343] |
| B. coagulans + B. thermoamylolavorans | 39.2 | 1.09 | | Kitchen refuse medium | [118] |
| B. coagulans IPE22 | 68.72 | 0.99 | 1.72 | Inedible starchy biomass | [344] |
| B. coagulans LA-15-2 | 117 | 2.79 | | White rice bran | [345] |
| B. coagulans A166 | 61.1 | 0.94 | | Municipal solid waste | [346] |
| B. subtilis ZM63, B. cereus, Paenibacillus polymyxa and B. cereus | 49.14–51.47 | 0.82–0.86 | 2.05–3.08 | Corn cob hydrolysate | |
| B. coagulans strain IPE22 | 180 | 0.98 | 1.61 | Glucose | [347] |
| B. coagulans | 180 | 0.98 | 1.61 | Glucose | [348] |
| B. coagulans | 180 | 0.96 | 2.4 | Cellulosic hydrolysate | [349] |
| E. coli | 40–62.2 | 0.80–0.90 | | Glucose | [350] |
| E. coli | 45.5–51.8 | 0.91–0.99 | | Glucose | [351] |
| E. coli | 60.7 | 0.93 | | Xylose | [352] |
| E. coli | 56.8 | 0.88 | 0.94 | Glycerol | [353] |
| E. coli | 85 | 0.85 | 1.0 | Sucrose | [354] |
| E. coli K12 strain | 32 | 0.85 | 0.44 | Glycerol | [355] |
| E. coli | 75 | 0.85 | 1.18 | Molasses | [356] |
| lactogenic Escherichia coli strain JU15 | 40 | 0.6 | | Corn stover | [357] |
| E. coli BW25113 (DpIA) (engineered) | 5.2 | 22.5 | 0.06 | Cellulobiose | [358] |
| E. coli | 4.3–5 | 0.22–0.25 | | Glucose | [359] |
|  | 5.3 | 29.6 | 0.11 | Glucose | |

(continued on next page)
| Organism                | Yield g/L | Productivity g/(L/h) | Source       | Reference |
|-------------------------|-----------|-----------------------|--------------|-----------|
| E. coli MG1655-LA02Δdld (engineered) | 45        | 0.83                  | Glycerol     | [59]      |
| E. coli strain CICIM B0013-070 (pUC-ldhA) (engineered) | 111.5     | 0.78                  | Glycerol     | [354]     |
| Engineered E. coli      | 50        | 0.90                  | Glycerol     | [53]      |
| Engineered E. coli RR1  | 62.6      |                       | Glucose      | [13, 14]  |
| Corynebacterium glutamicum | 120       | 0.865                | Glucose      | [48]      |
| C. glutamicum           | 33.3      | 0.93                  | Call potato glucose | [356]     |
| C. glutamicum           | 83        | 65%                   | Glucose      | [13, 14]  |
| C. glutamicum           | 71.5      | 71%                   | Glucose      | [13, 14]  |
| C. glutamicum L-arabinose | 40         | 78%                   | Glucose      | [13, 14]  |
| C. glutamicum           | 40        | 6.2                   | Glucose      | [13, 14]  |
| Achromobacter denitrificans NBRC 12669 | 3.9 | 0.41                  | Glycerol     | [195]     |
| Fungi                   |           |                       |              |           |
| Rhizopus sp.            |           |                       |              |           |
| R. oryzae ATCC 52311    | 83.0      | 0.88                  | Glucose      | [70]      |
| R. oryzae               | 62        | 72%                   | Glucose      | [13, 14]  |
| R. oryzae sp. MK-96-1196 | 33.3      | 0.93                  | Call potato glucose | [356]     |
| R. oryzae               | 83        | 65%                   | Glucose      | [13, 14]  |
| R. oryzae               | 71.5      | 71%                   | Glucose      | [13, 14]  |
| R. oryzae               | 40        | 78%                   | Glucose      | [13, 14]  |
| R. oryzae               | 40        | 6.2                   | Glucose      | [13, 14]  |
| R. oryzae               | 112-173   | 78-94%                | Glucose      | [357]     |
| R. oryzae               | 104.6     | 87                    | Glucose      | [13, 14]  |
| R. oryzae               | 60        | 2.9-6.2               | Glucose      | [13, 14]  |
| R. oryzae               | -         | 2.91                  | Glucose      | [72, 77]  |
| R. oryzae NBRL 395      | 104.6     | 0.87                  | Glucose      | [153]     |
| R. oryzae NBRL 395      | 0.87-0.90 | 1.8-2.5               | Glucose      | [86]      |
| R. oryzae R1021         | 0.77      |                       | Glucose      | [83]      |
| R. oryzae NBRL 395      | 1.65      | Corn                  | [86]        |
| R. oryzae RBU2-10       | 1.84      | Rice                  | [358]       |
| R. arrhizus DAR 36017   | 1.3-1.6   | Potato                | [172]       |
| R. oryzae H256         | 0.80      | 0.99                  | Corn cob     | [155]     |
| R. oryzae NRRL395       | 24.0      | 0.3                   | Corn cob     | [65]      |
| R. oryzae NRRL395       | 49.1      | 0.7                   | Waste paper  | [153]     |
| R. oryzae GY18         | 115       | 0.81                  | Glucose      | [359]     |
| R. oryzae GY18         | 80.1      | 0.89                  | Sucrose      | [359]     |
| R. oryzae GY18         | 68.5      | 0.85                  | Xylose       | [359]     |
| R. oryzae NBRC 5378     | 14.4      | 0.56                  | Xylose       | [69]      |
| R. oryzae ATCC 9363     | 113       | 4.3                   | Glucose      | [360]     |
| R. oryzae NBRL 395      | 91.0      | 2.02                  | Corn starch  | [13, 14]  |
| R. oryzae               | 103.7     | 2.16                  | Glucose      | [84]      |
| R. oryzae NBRC 5384     | 145       | 1.42                  | Glucose      | [361]     |
| R. oryzae Ac3.819       | 231       | 1.83                  | Glucose      | [361]     |
| R. oryzae               | 51.7      | 0.68                  | Oat          | [362]     |
| R. oryzae               | 173.5     | 1.45                  | Tobacco waste water-extract and glucose | [363] |
| R. oryzae NBRC 5384     | 145       | 1.42                  | Glucose      | [361]     |
| R. oryzae Ac3.819       | 231       | 1.83                  | Glucose      | [361]     |
| R. oryzae               | 51.7      | 0.68                  | Oat          | [362]     |
| R. oryzae               | 173.5     | 1.45                  | Tobacco waste water-extract and glucose | [363] |
| R. oryzae Ac3.819       | 80.2      |                       | Glucose      | [364]     |
| R. oryzae               | 463.18    | 2.76                  | Cassava pulp | [365]     |
| R. oryzae               | 75.28     | 1.05                  | Cassava pulp hydrolysates | [366] |
| R. arrhizus             | 68.8      | 0.72                  | Honeycomb matrix | [367] |
| R. arrhizus             | 75.1      | 1.54                  | Glucose      | [368]     |
| R. arrhizus             | 1.2       |                       | Pretreated dairy manure | [369] |
| R. arrhizus             | 34-60.3   | 0.34-0.60             | Xylo-oligosaccharides manufacturing | [370] |
| R. arrhizus UMIP 4.77   | 10        | 0.26                  | Wheat straw  | [371]     |

(continued on next page)
Table 1 (continued)

| Organism | Lactic acid | Yield (g/L) | Productivity (g/L/h) | Source | Reference |
|----------|-------------|-------------|-----------------------|--------|-----------|
| **Rhizopus sp.** | | | | | |
| R. arrhizus | 46.78 | 0.97 | | Animal feeds from Sophora flavescens residues [372] |
| R. microsorus | 84.3–119 | 0.84–0.93 | 1.25 | Liquefied cassava starch [373] |
| R. arrhizus | 103.8 | | | Waste potato starch [374] |
| Monascus ruber | 129–190 | 0.58–0.72 | 0.91–1.15 | Glucose [375] |
| Aspergillus niger | 13.1–32.2 | | 0.26–0.47 | Glucose [376] |
| **Yeast** | | | | | |
| Engineered P. stipitis: LDH from L. helveticus (integrated, 1 copy) | 15–58 | 0.58 | 0.6 | Glucose [100] |
| **Saccharomyces** | | | | | |
| Engineered S. cerevisiae LDH from L. casei (multicopy vector) | 12 g/L | | | Glucose [13, 14] |
| Engineered S. cerevisiae LDH from L. casei | 8.6 | 0.04 | | Glucose [13, 14] |
| Engineered S. cerevisiae LDH from B. taurus (integrated, 1 copy) | 20 | | | Glucose [13, 14] |
| Engineered S. cerevisiae LDH from B. taurus (multicopy plasmid) | 11.4 | | | Glucose [13, 14] |
| Recombinant Saccharomyces cerevisiae CENPB2 | 2.22 | | | Food waste biomass [378] |
| Engineered S. cerevisiae OC-2T T165R | 6.1 | −0.45–1.6 | | Glucose [379] |
| Engineered S. cerevisiae LDH from B. taurus (multicopy plasmid) | 58 | | | Glucose [380] |
| Engineered S. cerevisiae LDH from L. plantarum (integrated, 1 copy) | 1.6 mol/96h | | | Glucose [92] |
| Engineered S. cerevisiae LDH from B. taurus (integrated, 2 copies) | 50.6 | | | Glucose [381] |
| Engineered S. cerevisiae LDH from B. taurus (integrated, 6 copies) | 120 | | | Glucose [381, 382] |
| Engineered S. cerevisiae LDH from L. mesenteroides (D-LDH, integrated, 2 copies) | 53.2 | | | Glucose [383] |
| Engineered S. cerevisiae LDH from B. taurus (integrated, 2 copies) | 82.3 | | | Glucose [95] |
| Engineered S. cerevisiae HDH from R. oryzae (multicopy plasmid) | 38 | | | Glucose [96] |
| Engineered S. cerevisiae HDH from L. plantarum (multicopy plasmid) | 70 | 0.93 | | Glucose [98] |
| Engineered S. cerevisiae LDH from B. taurus (integrated, 8 copies) | 80 | | | Glucose [97] |
| Engineered S. cerevisiae LDH from B. taurus (integrated, 2 copies) | 74.1 | | | Glucose [97] |
| Engineered S. cerevisiae LDH from B. taurus (integrated, 2 copies) | 71.8 | | | Glucose [97] |
| Engineered S. cerevisiae | 122 | 0.61 | | Cane juice [67] |
| S. cerevisiae | 117 | 0.58 | | Glucose [384] |
| Recombinant Saccharomyces cerevisiae | 60.3 | 0.646 | 2.8 | Cane juice [385] |
| Engineered Issatchenkia orientalis: LDH from L. helveticus (integrated, 1 copy) | 66 | | | Glucose [386] |
| Engineered Issatchenkia orientalis: LDH from L. helveticus (integrated, 1 copy) | 70 | | | Glucose [387] |
| **Candida** | | | | | |
| Candida utilis | 93.9 | 0.91 | 2.18 | Xylose [388] |
| Engineered Candida utilis: LDH from B. taurus – optimised (integrated, 2 copies) | 103.3 | | | |
heterofermentative *Lactobacillus* spp. are *Lb. brevis*, *Lb. fermentum*, and *Lb. reuteri*.

### 2.1.2. *Bacillus strains*

*Bacillus* also has metabolic capacity to produce LA. There are several advantages to the use of *Bacillus* spp. relatively to the LAB. The use of *Bacillus* spp., allows reducing the LA production cost, because: (1) they can grow and ferment in mineral salt media with inexpensive nitrogen source; (2) allow fermentation in high pH (6-6.5); (3) media sterilization before the fermentation process can be avoided due to the high temperature of LA fermentation process (≥50 °C) and so do not need also cooling after medium sterilization, with considerable costs reduction; (3) they can utilize all sugars from lignocellulose biomasses, due to the ability to metabolize pentose sugars via the pentose phosphate pathway and hexose sugars via the EMP pathway; (4) all strains of *Bacillus* produce only L-LA [15]; (5) they can convert substrates to LA with high yield or high productivity; (6) some strains namely *B. coagulans* JJ12 was tolerant to both furfural (4 g/l) and acetate (20 g/l). Neither pre-detoxification nor separation of fermentable sugars from lignin was needed before the fermentation. Meng et al. [16] and Patel et al. [17] reported that the alkaliphilic *Bacillus* sp. WI-S20 and *B. coagulans* 36D1 produced L-LA at concentration and yield of (225 g/L and 0.993 g/g) and (92.0 and 0.96 g/g), respectively. *Alkaliphilic Bacillus* sp. WL-S20 generated L-lactic acid in fed-batch fermentation at pH 9.0, which would reduce a risk of the contamination during fermentation and also can produce lactic acid in thermal fermentation (≥50 °C) [16].

### Table 1 (continued)

| Organism | Lactic acid g/L (plasmid) | Yield g/ (g (g/L/h) | Productivity Source | Reference |
|----------|---------------------------|---------------------|---------------------|-----------|
| *Candida boidinii* | | | | |
| Engineered *Candida boidinii* DH from *B. taurus* – optimized (integrated, 1 copy) | 85.9 | | Glucose | [99] |

| *Candida sonorensis* | | | | |
| Engineered *Candida sonorensis* from *Homo sapiens* (integrated, 1 copy) | 25-105 | | Alkali-pretreated corn cob | [392] |

| *K. marxianus* | 8.8 | 0.24 | 4.3 | [219] |
| Engineered *K. marxianus* from *actobacillus plantarum* | 122-130 | | Jerusalem artichoke tuber powder | [391] |

| *Schizosaccharomyces* | | | | |
| Engineered *Schizosaccharomyces pombe* DH from *R. oryzae* | 80-100 | | Glucose | [393] |

| *Microalgae and cyanobacteria* | | | | |
| *Alkaliphilic Bacillus* sp. WL-S20 generated L-Lactic acid in fed-batch fermentation at pH 9.0, and 0.993 g/g) and (92.0 and 0.96 g/g), respectively. | | | | [403] |

Cases with no data indicate absence of results in the cited reference.
Bacillus spp. have been accredited by European Food Safety Authority (EFSA) and Food and Drug Administration (FDA) to the Qualified Pre-summation of Safety (QPS) list and Generally Recognized As Safe (GRAS) status for applications in livestock production [18]. Some Bacillus strains could produce LA, including B. coagulans [19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33], B. steatorrhoeus [13, 14], B. licheniformis [34] thermophilic B. licheniformis [35], B. subtilis [36], Bacillus sp [37, 38, 39, 40], and alkaliophilic bacilli such as B. circulans var. alkaliophilus ATCC 21783, B. alcalophilus sp. halodurans ATCC 27557, B. alcalophilus ATCC 27647, alkaliphilic B. sp. WI-S20 and B. sp. 17-1 ATCC 31007 [16].

2.1.3. Corynebacterium glutamicum

Corynebacterium glutamicum is an aerobic Gram-positive bacterium that has been reported to be able to excrete amino acids (L-lysine and L-glutamate) and also small amounts of mix-organic acids (LA, succinic acid (SA), and AA) in industrial production. The organic acids production reported has occurred under oxygen deprivation conditions (anaerobic condition) due to cell growth inhibition and acceleration of mix-organic acids production; from various sugars, including D-glucose [41, 42, 43]; L-arabinose [44]; D-glucose and L-arabinose [45] D-xylene and D-glucose [46] and D-xylene, D-cellobiose and D-glucose [44] in mineral salts medium [13]. C. glutamicum is engineered and has highly potential bacterium that can produce LA with high yield and productivity without requiring complex nutritional compounds. C. virtutminus MTCC 5488 produced 38.5 g/L LA in fed-batch fermentation [13]. Meanwhile, C. glutamicum, as well as E. coli (section 1.4), have extremely low tolerance to acidic condition; hence LA production needs to be performed at pH-values about 7.0.

However, the simultaneous production of LA and the formation of several organic acids such as AA and SA resulted in a low LA production yield which should be improved [47]. Several types of research strategies were attempted to increase the LA production by C. glutamicum fermentation, through the promotion of medium conditions changes or by using engineering methodologies, such as:

A) Inui et al. [41] and Okino et al. [48] reported a novel system which consists in a reactor containing high-density cells (HDC) of C. glutamicum (the cell concentrations were almost 10-fold higher than those commonly used for batch fermentation) that could lead to the high volumetric productivity of LA. According to the results of Yukawa et al. [49], LA was produced by using the C. glutamicum R strain under an HDC condition.

B) Manipulation of C. glutamicum could produce D-lactic acid at higher productivity and purity compared with the parental strain. Simultaneously knock out of the L-LDH gene, and over expression of the D-LDH encoding gene was performed by inserting this gene into C. glutamicum from Lb. delbrueckii [45] and Lb. Bulgaricus [42].

Song et al. [50] reported an engineered C. glutamicum strain that can produce D-lactyl-CoA (by D-LDH and propionyl-CoA transferase) and 3-hydroxybutyryl-CoA (by β-ketothiolase and NADP-dependent acetacetyl-CoA reductase) from glucose, under several enzymatic reactions. Copolymerization of 3-hydroxybutyryl-CoA and D-lactyl-CoA by using lactate polymerizing enzyme reaction resulted in the production of poly (LA-co-3HB) with high LA fractions (96.8 mol%) [50].

C) On the other hand, some studies reported that an engineered C. glutamicum could utilize pentose sugars including xylose [46] and arabinoise [45], as well as hexose sugars, such as galactose and glucose. Kawaguchi et al. [46] inserted the genes xylA and xylB from E. coli into the C. glutamicum R strain that encodes xylose isomerase and xylulokinase, respectively, using a multicopy plasmid under the controlled promoter condition. Both the expression of xylA and xylB genes with xylose utilization ability could enhance the growth rate and production pattern of organic acid including L-LA and SA with interesting productivities (29 and 17 mmol/L/h) and yields (0.53 and 0.25 g/L, respectively) [46]. Kawaguchi et al. [45] performed another study in order to gain arabinoise utilization ability, throughout the expression of genes araA, araB and araD (encoding arabinoase isomerase, ribulokinase, and ribulose-5-phosphate 4-epimerase, respectively) from E. coli into the C. glutamicum R strain. The results showed that the engineered C. glutamicum could consume arabinoise, through successful arabinoase genes expression, leading to the production of L-LA (3.4 mmol/L/g dry cell), SA and AA. This L-LA was produced using a mixture of sugars (arabinoise and glucose), being the glucose consumption rate (0.76 g/L/g dry cell) significantly higher than the arabinoase counterpart (0.06 g/L/g dry cell) [45].

D) Pyruvate kinase (Pyk) plays a key role in the production of pyruvate and ATP in glycolysis pathway and, moreover, as an essential factor in controlling the carbon flux distribution. C. glutamicum only contains one Pyk (pyk1NCgl2008). Moreover, recently Chai et al. [51] found NCgl22809 as another novel pyruvate kinase (Pyk2) in C. glutamicum. These authors grew an engineered C. glutamicum containing Pyk1 or Pyk2 on D-ribose conditions, being the LA production enhanced by overexpression of either Pyk1 or Pyk2, due to the increase of the activity of the Pyk enzyme. They found that fermentation by the overexpression of Pyk2 in WT&pyk1 C. glutamicum strain could increase LA production to 60.27 ± 1.40 g/L (about 47% higher than the parent strain) under oxygen deprivation condition.

2.1.4. Escherichia coli

Wild-type E. coli is capable of growing and producing LA using hexoses and pentoses sugars fermentation with production of a mixture of organic acids (AA, SA, and formic acid (FA)) and ethanol [47, 52]. Moreover, they can grow on broth with more straightforward nutrient requirements compared to the conventional LAB.

Engineered E. coli showed improved LA fermentation efficiency compared with wild E. coli [13, 14, 52]. These engineered strains were manipulated by (1) replacement of D-LDH with L-LDH from LAB, bovine and other sources [13, 14, 52]; (2) prevention synthesis of racemic mixtures of D- and L-lactates by omission of methylglyoxal bypass route and consequently its accumulation; (3) avoiding of the undesired utilization of L-lactate by blocking the aerobic L-LDH [53]. Engineered E. coli strains can grow and produce LA from several disaccharides including sucrose [54, 55] and monosaccharides (hexoses and pentoses) including glucose [13, 14, 52, 56, 57], xylose [56], and also glycerol [13, 14, 59, 60]. Some researchers reported that engineered E. coli strains produce D-LA by the homofermentative substrate pathway that causes over-expressing of LA. However, engineered E. coli strains had shown several disadvantages, such as low productivity (<1.04 g/L/h) and low tolerance to low pH conditions due to LA production, in comparison with LAB [13, 14, 57].

2.2. Filamentous fungi

Filamentous fungi are another microbial source that can produce LA. Numerous species of the genus Rhizopus such as R. oryzae and R. arrhizus can produce LA (as the main product) fumaric acid, and ethanol from different carbon sources [64]. Among carbon sources, they aerobically metabolize glucose to produce LA. However, there are several renewable carbon resources for LA production by Rhizopus strains, which include corn cob hydrolysate [61, 62, 65, 64, 65], xylose [66, 67], glucose [13, 14, 68], wheat straw [69], paper pulp sulfite liquor [70], chicken feather protein hydrolysate [71], molasses [71], cassava pulp hydrolysis [72], potato hydrolysate [73], and glycerol enriched with lucerne green juice and inorganic nutrients [74]. Media containing nitrogen sources lead to a fast growth that induces the production of chitin instead of LA [15]. On the other hand, lack of nitrogen source leads to a decreased cell activity and product formation in long-term cultivation [15]. Two solutions to overcome this drawback was: 1) cells morphology affected LA.
productivity and yield (for example, fungal pellets instead of spores [73]; 2) medium composition manipulation by using low nitrogen sources and high content of carbon sources could enhance LA production [73]. Urea is one of the nitrogen sources used by genus *Rhizopus* that when added periodically within the production phase can avoid biofilm overgrowth, postpone sporulation, and retain high cell viability and LA productivity [72].

There are some advantages and disadvantages of using *Rhizopus* strains for LA production. Some benefits of *Rhizopus* strains in comparison to LAB include: 1) their amyloytic properties (containing amyloytic enzyme activity) that can convert various starchy biomasses directly to L-LA without prior saccharification process [75]; 2) simple medium requirements [76-78]; 3) their filamentous or pellet growth in fermentation medium facilitate their separation from fermentation broth, which can lead to lower-cost downstream process [79]; 4) fungal biomass is a worth fermentation by-product. On the other hand, *R. oryzae* is an obligate aerobe and requires vigorous aeration, usually above an oxygen transfer rate of 0.3 g O₂/L/h [80, 81]. A disadvantage of using fungi is related with the different morphology of growth under fermentation, which includes extended filamentous appearances, pellets, mycelial mats, and clumps that significantly affect LA productivity and rheology of broth medium. Their morphology can affect the oxygen supply and mass transfer. In fungal fermentation, the low LA productivity (below 3 g/(L⋅h)) is a result of the low O₂ mass transfer and synthetic route shift toward production of other by-products such as ethanol and fumaric acid. The preferable fungal morphology for industrial fermentations is small pellets by several reasons: 1) improved rheology of broth fermentation; 2) enhanced mass transfer in fermentation broth; 3) can be continuously utilized by using repeated batch fermentation for long operations [82].

Some researchers investigated fungal morphology that enhances the LA productivity. Abdel-Rahman et al. [13, 14] verified that high LA production was obtained by cotton-like mycelial flops morphology, which was formed by the culture of *R. oryzae* in the air-lift bioreactor.

Several reports attempted to achieve high yield and productivity of pure L-LA with higher cell density by fungal fermentation [71, 83, 84], including the following:

1. Immobilization techniques, being *Rhizopus oryzae* immobilized for LA production [13, 14, 85, 86], but entrapment of fungal cells on matrixes revealed to be time-consuming.

2. Controlling the production of undesirable by-products, mainly ethanol and fumaric acid leads to higher LA productivity [87, 88, 89].

2.1. Addition of alcohol dehydrogenase (ADH) inhibitor into the fermentation medium (i.e., 1,2-diazole and 2,2,2-trifluoroethanol) as an active inhibitor to decrease ethanol production and lactate dehydrogenase (LDH), as a useful promoter to increase LA and cell biomass production [90].

2.2. Metabolic engineering of the strain by deleting the alcohol dehydrogenase and malate dehydrogenase genes, thus shifting the metabolic flux, increasing LA production and yield [89].

As far as we are aware, there are no reports that include other fungi to produce LA. The fungus, *Aspergillus niger* together with *Lactobacllus* sp. was used for LA production. The strategy, in this case, was that fungi enzymes would perform saccharification and de-polymerization of carbohydrate polymers to produce fermentable sugars to be used by the bacterium [10, 91].

2.3. Yeasts

Presently, LAB is the main microorganisms used to LA production. However, there is one problem associated to their use; their low pH sensitivity leads to the use of large amounts of neutralizing agents, including CaCO₃ and results in the production of gypsum in fermentation medium [92]. Comparatively, yeasts versus bacteria, yeasts can tolerate low pH which leads to a reduction for the need of neutralizing agents and downstream processing cost. The worst important disadvantage of using wild-type yeasts is the reduced LA production as the main product. Nevertheless, engineered yeasts are the best solution to overcome this drawback.

Engineering yeast manipulation has been studied to obtain high LA productivity and yield, due to cancelation of pyruvate decarboxylase and/or pyruvate dehydrogenase activities, which results in the partial or full substitution of ethanol by LA production [93]. In order to improve the natural acid resistance of yeasts, lactic acid productivity has been enhanced by inserting the gene encoding L(+)-LDH from heterologous sources. The bovine gene encoding LDH has been successfully expressed in both *Candida utilis* and *Saccharomyces cerevisiae*, and the gene encoding LDH from *Lb. helveticus* has been expressed in *Candida sonorensis* [1].

Different research teams have been attempting to produce lactate from engineered yeasts genera including *Saccharomyces cerevisiae* [13, 14, 92, 94, 95, 96, 97, 98], *Candida spp.* [99], *Kluyveromyces lactis* [13, 14, 93], *Torulaspora delbrueckii* [13, 14], *Pichia stipites* [100] and *Zygosaccharomyces bailii* [101].

2.3.1. *Saccharomyces cerevisiae*

*Saccharomyces cerevisiae* is one of the more permissive organisms used for LA production due to a high intrinsic tolerance to low pH-values. This characteristic should give to *S. cerevisiae* several advantages over LAB and *Bacillus* spp. Firstly, it is a microorganism resistant to low pH and can grow aerobically on glucose sources with the basic anaerobic growth factors including oleic acid, nicotinic acid, and ergosterol.

Engineered *S. cerevisiae* can efficiently produce d-lactic acid due to its capability to grow fast under anaerobic and aerobic conditions. In transgenic strains, the coding section of pyruvate decarboxylase 1 (PDC1) was completely eliminated, and one or several copies of the d-lactate dehydrogenase (d-LDH) gene resources were inserted into the genome from mammalian LAB such as *Leuconostoc mesenteroides* subsp. *mesenteroides* strain NBC3426. This study was for the first time performed by Porro et al., 1995, having achieved an LA production of 20 g/l and productivity up to 11 g/L/h using engineered *S. cerevisiae* [13, 14].

2.3.2. *Candida*

2.3.2.1. *Candida sonorensis*. *Candida sonorensis* as a methylotrophic yeast that can ferment hexose (i.e., glucose) and pentose sugars (i.e., xylose and arabinose) to ethanol. They tolerate acid environments and require simple growth medium. *C. sonorensis* was manipulated by insertion of L-LDH genes from *Lb. helveticus*, *B. megaterium*, and *R. oryzae*. Multiple LDH gene copies were expressed to produce suitable mutants for LA production, which produced LA and ethanol. In order to increase the LA productivity, ethanol production was stopped by the elimination of two pyruvate decarboxylase genes (PDC) 1 and 2, being these the primary enzymes contributing to ethanol production. This modification (*C. sonorensis* expressing *L. helveticus* LDH) did not affect cell growth and resulted in the accumulation of lactate up to 92 g/l with a yield of 0.94 g/g glucose without ethanol production [102]. In another work, engineered *C. sonorensis* (L-lactic acid dehydrogenase (IdhL) from *Lb. helveticus*) was reported to produce 31 g/l LA from 50 g/l-D-xylose free of ethanol [103].

2.3.2.2. *Candida boidinii*. Genetic engineering can be used to construct a crabtree-negative methylotrophic haploid of *Candida boidinii* that can efficiently produce high amounts of L-LA [99]. The ethanol production of *C. boidinii* was 17% reduced by knocking out of the PDC1 gene encoding pyruvate decarboxylase when compared with the wild-type strain and with simultaneous heterologous expression of the bovine LDH gene resulted in 85.9 g/l of LA with a productivity of 1.79 g/l/h [99].

2.3.2.3. *Candida utilis*. *Candida utilis* as crabtree-negative yeast is currently used for the production of several valuable chemicals,
including glutathione, single cell protein, and RNA. The most pertinent advantage of *C. utilis* for LA production is the use of inexpensive substrates for growing, which includes pulping-waste liquors. In the study performed by Ikushima et al. [104], an engineered *C. utilis* strain produced L-LA with high efficiency. These authors reduce ethanol production (as a by-product of L-LA) by knocking out the gene encoding pyruvate decarboxylase (CuPDC1), and then two copies of the bovine L-lactate dehydrogenase (L-LDH) gene were inserted into the CuPdc1-null strain genome. The engineered *C. utilis* produced 103.3 g/l of L-LA with 95.1% conversion of basal medium and 99.9% purity.

2.3.3. Kluyveromyces

2.3.3.1. *Kluyveromyces lactis*. *Kluyveromyces lactis* is crabtree-negative yeast which was used for LA production after genetic modification. In comparison with some other yeasts strains, such as *S. cerevisiae*, which have a pyruvate decarboxylase (PDC) with two active structural genes (PDC1 and PDC5) [93], *Kluyveromyces lactis* has expressed PDC activity with a single gene, *KIPDC1*. The omission of *KIPDC1* leads to production strains without PDC activity and increase LA production with free ethanol. The intense competition for pyruvate consumption by homologous PDC and heterologous LDH activities leads to a low LA yield, due to the simultaneous production of ethanol and LA. On the other hand, the elimination of pyruvate decarboxylase gene (KlPDC1), as a single gene with PDC activity in *K. lactis*, resulted in no ethanol production [93]. In this yeast, the bovine L-lactate dehydrogenase gene (LDH) insertion and decarboxylase gene deletion were sufficient to increase the LA production to 109 g.l⁻¹, with a productivity of 0.91 g.l⁻¹.h⁻¹, and yield 1.19 mol.mol⁻¹ of consumed glucose [13, 14]. In another study, the KIPDC1 and pyruvate dehydrogenase (PDH) genes were deleted, being the LDH gene inserted into a wild-type of *K. lactis*. The LA production improved by shifting of pyruvate flux toward homolactic fermentation with a yield level of 0.85 g g⁻¹ (being the maximum theoretical yield 1 g.g⁻¹) [93].

2.3.3.2. *Kluyveromyces marxianus*. *Kluyveromyces marxianus* has several advantages which make it economically attractive for commercial-industrial applications, including 1) proliferation occurs at high temperatures (up to 52 °C), reducing contamination control in commercial cultivation, whereas most organisms in an industrial environment cannot be cultivated well at this temperature [105]; 2) *K. marxianus* in enriched media conditions, can grow rapidly with doubling times of 0.75–1 h (37 °C) [105]; 3) Many *K. marxianus* strains can utilize various inexpensive carbon sources and require few additional nutrients [105]. In this yeast, the LA concentration was improved by the insertion of the LDH gene from *B. megaterium* [105]. Also, Hause et al. [106] transformed *K. marxianus* by insertion of the LDH gene (from *Lb. helveticus* and integrated into PDC1 locus) and verified an L-LA production at 9.1 g/L.

2.3.4. *Zygosaccharomyces*

*Zygosaccharomyces bailii* has been suggested as another host for LA [107], due to its ability to tolerate environmental restrictions, including high sugar concentrations, acidic conditions, relatively high temperatures (higher than fermentation process) and LA production levels compared with *S. cerevisiae*. *Z. bailii* has a high growth rate and biomass yield which could improve the fermentation processes of LA production.

---

**Figure 2.** Pathways of lactic acid production from pentose sugars obtained from lignocellulose hydrolysate. Genes *AraA*, *AraB*, and *AraD* encoding arabinose isomerase, ribulokinase, and ribulose-5-phosphate 4-epimerase, respectively. *XylA*, and *xylB* encodes xylose isomerase, and xylulokinase. (1) arabinose isomerase; (2) ribulokinase; (3) ribulose-5-phosphate 3-epimerase; (4) xylene isomerase; (5) xylulokinase; (6) phosphoketolase; (7) acetate kinase; (8) phosphotransacetylase; (9) aldehyde dehydrogenase; (10) alcohol dehydrogenase; (11) lactate dehydrogenase; (12) transketolase; (13) transaldolase; (14) 6-phosphofructokinase; (15) fructose-bisphosphate aldolase; and (16) triosephosphate isomerase. PK pathway and PP pathway are phosphoketolase and pentose phosphate pathway. GA3P: glyceraldehyde-3-P, DHAP: Dihydroxyacetone-P.
An engineered *Z. bailii* was produced by heterologous LDH gene expression (from the bacterial L-LDH) to induce the shift of the glycolytic flux towards the lactate production [101, 107] to improve LA production efficiency.

### 2.3.5. *Pichia stipitis*

*Pichia stipitis* can utilize pentose and hexose sugars from lignocellulose hydrolysates as substrates to produce ethanol. The deletion of alcohol dehydrogenase 1 (ADH 1) and insertion of L-LDH (from heterologous *Lb. helveticus*) under the ADH1 promoter, led to an engineering *P. stipitis* producing 58 and 41 g/l of LA from 100 of xylose and 94 g/l glucose, respectively. Moreover, ethanol production was reduced by 15–30% and 70–80% compared with the wild-type strain, by xylose and glucose utilization, respectively [100].

### 2.4. Microalgae and cyanobacteria

Algae and cyanobacteria are included in the category of photosynthetic microorganisms, and they can grow almost anywhere, with a short harvesting cycle of about 1–10 days and produce various chemicals (including biofuels (H₂), ethanol, lactic, AA and FA). Algal biomass can be proposed as an alternative candidate to LA production without carbohydrate feed medium costs, being induced in high content of carbohydrates and proteins and also lack lignin [15, 108].

A few reports have evaluated the content of LA production by microalgal species, such as:

1. *Scenedesmus obliquus* strain D3 could produce d-LA as the main fermentation product [13, 14];
2. *Nannochlorum* sp. 26A4 produced LA at 26 g/L with a yield of 70% and optical purity of 99.8% from starch (40% content per dry weight) under dark and anaerobic conditions [109];

3. Biomass of *Nannochloropsis salina* contains 40% lipids, 20% carbohydrates, and 40% proteins. The neutralized and concentrated lipid-free residue has 64.3% of sugars (glucose and xylose). Co-fermentation of *N. salina* and *L. pentosus* under anaerobic fermentation could yield 10.1 g/L of LA with 92.8% of the conversion [110].

4. *Synechococcus elongates* PCC7942 engineered with simultaneous genes expression encoding glucose; lactate and fructose-facilitated diffusion transporter; L-LDH (from *E. coli*) and invertase could produce 600 μM of LA. Similarly, engineered *Synechocystis* sp. PCC6803 by insertion L-LDH gene (derived from *B. subtilis*) could produce of 3.2 mM LA [111].

3. Substrates for lactic acid production

3.1. Food waste

Food waste can include any compounds from the food production process to the wastes formed by the final consumer. Food waste contain a high amount of carbohydrate which causing it suitable as a substrate for lactic acid fermentation. Regarding to Table 1, numerous studies stated food waste are suitable for lactic acid production such as kitchen residues/refuse and municipal solid wastes [112], model kitchen refuse medium contain water, vegetables, meat/fish and cereals [113], mixes of cooked rice, vegetables, meat, and bean curd [113, 114]; rice, noodles, meat, and vegetables [115, 116]; vegetables such as carrot peel, cabbage, and potato peel, fruit such as banana peel, apple peel, and orange peel, baked fish, rice, and used tea leaves [117, 118]; rice, noodles, meat and vegetables, and unsold bakery products including cakes, breads and pastries [119]; rice, vegetables, and meat [120]; coffee mucilage [119]; and coffee pulp [121].

3.2. Carbohydrates

3.2.1. Starchy biomass and sugar plant wastes (malt, molasses and sugar beet juice)

Lactic acid can be produced from sugar plant wastes (molasses and sugar beet juice), starchy, and lignocellulosic biomasses (Figure 2). Disaccharides (lactose and sucrose) and monosaccharides hexoses (glucose, fructose, and galactose) and pentoses (xylose and arabinose) sugars can be fermented by LAB via EMP and/or the pentose PK pathway [122]. Molasses are waste products containing a large amount of sucrose...
and other essential nutrients, which can derive from sugar cane and sugar beet from sugar manufacturing plants. Several microorganisms can use molasses as a substrate including *Lb. delbrueckii* subsp. *delbrueckii* mutant Uc-3 [123], *Lb. delbrueckii* NCIM 2025 [124]; *Lb. delbrueckii* NCIM 8130 [125]; *Lb. delbrueckii* C.E.C.T. 286 [13,14], *Lb. delbrueckii* IPO 3202 [13, 14], *Lb. delbrueckii* [126], *Lb. plantarum* [127], *Sporolactobacillus cellulolysans* [13, 14], *Rhizopus arrhizus* [128], *Lb. casei* M-15 [129], *Bacillus* sp. X219 [29] and *E. faecalis* [130]. Shukla et al. (2004) also reported that recombinant *E. coli* strain could produce D-lactic acid from molasses [131]. Raw sugar beet juice with a Brix of at least 60 was used for LA production by lactic acid-producing microorganisms including bacteria (lactobacilli and moderately thermostable bacilli due to fermentation at relatively high temperature such as *B. coagulans, B. thermoamylovorans, Geobacillus stearothermophilus* and *B. smithii*), yeasts and fungi, such as, *Rhizopus* and *Aspergillus* [132]. Malt and date juice are another source for LA production by *Lb. casei* subsp. *rhamnosus* in batch and fed-batch cultures with a maximum LA production level of 89.2 g/L already achieved [133, 134].

There is a great interest to introduce cellulosic and starchy materials as substrates for LA production due to their abundance, low price and for being derived from renewable sources [135]. Amylolytic lactic acid bacteria (ALAB) such as *Lb. plantarum, L. fermentum* and *Lb. manihotivorans*, *Lb. amylophilus* and *Lb. amylovorus* can ferment starchy biomass into LA due to their α-amylase activities [13, 14, 136, 137]. Some ALAB were isolated from various amylaceous compounds, which include maize and maize-based fermented products [13, 14, 138], potato [13, 14, 139], sweet potato [13, 14, 140], sweet sorghum [13, 14], wheat [13, 14, 136, 141], rye [13, 14], oat [13, 14], barley [13, 14, 136] and other starchy substrates [134, 137, 142, 143, 144, 145, 146, 147].

### 3.2.2. Lignocellulosic biomass

Worldwide, there are abundant and cheap lignocellulosic materials, that include agricultural residues (corn stover, bagasse, and rice husk), forestry residues (sawdust), portions of municipal solid wastes (waste that include agricultural residues (corn stover, bagasse, and rice husk), forestry residues (sawdust), portions of municipal solid wastes (waste), chemical detoxification products with a maximum LA production level of 89.2 g/L already achieved [135, 136].

The addition of pectinases and cellulases in the fermentation medium can enhance LA production [150]. However, fermentation of lignocellulosic hydrolysates is prevented by the inhibitory effect of some compounds including acetic acid, furfural and 5-hydroxymethylfurfural, which are formed during pre-treatment of lignocellulose [150]. To reduce this inhibition, studies were performed through physical and chemical detoxification of the hydrolysate, being this mentioned as the challenges that must be overcome for their efficient utilization [14]. For LA production, several cellulosic materials can be used as substrate, such as: pure cellulose [13, 14, 151], lignocellulosic pentoses including xylose and arabinose (Figure 1) [13, 14, 63, 65, 66, 152] corncob [63, 65] waste paper [13, 14, 153, 154], and wood [64, 130, 155].

Yadav et al. (2020) indicated that *P. pentosaceus* SKL-7, *Lb. plantarum* SKL-19, *Lb. flavus* SKL-15, *Lb. plantarum* SKL-22, and *Lb. paracasei* SKL-21 grew well in presence of 1-Ethyl-3-methylimidazolium-acetate, 1-Butyl-3-methylimidazolium methane-sulfonate and 1-Butyl-3-methylimidazolium chloride. The *L. plantarum* SKL-22 demonstrated relatively high tolerance with greatest specific growth rates in presence of 0.5% and 1% 1-Butyl-3-methylimidazolium methane-sulfonate and 1-Butyl-3-methylimidazolium chloride. *L. plantarum* SKL-22 formed reasonable good content of lactic acid 34.26 g/L, so promising strain for production of lactic acid from lignocellulosic biomass [156].

### 3.3. Dairy wastes

#### 3.3.1. Cheese whey

Whey is the primary by-product of the dairy industry, containing proteins, lactose, fats, water-soluble vitamins and minerals. Lactose can be hydrolyzed into glucose and galactose by entering the cell via a permease and β-galactosidase (Figure 1) and can produce four LA moles [122, 177]. LAB are fastidious microbes that require complex macro and microelements since they don’t have enough proteolytic enzyme activity to utilize whey proteins [178]. For complete utilization of whey lactose and proteins, the addition of supplementary components with a nitrogen source such as yeast extract, peptone, and soy flour or steep corn liquor is necessary. Enriched whey showed a significant improvement in LA production [13, 108, 122, 177]. For instance, whey supplemented with whey protein hydrolysate or yeast extract enhanced the LA production and decreased the unused nutrients loss during bioprocessing [178, 179].

Several strains have been used for LA production from whey, including *Lb. plantarum, Lb. helveticus, Lb. acidophilus, Lb. delbrueckii* subsp. *bulgaricus, L. casei, L. lactis, and K. marxianus*. However, in conventional batch fermentation, there is a long lag phase in LA production from whey. To overcome this problem, a greater fermenter capacity is required, but this subsequently increases the operational costs [13, 14, 179]. On the other hand, continuous whey fermentation (without the requirement of high-volume) allowed obtaining a high LA productivity [13, 14, 180]. Semi-continuous fermentation conditions with nanofiltration membranes for recycling lactose and cells increased twice the LA production [181]. *Lactobacillus* and *Lactococcus* genus are the major LA producers who could efficiently utilize lactose and proteins, present in whey, with high conversion rates [13, 14, 179, 182, 183]. *Lb. sp. RKY2*, *Lb. casei* NRRL B-441 and *L. lactis* subsp. *cremoris* produced LA at 6.34, 3.97 and 4.6 g L⁻¹ h⁻¹; with a yield of 0.98, 0.93 and 0.88 g/g lactose, respectively [13, 14, 182, 184]. Also, *B. longum* NCFB 2259 could produce LA with a yield of 0.81 g/g whey lactose as a sole medium in a batch fermentation reactor [181]. On the other hand, LA initially present in whey could have an inhibitory effect in whey fermentation which can be reduced to a certain content by the application of mono or dipolar membranes in an electrodialysis system [185] or using a hollow fiber fermenter by a continuous dialysis process [13, 14].

#### 3.3.2. Yogurt

There is a huge amount of damaged or expired yogurt as waste products, which could provide a good resource for LA production [186]. Sweetened yogurt contains additional sugars, including sucrose and glucose, which would lead to a higher LA production, in comparison to cheese whey, which has fewer sugars. From yogurt whey LA was obtained with a productivity of 0.76 g/L/h and a yield of 0.9 g/g by *Lb. casei* ATCC 393 with bioconversion of about 44% of total sugars, with increasing order of consumption glucose > sucrose > lactose [186].

### 3.4. Industrial waste

This category includes glycerol from biodiesel industry and petroleum-based polymers. Glycerol is a byproduct of biodiesel industry that can be produced at a weight ratio of 1:10 (glycerol:biodiesel) [187].
There is abundantly glycerol being a cheap raw material that could be utilized by several microorganisms, which can convert glycerol to LA, such as Klebsiella pneumonia [188], Clostridium pasteurianum [189], Lb. Reuteri [13, 14], Lb. Brevis [13, 14], Lb. Buchneri [13, 14], wild-/engineered E. coli [55, 190, 191, 192, 193]. Engineered Enterococcus faecalis [194], and Achromobacter denitrificans NBRC 12669 [195]. According to Mazumdar et al. (2010) [53] and Posada et al. (2012a, b) [59, 187,196,197], the over expressing pathways in engineered E. coli strains via homofermentative route could convert glycerol to D-lactate [59, 187, 196].

3.5. Microalgae

Algal biomass is another source for LA production [15, 108, 134]. Some advantages of these substrates include: 1) the richness in carbohydrates, essential fatty acids, vitamins, and proteins; 2) the lignin absence in microalgae could simplify its conversion into fermentable sugars [198,199]; 3) the growth can be almost anywhere with extremely short harvest cycles of about 1–10 days [197]. 4) The use of microalgae and cyanobacteria is capable to decrease the feedstock cost, as a result of their ability to utilize light energy to fix CO2 [134]. The microalgae Hydrodictyon reticulum has been utilized as a substrate for the production of L-LA by Lb. paracasei LA104 and Lb. coryniformis subsp. Torquens [198]. Lb. paracasei LA104 and Lc. coryniformis subsp. torquens, by simultaneous saccharification and co-fermentation, achieved values of 37.1 g/l and 36.6 g/l LA and D-LA, respectively, from 80 g of L-lactate by Hydrodictyon reticulum (47.5%) [198, 199]. Lipid-free microalgae are good sources for LA production, such as Nannochloropsis salina for Lb. Pentosus [199], Chlamydomonas reinhardtii, Chlorell pyrenoidosa, and Dunaliella tertiolecta for L. amylvable [13, 14].

3.6. Feed stock pretreatment

Generally, three leading stages could be demonstrated for efficient fermentative LA production mainly (i) feedstock pretreatment, (ii) mixed and other substrates for LA production, (iii) ion requirement [10, 134, 147, 200].

The chemical composition of substrate mainly consist of carbon and nitrogen compounds. A lignocellulosic agricultural residue as worldwide resource is comprised of three main polymers: cellulose, hemicellulose and lignin, linked by covalent and non-covalent bonds. Not only, this organised structure cause to prevent cellulose and hemicelluloses hydrolysis into fermentable sugars, but also inhibit the valorisation of lignin into chemicals. The impacts of various pretreatment methods upon diverse lignocellulosic materials, e.g., wheat straw, corn stover, rice straw, switchgrass, and sugarcane bagasse have been demonstrated [10, 14, 134, 147, 200]. The pretreatment process is extremely crucial stage in lignocellulose bioconversion. If it is too intense, toxic compounds can be generated which prevent microbial metabolism and growth. In contrast, insufficient pretreatment will cause, the resultant residue is not easily saccharified through hydrolytic enzymes. Therefore, pretreatment has a great potential to affect the downstream costs due to enzymatic hydrolysis rates, enzyme loading, determining fermentation toxicity, mixing power, power generation, product purification, product concentrations, waste treatment demands, and other process variables. Numerous pretreatments for lignocellulosic materials are suggested as follow:

3.6.1. Physical pretreatment

1) Milling is being conducted for approximately all solid feedstocks to decrease particle size and cause it more accessible to other treatments or hydrolysis.

In order to improve fermentation, hydrolysis of carbohydrates to fermentable sugars is performed to facilitate microorganisms growth and their accessibility for biochemical conversion to LA. The hydrolysis of starchy substrate is carried out by amylolytic enzymes upon gelatinization, liquefaction and saccharification. The optimization of hydrolysis could be conducted for numerous substrates, temperature, time and mixing conditions etc [10, 14, 134, 147, 200]. 2) Liquid hot water and emerging technologies including pulsed electric field, high hydrostatic pressure and high pressure homogenization, ionizing (X-ray, beam) and non-ionizing (microwaves) radiation and non-thermal plasma can be also suitable as pretreatments or co-treatments during hydrolysis in bio-refinery processes, predominantly for lignocellulosic substrates and other substrates [10, 14, 134, 147, 200].

3.6.2. Chemical pretreatment

Combination of thermal pretreatments with alkaline, lime, organosolv, ammonia fiber explosion and ammonia recycle percolation, ionic liquid, natural deep eutectic solvents are “greener” method, and acids, making changes in all three portions of lignocellulose substrate [10]. Acid treatment was predominantly applied in the hydrolysis of lignocellulose. Dilute acid pretreatment reaction can cleave labile ester groups and catalyze the hydrolysis of the glycosidic bonds of hemicellulose and lignin. Hydrolysis of both hemicellulose and lignin, in turn, production of toxic by-products. Although, it minimizes the requirement for using hemicelluloses, acid hydrolysis cannot be combined with further enzymatic steps. Moreover, thermo-chemical pretreatments are considered as energy demanding and not environment friendly. The major drawback in the production of LA on lignocelluloses is formation of numerous undesirable compounds including furfural, uronic acid, vanillic acid, 4-hydroxybenzoic acid lignin or salts can influence microbial growth during fermentation and slow-down the fermentation and increase purification costs [10, 14, 134, 147, 200].

3.6.3. Biological pretreatments

This category of pretreatment is greater eco-friendly method than others and consists of various methods including:

1) Utilization of more productive species to decline time necessary for microbial growth and formation of enzymes and hence cause to increase efficiently and economically processes. For instance, basidiomycetes or their enzymes (lignin peroxidase, laccase and manganese peroxidase) to degrade lignocellulosic biomass [10, 14, 134, 147, 200].

2) Enzymatic hydrolysis is the abundant method to produce fermentable sugars from pretreated lignocellulosic biomass via depolymerizes the polysaccharides in the water-insoluble solid fraction. Therefore, it is critical step to consume polysaccharides as a carbon source by LAB [14]. Cellulases and hemicellulases enzymes can convert cellulose and hemicellulose into soluble sugars, respectively. In order to enhance enzymatic hydrolysis efficiency, mixtures of these enzymes are required to improve hemicellulose hydrolysis and then rise the access of cellulase, inducing to a reduced hydrolysis time and process cost [14]. Effective degradation and saccharification of cellulose demand a synergistic reaction of the 3 categories of cellulolytic enzymes in order: (i) Endo-β-1,4-glucanases (EG; EC 3.2.1.3) can randomly disassociate accessible intramolecular β -1,4-glucosidic bonds of cellulose chains, generating a new reducing and non-reducing chain end pair. (ii) Exo- β -1,4-glucanases or cellobiohydrolases (CBH; EC 3.2.1.91) can hydrolyze cellulose chains at the ends of the polymer, forming soluble cellubiose or glucose. (iii) β -Glucosidases (β-G; EC 3.2.1.21) (cellobiohases or glucose hydrolases) are capable complete the hydrolysis by cleaving cellubiose into 2 glucose molecules. They are also active on cellobioolsaccharides. Besides, there are accessory or “helper” enzymes that play a main role in hydrolysis by clearing the access of the leading enzymes to cellulose due to attack hemicellulose and lignin. Xylan does not generate tight crystalline structures, so the substrate is more easily accessible. However, in contrast to cellulose, xylans are chemically quite complex, and their hydrolysis needs multiple enzymes. Enzymatic hydrolysis of hemicellulose was performed by β

E. Abedi, S.M.B. Hashemi Heliyon 6 (2020) e04974
3.6.4. Mixed and other substrates for LA production

Wastes or by-products are main representatives of mixed substrates with different composition of carbohydrates and proteins. Meanwhile, they contain low nutritional values, so require additional fortification and often some treatment. Inhibitory or toxic components in these media have to be evaluated, also. Instead of consumption yeast extract or other Unconventional and expensive nitrogen sources, numerous agricultural residues or byproducts namely soya bean hydrolysate, corn steep liquor, corn meal and wheat bran hydrolysate, chicken feather hydrolysate, by-products from melting and brewing and oil production can be utilized as cheaper nitrogen sources [10, 14, 134, 147, 200] (Table 1). Substantial studies were demonstrated in the case of free amino nitrogen content such as amino acids, and phosphate to LA production. Complementary substrates in nitrogen and carbohydrate sources were combined for LA fermentation. For instance sugar beet molasses (rich in carbohydrates) and distillery stillage from bioethanol production from waste potato (rich in nitrogen source) were used for LA production by Lactobacillus paracasei. Many studies have shown that how to determine carbon to nitrogen ratio and correlate it with LA productivity. Carbon/nitrogen ratio significantly effects on LA yield and cell growth. When the carbon and nitrogen content are provided only from fermentable sugars and free amino nitrogen content, accurate optimization of media composition for LA production would be performed [10, 14, 134, 147, 200].

3.6.5. Ion requirement

It is obvious that metals play a key role in the biological processes, such as activating major enzymes in metabolism as cofactor, improving the growth of microbial cells and activation of organic acid synthesis by fungal and bacterial species [201].

3.6.5.1. Copper. Copper (II) by far has acted as a cofactor within numerous copper-dependent enzymes [201]. Furthermore, the microbial populations including LAB are more affected in the presence of copper (II) [202, 203, 204]. There are several hypotheses to improve lactic acid production in the presence of copper: a) it was proved that copper (II) inhibited the conversion of D-lactic acid to pyruvate via preventing the activity of NAD independent D-lactate dehydrogenase (id-LDH) in the pure culture, b) carbohydrate hydrolysis and glycolysis pathway were both strengthened that resulted in the promoting of lactic acid production from organic waste. The amount of copper (Cu-15; 15 μM/g, Cu-30; 30 μM/g and Cu-70; 70 μM/g) influence on the production of lactic acid (23.21 g/L), (17.44 g/L) and (16.53 g/L), respectively. It is indicated that the maximum concentration of lactic acid increased in the presence of copper compared to that of Blank (15.11 g/L). Nevertheless, continuously raising the copper level gradually reduced the production of lactic acid imply that that 70 μM-Cu2+/g VSS might exceed the tolerance of Lactobacillus and variation of functional genes revealed that the suggested homeostatic system towards copper (II) was activated at pretty low content that cause to facilitate the membrane transport function as well as carbohydrate metabolism [201].

3.6.5.2. Zinc. Regarding to Mumtaz et al., 2019, ZnO solubilization was associated to the synthesis of specific organic acids like Lactic and acetic acids. The culture medium was acidified and then ZnO solubilized. Two Zn- and acid-tolerant strains. Rhizosphere isolate Bacillus sp. ZM20 and B. cereus—culture-collection strain generated various organic acids at a remarkably greater content than less tolerant strains when cultured in the presence of inhibitory but non-lethal levels of ZnO. It is supposed that the enhanced synthesis of these acids is due to a generalized stress response [205].

4. Conclusions

The capacity of several microorganisms for production of LA was studied. Some of these microorganisms such as LAB require complex nutrients and low fermentation temperatures, which lead to increased costs and contamination risk. However, some of them like Bacillus spp., reduce the LA production cost due to fewer nutrition demands and a high temperature of fermentation. Agro-industrial waste or sub-products with a lower value such as molasses, juices waste, starchy biomass, agricultural residues, forestry residues that are rich in mono and disaccharides, which in some cases need to be hydrolysed by pectinases to enhanced the LA production. To use dairy wastes as a substrate, mainly whey, it is necessary to use an enriched mediums, due to insufficient proteolytic enzyme activity.

Declarations

Author contribution statement

All authors listed have significantly contributed to the development and the writing of this article.

Funding statement

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Competing interest statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

References

[1] B.P. Upadhyaya, L.C. DeVeaux, L.P. Christopher, Metabolic engineering as a tool for enhanced lactic acid production 32 (2014) 637–644.
[2] R.A. de Oliveira, A. Komen, C.E.V. Rosnell, R. Maciel Filho, Challenges and opportunities in lactic acid bioprocess design – from economic to production aspects, Biochem. Eng. J. 153 (2018) 219–239.
[3] D. Fleissner, P. Demichelis, M. Mariano, S. Fiore, L.M. Navarro Guiérrez, R. Schneider, J. Venus, Direct production of lactic acid based on simultaneous saccharification and fermentation of mixed restaurant food waste, J. Clean. Prod. 143 (2017a) 615–623.
[4] T. Payot, Z. Chemaly, M. Fick, Lactic acid production by Bacillus coagulans—kinetic studies and optimization of culture medium for batch and continuous fermentations, Enzym. Microb. Technol. 24 (1999) 191–195.
[5] K. Kyla-Nikkilä, M. Hujanen, M. Leinola, A. Palva, Metabolic engineering of lactobacillus helveticus CNRZ32 for production of pure(−)-lactic-α-lactid, Appl. Environ. Microbiol. 66 (2000) 3835–3841.
[6] G. Reddy, M. Altat, B. Naveena, M. Venkateshwar, E.V. Kumar, Amylolytic bacterial lactic acid fermentation—a review, Biotechnol. Adv. 26 (2008) 22–34.
[7] S.K. Singh, S.U. Ahmed, A. Pandey, Metabolic engineering approaches for lactic acid production, Process Biochem. 41 (2006) 991–1000.
[8] J. Zheng, S. Wittouck, E. Salvetti, C.M.A.P. Franz, H.M.B. Harris, P. Mattarelli, A-Nikkilä, S. Lebeer, A taxonomic note on the genus Lactobacillus: description of Lactobacillus paracasei subsp. B. cereus—culture-collection strain generated various organic acids at a remarkably greater content than less tolerant strains when cultured in the presence of inhibitory but non-lethal levels of ZnO. It is supposed that the enhanced synthesis of these acids is due to a generalized stress response [205].
L. Wang, B. Zhao, L. Wang, B. Yu, Y. Ma, C. Ma, H. Tang, J. Sun, P. Xu, Non-sterilized fermentative production of polymer-grade L-lactic acid by a newly isolated thermophilic strain Bacillus sp. 2–6, Plos One 4 (2009) e4559.

B. Zhao, L. Wang, C. Tan, X. Lian, X. Zhang, L. Xu, Y. Ma, Repeated open fermentative production of optically pure L-lactic acid using a thermophilic Bacillus sp. strain, Biotechnol. Biofuels 10 (2017) 649–6498.

M. Inui, S. Murakami, S. Okino, H. Kawaguchi, A.A. Vertes, H. Yukawa, Metabolic analysis of Corynebacterium glutamicum during lactate and succinate productions under oxygen deprivation conditions, J. Mol. Microbiol. Biotechnol. 7 (2004) 182–196.

K. Liu, S. Li, S. Li, J. Wen, D-lactic acid production by a genetically engineered strain Corynebacterium glutamicum, World J. Microbiol. Biotechnol. 27 (2011) 2117–2124.

S. Okino, M. Suda, K. Fujioka, M. Inui, H. Yukawa, Production of D-lactic acid by Corynebacterium glutamicum under oxygen deprivation, Appl. Microbiol. Biotechnol. 78 (2008) 449–454.

M. Sasaki, T. Jojima, M. Inui, H. Yukawa, Simultaneous utilization of D-cellulose, D-glucose, and D-xylene by recombinant Corynebacterium glutamicum under oxygen-deprived conditions, Appl. Microbiol. Biotechnol. 81 (2008) 691–699.

H. Kawaguchi, M. Sasaki, A.A. Vertes, M. Inui, H. Yukawa, Engineering of an L-arabinose metabolic pathway in Corynebacterium glutamicum, Appl. Microbiol. Biotechnol. 77 (2008) 1053–1062.

H. Kawaguchi, A.A. Vertes, S. Okino, M. Inui, H. Yukawa, Engineering of a xylose metabolic pathway in Corynebacterium glutamicum, Appl. Environ. Microbiol. 72 (2006) 3418–3428.

K. Tominaga, T. Tanaka, C. Ogino, H. Fukuda, A. Kondo, Biotechnological production of enantiomerically pure lactic acid from renewable resources: recent achievements, perspectives, and limits, Appl. Microbiol. Biotechnol. 85 (2010) 413–423.

S. Okino, M. Inui, H. Yukawa, Production of organic acids by Corynebacterium glutamicum under oxygen deprivation, Appl. Microbiol. Biotechnol. 68 (2005) 475–480.

H. Yukawa, C.A. Osumanaba, H. Nonaka, P. Kos, N. Okai, N. Suzuki, M. Suda, Y. Tsuge, J. Watanabe, Y. Ikeda, Comparative analysis of the Corynebacterium glutamicum group and complete genome sequence of strain R, Microbiology 153 (2007) 1042–1058.

Y. Song, K.I. Matsumoto, M. Yamaoda, A. Gohda, C.J. Brigham, A.J. Sänksy, S. Taguchi, Engineered Corynebacterium glutamicum as an endotoxin-free probiotic strain for lactic acid and polymer production, Appl. Microbiol. Biotechnol. 93 (2012) 1917–1925.

X. Chai, X. Shang, Y. Zhang, S. Liu, Y. Liang, Y. Zhang, T. Wen, A novel pyruvate kinase and its application in lactic acid production under oxygen deprivation in Corynebacterium glutamicum, BMC Biotechnol. 16 (2016) 79.

S. Zhou, T. Causby, A. Hasona, K. Shanmugam, L. Ingram, Production of optically pure D-lactic acid in mineral salts medium by metabolically engineered Escherichia coli W3110, Appl. Environ. Microbiol. 69 (2003) 599–407.

S. Mazumdar, M.D. Blankschien, J.M. Cloumborg, R. Gonzalez, Efficient synthesis of L-lactic acid from glycerol by metabolically engineered Escherichia coli, Microb. Cell Factories 12 (2013) 7.

W. Yang, T. Tian, J. Shang, W. Jiang, T. Yan, L. Yu, Z. Li, G. Fan, J. Han, Engineering of a D-lactic acid producer by expressing the ldhL gene from Pediococcus acidilactici, Enzym. Microb. Technol. 38 (2006b) 569–576.

M. Rosenberg, M. Rebrot, L. Kristoffikova, K. Mahalova, High temperature lactic acid production by Bacillus coagulans immobilized in LentiKats, Biotechnol. Lett. 27 (2005) 1943–1947.

K. Sakai, Y. Ezaki, Open lactic acid fermentation of food refuse using thermophilic Bacillus coagulans and florescence in situ hybridization analysis of microflora, J. Biosci. Bioeng. 101 (2006) 457–463.

S.L. Walton, K.M. Bischoff, A.R. van Heiningen, G.P. van Walsum, Production of lactic acid from hexose and pentose sugars, J. Ind. Microbiol. Biotechnol. 168 (2012) 2387–2397.

M. Inui, T. Maeda, H. You, T. Shirai, Open fermentative production of l-lactic acid with high optical purity by thermophilic Bacillus coagulans using excess sludge as nutrient, Biotechnol. Biofuels. 15 (2014) 28–35.

M. Rosenberg, M. Rebrot, L. Kristoffikova, K. Mahalova, High temperature lactic acid production by Bacillus coagulans immobilized in LentiKats, Biotechnol. Lett. 27 (2005) 1943–1947.

K. Sakai, Y. Ezaki, Open lactic acid fermentation of food refuse using thermophilic Bacillus coagulans and florescence in situ hybridization analysis of microflora, J. Biosci. Bioeng. 101 (2006) 457–463.

S.L. Walton, K.M. Bischoff, A.R. van Heiningen, G.P. van Walsum, Production of lactic acid from hexose and pentose sugars, J. Ind. Microbiol. Biotechnol. 168 (2012) 2387–2397.

M. Inui, T. Maeda, H. You, T. Shirai, Open fermentative production of l-lactic acid with high optical purity by thermophilic Bacillus coagulans using excess sludge as nutrient, Biotechnol. Biofuels. 15 (2014) 28–35.

M. Inui, T. Maeda, H. You, T. Shirai, Open fermentative production of l-lactic acid with high optical purity by thermophilic Bacillus coagulans using excess sludge as nutrient, Biotechnol. Biofuels. 15 (2014) 28–35.

M. Inui, T. Maeda, H. You, T. Shirai, Open fermentative production of l-lactic acid with high optical purity by thermophilic Bacillus coagulans using excess sludge as nutrient, Biotechnol. Biofuels. 15 (2014) 28–35.

M. Inui, T. Maeda, H. You, T. Shirai, Open fermentative production of l-lactic acid with high optical purity by thermophilic Bacillus coagulans using excess sludge as nutrient, Biotechnol. Biofuels. 15 (2014) 28–35.

M. Inui, T. Maeda, H. You, T. Shirai, Open fermentative production of l-lactic acid with high optical purity by thermophilic Bacillus coagulans using excess sludge as nutrient, Biotechnol. Biofuels. 15 (2014) 28–35.
A. Nancib, N. Nancib, J. Boudrant, Production of lactic acid from date juice extract

Y.-J. Wee, J.-S. Yun, D.-H. Park, H.-W. Ryu, Biotechnological production of L (V. Shukla, S. Zhou, L. Yomano, K. Shanmugam, J. Preston, L. Ingram, Production of B. Naveena, C. Vishnu, M. Altaf, G. Reddy, Wheat bran an inexpensive substrate

Y. Zhang, P.-j. He, N.-f. Ye, L.-m. Shao, Enhanced isomer purity of lactic acid from (2006) 1036–1043.

R. Y. Connor, The eco-pro...A.H. Jawad, A.F. Alkarkhi, O.C. Jason, A.M. Easa, N.N. Norulaini, Production of H.K. Sreenath, A.B. Moldes, R.G. Koegel, R.J. Straub, Lactic acid production from B. Zhang, P.-j. He, N.-f. Ye, L.-m. Shao, Enhanced isomer purity of lactic acid from A. Jukonyte, Z. Daiva, E. Bartkiene, V. Lele, D. Cernauskas, S. Suproniene, G. Juodeikiene, A potential of brown rice polish as a substrate for the lactic acid bioconversion of A.B. Moldes, J.K. Alonso, J.C. Parajo, Strategies to improve the bioconversion of coagulans at laboratory and pilot scales, Biotechnol. (2016) 100423.

A. K. Thakur, S. Bhatt, S. Srivastava, Lactic acid production from cane molasses by Lactobacillus perfringens strain, J. Food Sci. Technol. 56 (2019) 3357–3364.

A. Pande, S. Bhatt, S. Srivastava, Lactic acid production from grape molasses by Lactobacillus plantarum, J. Sci. Ind. Res. 77 (2018) 774–778.

A. Pradhan, S. Bhatt, S. Srivastava, Lactic acid production from sugarcane bagasse waste using Lactobacillus plantarum, J. Ind. Microbiol. Biotechnol. 44 (2017) 1253–1258.

A. Pradhan, S. Bhatt, S. Srivastava, Lactic acid production from grape molasses by Lactobacillus plantarum, J. Ind. Microbiol. Biotechnol. 44 (2017) 1247–1252.

A. Pradhan, S. Bhatt, S. Srivastava, Lactic acid production from sugarcane bagasse waste using Lactobacillus plantarum, J. Ind. Microbiol. Biotechnol. 44 (2017) 1253–1258.

A. Pradhan, S. Bhatt, S. Srivastava, Lactic acid production from sugarcane bagasse waste using Lactobacillus plantarum, J. Ind. Microbiol. Biotechnol. 44 (2017) 1247–1252.
Y. Zheng, Y. Wang, J. Zhang, J. Pan, Using tobacco waste extract in pre-culture fermentation of L-lactic acid using white rice bran by simultaneous saccharification and fermentation of crude feedstock fermentation products.

K. Xu, P. Xu, Lactic acid production from cellulosic biomass by Rhizopus oryzae fermentation using b-glucosidase-displaying Escherichia coli, J. Biosci. Bioeng. 115 (2013) 90

C. Ishida, C. Aranda, L. Valenzuela, L. Riego, A. DeLuna, F. Recillas-Targa, N. Ishida, S. Saitoh, T. Onishi, K. Tokuhiro, E. Nagamori, K. Kitamoto, J.Y. Lee, C.D. Kang, S.H. Lee, Y.K. Park, K.M. Cho, Engineering cellular redox balance in Saccharomyces cerevisiae to enhance production of L-lactic acid, Biotechnol. Bioeng. 114 (2017) 2075–2086.

E.N. Efremenko, O.V. Spiricheva, D.V. Veremeenko, A.V. Baibak, V.I. Lozinsky, Lactobacillus plantarum. Journal of Biological and Engineering 102 (2006) 227–232.

Y. Li, R. Ruan, P.L. Chen, Z. Liu, X. Pan, X. Lin, Y. Liu, C. Mok, T. Yang, Enzymatic hydrolysis of corn stover pretreated by combined dilute alkaline treatment and steam explosion. Bioresour. Technol. 148 (2013) 394–400.

M.A. Patel, M.S. Ou, L.O. Ingram, K. Shanmugam, Simultaneous saccharification and fermentation of cellulose and hemicellulose from sugarcane bagasse. Bioresour. Technol. 153 (2015) 132–140.

D. Dettt, R. Schneider, F. Papendiek, J. Venema, Leguminose green juice as an efficient nutrient for L(+)-lactic acid production, J. Biotechnol. 236 (2016) 26–34.

J.P. Liao, M. Latorre-Sanchez, C. Collazo Lozano, J. Venema, Organic fraction of municipal solid waste for the production of L-lactic acid with high optical purity, J. Clean. Prod. 247 (2020) 119165.

K. Sakai, N. Fugi, E. Chakraborti, Racemization of L-lactic acid in pH-swollen open fermentation of lactic acid production by Lactobacillus plantarum. Journal of Biological Science and Engineering 102 (2006) 227–232.

Y. Guo, Q. Yan, Z. Jiang, C. Teng, X. Wang, Exploring the potential of lactic acid production from inedible starchy biomass by thermophilic Lactobacillus plantarum. Process Biochem. 9 (2020) 132.

P. Qin, Lactic acid production from pretreated corn stover with recycled streams, Bioresour. Technol. 98 (2007) 1247–1251.

B.K. Ahring, J.J. Traverso, N. Murali, K. Srinivas, Continuous fermentation of L-lactic acid using immobilized Rhizopus oryzae fungal cells. Journal of Chemical Technology and Biotechnology: International Research in Process, Environ. Clean Technol. 81 (2006b) 519–525.

J. Sun, J. Zhu, W. Li, L(+)-lactic acid production by Rhizopus oryzae using pretreated dairy manure as carbon and nitrogen source, Biomass Bioenergy 7 (2012) 442–450.

L. Jiang, X. Li, Q. Yong, S.T. Yang, J. Ouyang, S. Yu, Simultaneous saccharification and fermentation of oxalyl-oligosaccharides manufacturing waste residue for l-lactic acid production by Rhizopus oryzae. Bioeng. Chem. 9 (2015) 92–99.

K. Vially, R. Marchal, N. Guibert, L(+)-lactic acid production from carbohydrate- and lignocellulosic materials by Rhizopus oryzae UMP1 4.77, World Microbiol. Biotechnol. 26 (2010) 607–614.

X. Ma, M. Gao, Z. Yin, W. Zhu, S. Liu, Q. Wan, Lactic acid and animal feeds production from Sophora flavescens residues by Rhizopus oryzae fermentation process. Bioeng. Chem. 9 (2020) 401–408.

S. Trakarpaloon, B. Srirukkunl, S.T. Wang, V. Kittpeeravanich, L-lactic acid production from liquefied cassava starch by thermotolerant Rhizopus microsporus: characterization and optimization. Process Biochem. 63 (2017) 26–34.

Z. Zhang, B. Jin, L(+)-lactic acid production using sugarcane molasses and waste potato starch: an alternative approach. Int. Sugar J. 112 (2010) 17.

R. Areshrath, E. Ais, K. Dhole, S. Jadhav, H. van der Wal, T.G. de Vrije, M. Levinson, A. Leprinse, G.B. Houweling-Tan, A.P.H.A. Moors, S.N. A Hendriks, O. Mendes, Y. Griessknoop, M.W.T. Werten, P.J. Schaap, J. van der Oost, G. Eggink, Monascus ruber as cell factory for lactic acid production at low pH, Metab. Eng. 14 (2012) 66–72.

M. Naou, M.N. Rosso, N. Fabre, S. Crapart, I. Herpoil-Gimbet, J.C. Sigismondo, S. Racoue, A. Levasseur, L-lactic acid production by Aspergillus brasiliensis overexpressing the heterologous lidha gene from Rhizopus oryzae, Microb. Cell Fact. 14 (2015) 1–10.

K.K. Dev, P. Sneh, Explorations of lactic acid dehydrogenase in Aspergillus niger for L-lactic acid production, PloS One 10 (2015), e0145459.

Y.S. Kim, Y.J. Jang, S.J. Park, B.H. Um, Dilute sulfuric acid fractionation of Korean food waste for ethanol and lactic acid production by yeast, Waste Manag. 74 (2018) 231–240.

M.T. Gao, T. Shimamura, N. Ishida, H. Takahashi, Fertilemicytic lactic acid production with a metabolically engineered yeast immobilized in photo-crosslinkable resins, Biochem. Eng. J. 47 (2009) 66–70.

S. Colombié, S. Dequin, J. Sablayrolles, Control of lactic acid production by Saccharomyces cerevisiae expressing a bacterial LDH gene, Enzym. Microb. Technol. 33 (2003) 317–322.

A. Zorzi, P. Suominen, A. Aristidou, B.M. Hause, P. Van Hoek, C.A. Dundon, L(+)-lactic acid production from biomass by a recombinant Candida utilis strain, J. Biosci. Bioeng. 113 (2012) 73–78.

M. Miller, P. Suominen, A. Aristidou, B.M. Hause, P. Van Hook, C.A. Dundon, Lactic acid-producing yeast cells having non-functional L-or D-lactate: ferricytochrome c oxidoreductase cells, Google Patents (2012).

C. Ishida, C. Aranda, L. Valenzuela, L. Riego, A. DeLuna, F. Recillas-Targa, P. Filetici, R. Lopez-Revilla, A. Gonzalez, The UGA3-GLTI intergenic region constitutes a promoter whose bidirectional nature is determined by chromatin organisation in Saccharomyces cerevisiae, Mol. Microbiol. 59 (2006a) 1790–1806.

J.Y. Lee, C.D. Kang, S.H. Lee, Y.K. Park, K.M. Cho, Engineering cellular redox balance in Saccharomyces cerevisiae for improved production of L-lactic acid, Bioresour. Technol. 118 (2013) 75–84.

R. Yamada, K. Wakita, R. Mitsu, H. Ogino, Enhanced D-lactic acid production by recombinant Saccharomyces cerevisiae following optimization of the global metabolic pathway, Biotechnol. Bioeng. 114 (2017) 2075–2084.

M. Miller, P. Suominen, A. Aristidou, B.M. Hause, P. Van Hook, C.A. Dundon, Production of L-lactic acid by the yeast Candida sonorensis expressing heterologous pyruvate decarboxylase gene knockout in Saccharomyces cerevisiae on L-lactic acid production, Biosci. Biotechnol. Biochem. 70 (2006b) 1148–1153.
[391] J.-H. Bae, H.-J. Kim, M.-J. Kim, B.H. Sung, J.-H. Jeon, H.-S. Kim, Y.-S. Jin, D.-H. Kweon, J.-H. Sohn, Direct fermentation of Jerusalem artichoke tuber powder for production of L-lactic acid and D-lactic acid by metabolically engineered Kluyveromyces Marxianus, J. Biotechnol. 266 (2018) 27–33.

[392] X. Kong, B. Zhang, Y. Hua, Y. Zhu, W. Li, D. Wang, J. Hong, Efficient L-lactic acid production from corn cob residue using metabolically engineered thermo-tolerant yeast, Bioreour. Technol. 273 (2019) 220–230.

[393] S.S. Pavlovich, V.M. Mikhajlovic, J.T. Vladimirovich, R.J. Aleksandrovich, R.E. Isakovna, T.N. Georgievna, V.M. Aleksandrovna, A.A. Mikhajlovna, D.V. Georgievich, Method for Microbiological Synthesis of Lactic Acid and Recombinant Strain of Yeast Schizosaccharomyces pombe for its Realization, 2006. Russian Patent Application RU000002268304.

[394] A. Ozaki, R. Konishi, C. Otomo, M. Kishid, S. Takayama, T. Matsumoto, T. Tanaka, A. Kondo, Metabolic engineering of Schizosaccharomyces pombe via CRISPR-Cas9 genome editing for lactic acid production from glucose and cellobiose, Metabol. Eng. Commun. 5 (2017) 60–67.

[395] R. Yamada, K. Wakita, R. Mitsui, H. Ogino, Enhanced D-lactic acid production by recombinant Saccharomyces cerevisiae following optimization of the global metabolic pathway, Biotechnol. Bioeng. 114 (2017) 2075–2084.

[396] S.H. Baek, E.Y. Kwon, Y.H. Kim, J.S. Hahn, Metabolic engineering and adaptive evolution for efficient production of d-lactic acid in Saccharomyces cerevisiae, Appl. Microbiol. Biotechnol. 100 (2016) 2737–2748.

[397] A.M. Varman, Y. Yu, L. You, V.J. Tang, Photoautotrophic production of D-lactic acid in an engineered cyanobacterium, Microb. Cell Factories 12 (2013) 117.

[398] J. Li, W. Zhang, X. Li, T. Ye, Y. Gan, A. Zhang, H. Chen, G. Xue, Y. Liu, Production of lactic acid from thermal pretreated food waste through the fermentation of waste activated sludge: effects of substrate and thermal pretreatment temperature, Bioresour. Technol. 247 (2018) 890–896.

[399] S. Akao, H. Tsuno, J. Cheon, Semi-continuous L-lactate fermentation of garbage without sterile condition and analysis of the microbial structure, Water Resour. 41 (2007) 1774–1780.

[400] Y. Itoh, K. Tada, T. Kanno, J.I. Horiuchi, Selective production of lactic acid in continuous anaerobic acidogenesis by extremely low pH operation, J. Biosci. Bioeng. 114 (2012) 537–539.

[401] D.H. Kim, W.T. Lim, M.K. Lee, M.S. Kim, Effect of temperature on continuous fermentative lactic acid (LA) production and bacterial community, and development of LA-producing UASB reactor, Bioreour. Technol. 119 (2012) 355–361.

[402] T. Maeda, T. Yoshimura, T. Shimazu, Y. Shirai, H.I. Ogawa, Enhanced production of lactic acid with reducing excess sludge by lactate fermentation, J. Hazard Mater. 168 (2009) 656–663.

[403] Y. Sun, Z. Xu, Y. Zheng, J. Zhou, Z. Xiu, Efficient production of lactic acid from sugarcane molasses by a newly microbial consortium CEE-DL15, Process Biochem. 81 (2019) 132–138.

[404] J. Tang, X.C. Wang, Y. Hu, Y. Zhang, Y. Li, Effect of pH on lactic acid production from acidogenic fermentation of food waste with different types of inocula, Bioreour. Technol. 224 (2017b) 544–552.