fermentation

Review

Sourdoughs as Natural Enhancers of Bread Quality and Shelf Life: A Review

Ricardo H. Hernández-Figueroa, Emma Mani-López, Enrique Palou * and Aurelio López-Malo

Chemical, Food, and Environmental Engineerinng Department, Universidad de las Américas Puebla, San Andrés Cholula, Puebla 72810, Mexico; ricardoh.hernandezf@udlap.mx (R.H.H.-F.); emma.mani@udlap.mx (E.M.-L.); aurelio.lopezm@udlap.mx (A.L.-M.)
* Correspondence: enrique.palou@udlap.mx

Abstract: Sourdough is a key component in traditional and artisanal bread making. It imparts unique flavors and textures to bread, which are highly sought after by consumers. The use of sourdoughs to prepare bakery products has been researched for more than 30 years, and accumulated research shows the performance of sourdoughs as an alternative to improve the organoleptic characteristics of bread and its shelf life. The purpose of this review is to present an overview of the research carried out on the use of sourdoughs from lactic acid bacteria and their benefits in the quality characteristics of bread, as well as to present relevant and recent information on the use of sourdoughs and their aqueous extracts for the preservation of bakery products. Also, the advances in the identification of antifungal compounds have been revised. In general, it has been shown that incorporating sourdoughs into the bread formulation positively impacts the product's flavor and helps slow down the bread's aging process and spoilage. Also, it has been observed that the bioactive compounds formed by lactic acid bacteria (LAB) during sourdough fermentation and their extracts have an antimicrobial, especially antifungal, capacity that significantly helps increase bread's shelf life. Studying sourdough as part of fermentation processes and product development is essential to improve bread production's quality, diversity, and sustainability, and to advance our understanding of the science behind this food tradition.

Keywords: sourdough; lactic acid bacteria; bread quality; antifungals; shelf life

Citation: Hernández-Figueroa, R.H.; Mani-López, E.; Palou, E.; López-Malo, A. Sourdoughs as Natural Enhancers of Bread Quality and Shelf Life: A Review. *Fermentation* **2024**, *10*, 7. https://doi.org/10.3390/fermentation10010007

Academic Editor: Ronnie Willaert

Received: 16 November 2023
Revised: 14 December 2023
Accepted: 18 December 2023
Published: 21 December 2023

1. Introduction

Bread is one of the most consumed fermented foods in the world and is an important part of the food base of many countries [1]. In general, bread is a product made by baking a dough previously fermented with yeast and, in some types of bread, other micro-organisms that give it the important characteristics and quality attributes of this product. However, fresh bread has a short shelf life, governed mainly by physicochemical alterations known as aging and mold growth on the product's surface. To improve the shelf life of bakery products, the baking industry has used the incorporation of synthetic additives and antimicrobial agents, which have been shown to have the ability to reduce both the aging process of bread and the growth of molds on the surface of baking products. However, consumer demand for natural products or products without synthetic additives has generated the search for new "natural" alternatives that help replace these synthetic additives and maintain the shelf life of bread [2,3].

One of the oldest ways of bread leavening is sourdough fermentation, converting cereal flour into attractive, tastier, and more digestible products [1,4]. An alternative approach that has attracted the attention of the scientific community in recent years is the use of sourdough to leaven various bakery products, as well as to incorporate it into the formulation of other products, which creates research opportunities in the use of sourdoughs and their fermentation products with very diverse applications and approaches [1,5]. An alternative that has attracted attention in recent years is to use sourdough together with baker's yeast to produce bread at an industrial level and have the benefits of its incorporation in the formulation [6]. For many years, sourdoughs have been used in the European and Western regions to make bread [7] since it has been observed that incorporating them helps maintain the product's organoleptic characteristics and delays the growth of molds on the product's surface. This fermented dough has a complex microbiome that mainly includes lactic acid bacteria and yeasts [4]. It has been shown that during the formation of sourdoughs, compounds such as organic acids, peptide compounds, and exopolysaccharides are formed, which help maintain the shelf life of the product, preserving the quality characteristics of the bread and reducing the rate in the growth of molds on bread surface [3,8–11]. Likewise, in recent years, the ability of aqueous extracts from fermented sourdoughs to inhibit the growth of the main molds that spoil bread has been demonstrated, thus generating promising alternatives as natural antimicrobials in bakery products [11–15].

Bread is highly perishable due to its composition, leading to a quality decline from physicochemical and microbiological changes after baking. Post-baking cooling results in moisture loss, affecting crumb and crust texture. Over time, starch retrogradation and moisture loss increase hardness. Mold growth on the bread surface poses a significant economic challenge for the baking industry [16].

Molds proliferate easily in bread because it is rich in carbohydrates (70–80 g carbohydrates/100 g bread), with water activity values between 0.94–0.97 and pH values around 6, which are optimal conditions for mold growth. Contamination of bakery products with mold spores, which are naturally found in the bakery environment, has been shown to occur after the baking process, during cooling, slicing, and packaging of the product, these last stages being the determinants to define the microbiological quality of these products [16,17].

Penicillium and *Aspergillus* are common molds that cause bread spoilage due to their ability to thrive in diverse conditions, produce numerous spores, and exist in the environment. Notable species include *Penicillium roqueforti*, *P. paneum*, *P. corylophilum*, *P. chrysogenum,* and others, leading to blue-green spots on bread. *Aspergillus* species such as *A. chevalieri* and *A. niger* cause colored spots, ranging from green to black, with some producing yellow pigments. Additional filamentous molds like *Rhizopus*, *Mucor*, and *Neurospora*, while present in various baking products, are less significant than *Penicillium* and *Aspergillus* [16,17].

Bacteria such as *Serratia marcescens* and *Endomyces fibulger* can cause red or white stains on bread. Ropy bread, characterized by yellow color and sticky viscosity, results from specific strains of *Bacillus subtilis*. However, bacterial growth on bread is infrequent compared to mold growth, leading the baking industry to prioritize the elimination of mold contamination [17,18].

The baking industry, facing substantial economic losses from mold spoilage of bread, is increasingly developing preservation methods. Propionic, sorbic, and acetic acids, and their salts, are common antifungals for mold prevention [14]. In response to consumer demand for "natural" additives, research explores new compounds to enhance the shelf life of baking products. Utilizing sourdoughs or their aqueous extracts in bread formulation is considered an alternative, with numerous studies describing their effectiveness as antifungals.

This review focuses on recent developments in the utilization of sourdoughs, specifically those fermented with lactic acid bacteria and their corresponding aqueous extracts, aimed at augmenting bread quality and prolonging shelf life. The investigation examines the fundamental roles played by lactic acid bacteria and yeasts in generating organic acids, peptide compounds, and exopolysaccharides within sourdoughs. Additionally, it highlights the potential of aqueous extracts derived from sourdoughs to serve as natural antimicrobials, with a targeted focus on molds that compromise bread quality. Also, it attempts to identify the specific compounds inherent in sourdough that are responsible for its antifungal properties. Through this identification, the research aims to elucidate potential paths for future studies and the development of various bakery products where sourdough can be an alternative. As the baking industry contends with substantial economic losses from mold spoilage, this review contributes to evaluating the possibility of transforming the baking industry towards natural and sustainable conservation methods, emphasizing the multifaceted advantages of sourdough fermentation, thereby contributing to the ongoing scientific search for high-quality bakery products that align with evolving consumer preferences.

2. Sourdoughs

Sourdough is one of the oldest examples of natural starters, mostly used for making fermented bread as an alternative to baker's yeast and chemical leavening. The term "sourdough" can vary in different countries and languages. However, the different linguistic expressions capture the idea of a natural leaven or sourdough starter, such as in French: *levain*, Italian: *lievito madre*, German: *Sauerteig*, Spanish: *masa madre* or *levadura madre*, Portuguese: *fermento natural*, Dutch: *zuurdesem*, and many others. Sourdoughs are the result of spontaneous fermentations that are obtained when flours from different grains (mainly wheat or barley) are mixed with an adequate amount of water and maintained under conditions of temperature and time favorable for the growth of microorganisms inherent to the flour or intentionally inoculated [19]. In many countries worldwide, sourdoughs continue to be used as part of their formulation due to their unique texture and flavor characteristics in the final product [20]. During sourdough fermentation, metabolite production and chemical reactions occur, giving the product distinctive characteristics and a high sensory quality [5]. Likewise, in recent years, the use of sourdough in the baking industry has increased significantly due to the discovery of nutritional improvements, such as the enhancement of the bioavailability of minerals, the production of peptides with antioxidant activity, and the preservative effects on bread, which improve the shelf life [3,21].

Microbial analyses and investigations of sourdough microbiota have shown that two types of microorganisms coexist within this ecosystem: lactic acid bacteria (LAB) and yeasts [22]. A majority of sourdoughs that are used in bakeries as sole leavening agents include *Fructilactobacillus sanfranciscensis* (formerly *Lactobacillus sanfranciscensis*), which is one of the dominant fermentation microbes [23,24]. In sourdoughs fermented to achieve high acidity levels, *Limosilactobacillus* and *Lactobacillus* species typically dominate [24]. In most analyses, the LAB commonly isolated from sourdoughs are of the *Lactobacillus* genus, whereas *Saccharomyces* spp. and *Candida* spp. have mostly been isolated and identified as yeasts. The biodiversity of both LAB and yeasts in sourdoughs mainly depends on their type and production process [25,26]. De Vuyst et al. [27] provide the most recent comprehensive compilation of lactobacilli in sourdoughs (more than 700) used for bread making.

2.1. Classification of Sourdoughs

According to the preparation process and the metabolic activity of the main LAB and yeasts found in sourdoughs, these doughs can be classified into three or four types [28]. Type I sourdough is a mixture of flour and water subjected to incubation at temperatures below 30 °C, inoculated with a previously fermented sourdough, to keep the microorganisms' metabolic activity high. Type I sourdoughs traditionally use the fermented dough as the single leavening agent [28]. Examples include the sourdoughs used for sourdough bread, panettone, and San Francisco rye bread. Type I sourdoughs are generally firm doughs with a pH range between 3.8 and 4.5 and are fermented in a temperature range of 20 to 30 °C [29].

In type II sourdough, the mixture of flour and water is incubated at temperatures above 30 °C for extended fermentation times (up to 5 days). In Type II sourdoughs, *Saccharomyces cerevisiae* is added to leaven the dough; *Lactobacillus* species are the dominant members of type II sourdoughs. This sourdough can be liquid and is widely used as an acidifying agent and aroma generator in bakery products. This process was adopted by the industry, in part, due to the simplification of the multiple-step build typical of type I sourdoughs [30].

Type III sourdough is a dough that goes through a drying process, generally by spraying, known as "ready-to-use" [28]. Microorganisms in an active state are first transformed to a dormant state by drying and then require reactivation and resuspension with water before being used as a bread ingredient. Type III sourdough is used most for large-scale baking products as a premix starter due to its easy handling and long shelf life. However, it is important to mention that the number of viable microorganisms in this dough depends on the drying conditions [25,26,31]. Drying-resistant LAB, such as *Pediococcus pentosaceus*, *Lb. plantarum*, and *Lb. brevis* predominate in this sourdough. The drying conditions, time, and temperature depend on the desired characteristics and caramelization of the baked product. *Pediococcus pentosaceus* SP2 (isolated from kefir grains) was evaluated by Plessas et al. [32] as the starter in sourdough bread making when applied in fresh, freeze-dried, and freeze-dried immobilized (on wheat bran). The freeze-dried immobilized cells led to higher total titratable acidity values, and the bread presented higher resistance to mold and rope spoilage. Finally, type IV ferment (mixed ferment) was more recently characterized and consists of a mixture of types I and II [28].

2.2. Lactic Acid Bacteria in Sourdoughs

Sourdough microbiota generally comprise two types of microorganisms: LAB and yeasts. Table 1 shows the common LAB and yeasts isolated from different types of sourdoughs. The populations of the microorganisms can range from 10^6 to 10^9 CFU/g, and the proportion of LAB to yeasts is approximately 100:1; in consequence, the most significant contribution to the production of compounds during the fermentation of sourdoughs is provided by LAB [3,31,32].

Table 1. Main lactic acid bacteria (LAB) and yeasts isolated from different types of sourdoughs.

Type of Sour-Dough	Microorganism			
	Obligate Heterofermentative LAB	**Facultative Heterofermentative LAB**	**Obligate Homofermentative LAB**	**Yeasts**
Type I	*Lactobacillus sanfrancisencis* *Lactobacillus brevis* *Lactobacillus reuteri* *Lactobacillus fermentum* *Lactobacillus fructivorans* *Lactobacillus pontis*	*Lactobacillus alimentarius* *Lactobacillus casei* *Lactobacillus plantarum* *Lactobacillus paralimentarius*	*Lactobacillus acidophilus* *Lactobacillus delbrueckii* *Lactobacillus amylovorus* *Lactobacillus farciminis* *Lactobacillus mindensis*	*Candida humilis* *Candida milleri* *Issatchenkia orientalis* *Candida krusei*
Type II	*Lactobacillus brevis* *Lactobacillus frumenti* *Lactobacillus pontis* *Lactobacillus panis* *Lactobacillus reuteri* *Lactobacillus sanfrancisencis* *Weisella confusa*		*Lactobacillus acidophilus* *Lactobacillus delbrueckii* *Lactobacillus amylovorus* *Lactobacillus farciminis* *Lactobacillus johnsonii*	*Saccharomyces cerevisiae* (added)
Type III	*Lactobacillus brevis*	*Lactobacillus plantarum* *Pediococcus pentosaceus*		
Type IV	Similar to Types I and II	Similar to Types I and II	Similar to Types I and II	Similar to Types I and II

Adapted from: [3,25].

LAB from the genera *Enterococcus*, *Weissella*, *Lactococcus*, *Leuconostoc*, *Pediococcus*, and *Lactobacillus* have been identified in sourdoughs, *Lactobacillus* being the most important since more than 60 species of this genus have been isolated. Despite the vast diversity of LAB identified, only some species of lactobacilli survive the maintenance process and feeding cycles to which sourdoughs are subjected [33]. In general, obligate heterofermentative LAB survive these processes mainly due to their ability to metabolize carbohydrates, assimilate various amino acids, and resist the acidic environment caused by the production of acids. The species *Lb. plantarum* and *Lb. sanfrancisencis* have been identified as the LAB with the highest presence and resistance in sourdoughs. It has been reported that around 50% of fermented sourdoughs present this type of LAB growth during the different feeding cycles [20].

The feeding cycles of sourdoughs, which consist of adding new flour and water to the dough once the fermentation time has been completed, significantly affect the doughs' microbiota diversity. Different investigations have demonstrated that, with feeding cycles increasing, the diversity of sourdough microbiota decreases significantly; *Lb. plantarum* and *Lb. sanfrancisencis* predominate from the tenth day of feeding since they present the greatest ability for adaptation and resistance to this process [20,34–36]. Meanwhile, species such as *Lb. brevis*, *Lb. paralimentarius*, *Lb. fermentum*, and *Lb. casei* have a low capacity to adapt to the environment after several cycles of sourdough feeding [20,25,36]. Plessas [32] remarked that many factors are important for sourdough preparations; however, the starter culture selection is considered the most critical. Arena et al. [37] investigated the diversity of LAB and yeasts in six spontaneous sourdough fermentations from Italy (Apulian region); the authors reported the identification of *Lb. plantarum* as the dominant LAB and *S. cerevisiae* as the main yeast in the analyzed samples. Developments in the last decade have changed the selection criteria used to select sourdough cultures and have expanded the tools used to assess the metabolic potential of specific strains, species, or genera [6].

2.3. Metabolic Pathways of LAB during Sourdough Fermentation

The metabolic pathways or processes during lactic acid fermentation depend directly on the type of LAB [6] in the sourdough (Figure 1). Microorganisms' metabolic activity in sourdough affects the dough's technological functionality and the bread's nutritional properties, aroma profile, shelf life, and overall quality [19]. From glucose, homofermentative LAB mainly produce lactic acid/lactate (>90%) through glycolysis (homolactic fermentation), while heterofermentative LAB, in addition to lactic acid (around 50%) production, generate CO_2, acetic acid, or other acids, and ethanol through the 6-phosphoglucanate/phosphoketolase (6-PG/PC) pathway. Hexoses other than glucose enter the main glycolytic pathways at glucose-6-phosphate or fructose-6-phosphate, after the isomerization process and/or phosphorylation [3].

In the presence of electron acceptors, obligate heterofermentative LAB reduce fructose to mannitol and produce acetate and ATP, while mannitol can be fermented to lactate. The use of pentoses is not restricted to the LAB type and their type fermentation; facultative heterofermentative LAB, which ferment hexoses through glycolysis, ferment pentoses in the same way as obligate heterofermentative species, with the help of the enzyme fructose-1-6 diphosphate aldose. Pentose fermentation produces equimolar amounts of lactic and acetic acid without the formation of CO_2 [3].

LAB from sourdoughs have proteases, peptidases, and amino acid-converting enzymes, which break down cereal proteins, generating both compounds with bioactive properties and compounds that directly impact the bread's flavor [5]. The LAB proteolytic enzymatic system consists of an extracellularly located serine proteinase, specific transport systems for di/tripeptides and oligopeptides (>3 amino acid residues), and a variety of intracellular peptidases [3,38]. The transformation of amino acids by LAB into compounds that improve the bread's flavor and aroma is produced by transamination reactions, which require the presence of both an electron acceptor and an amino group, preferably α-ketoglutarate.

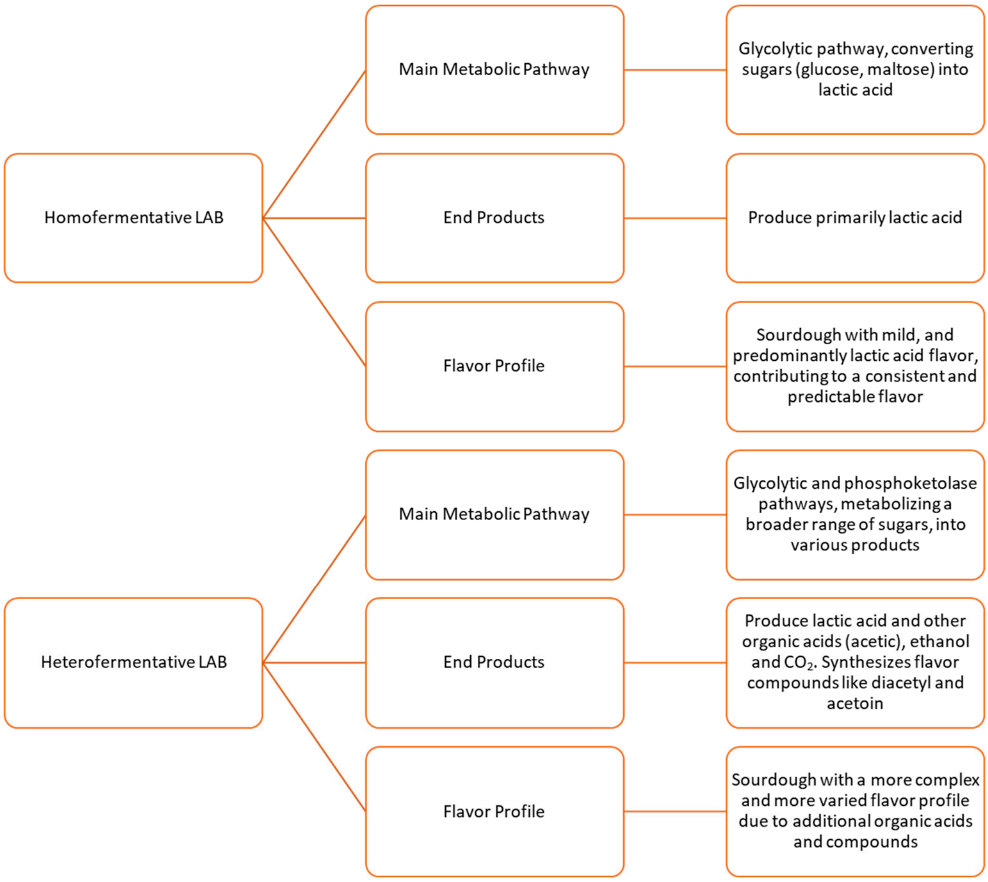

Figure 1. Products generated by homofermentative and heterofermentative lactic acid bacteria (LAB) metabolic routes during sourdough fermentation.

Protein metabolism in lactic acid bacteria can involve the breakdown of various free amino acids, specifically, catabolic reactions involving phenylalanine, where LAB catabolic enzymes generate bioactive compounds such as phenylactate and phenylacetate (Figure 2) [3,38].

Figure 2 provides an overview of the protein metabolism by LAB during sourdough fermentation. LAB hydrolyze proteins from the dough into amino acids and perform various metabolic reactions, including decarboxylation and deamination, which produce organic acids (such as lactic acid) and biogenic amines. These metabolic processes lead to the acidification of the sourdough and the development of characteristic flavors. The sourdough used in bread fermentation is crucial in leavening and flavor development [39].

3. Sourdough and Its Effect on Bread Properties

It has been observed that the fermentation processes of sourdoughs play a significant role in improving the bread's organoleptic attributes. The compounds formed in lactic acid fermentations and their concentration are directly related to improving bread's flavors and textures [3,39,40].

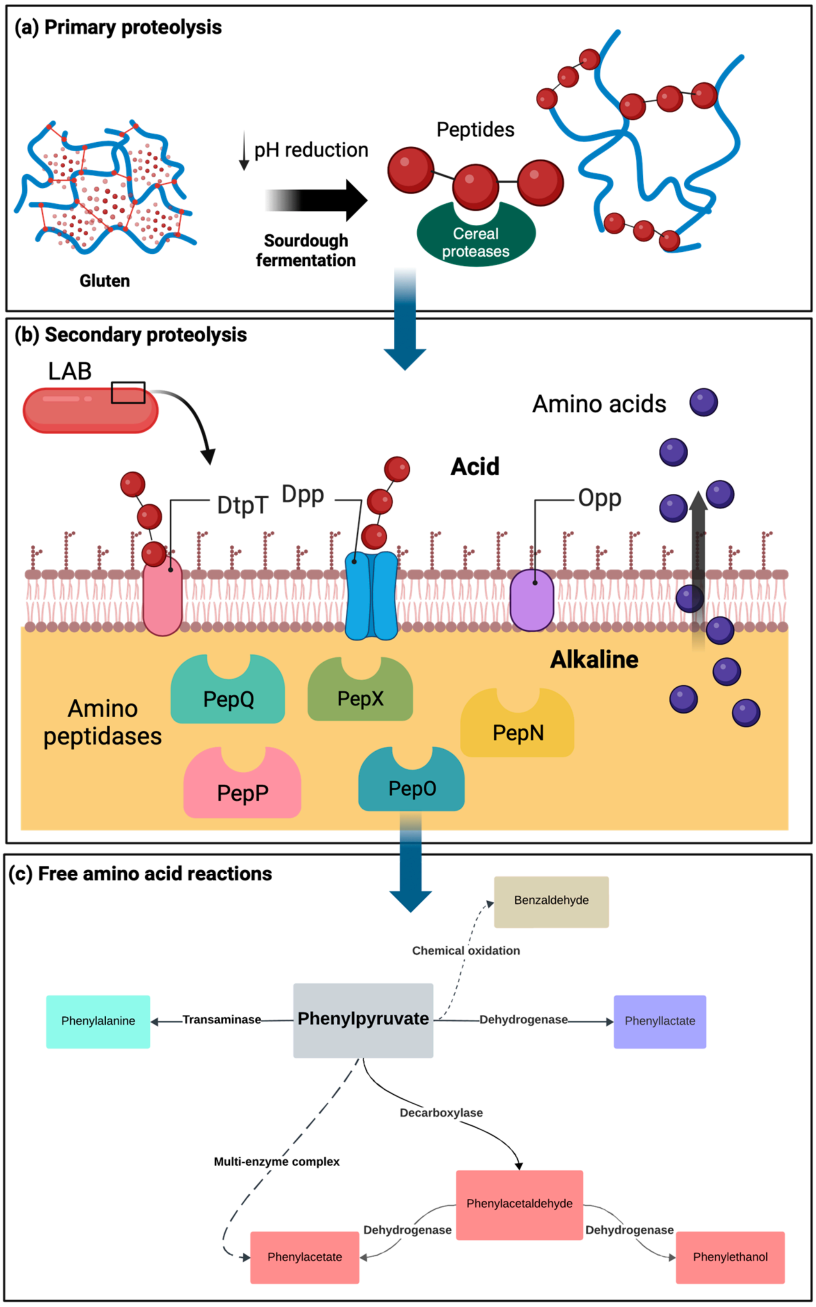

Figure 2. Protein metabolism by lactic acid bacteria (LAB) during sourdough fermentation. (**a**) Primary proteolysis, acidifying and reducing disulfide bonds in gluten, stimulating cereal proteases, and releasing polypeptides, (**b**) Intracellular peptidases secondary proteolysis to free amino acids, and (**c**) LAB catabolism of free amino acids (phenylalanine case). Peptide transport systems: oligopeptide permease (Opp), dipeptide permease (Dpp), transporter for di- and tripeptides (DtpT). PepQ (Prolidase EC 3.4.13.9), PepX (X-prolyl dipeptidyl aminopeptidase EC3.4.14.5), PepN (Aminopeptidase type N 3.4.11.11), PepP (prolyl endopeptidyl peptidase EC 3.4.21.26), and PepO (endopeptidase EC3.4.23). Adapted from Gänzle et al. [41] and Gobbetti et al. [38].

3.1. Texture

In general, sourdough fermentation affects dough rheology on two levels: in the sourdough itself and in dough that has had sourdough added to it [3]. Various studies have assessed the effect of sourdough on bread formulation and the resulting bread texture. In general, the addition of sourdoughs decreases the resistance to extension, reduces the elasticity of the dough, and increases the degree of softening, obtaining a crumb with greater CO_2 retention capacity (a greater number of alveoli of a larger size), a firmer crust, and better texture. These changes, both in the structure of the crumb and in the dough, have been attributed by several authors to the proteolysis of gluten proteins caused primarily by the increase in acidity due to the production of organic acids during the sourdough fermentation [8,40,42–47].

Many LAB associated with sourdoughs, especially the *Lactobacillus* genus, produce a variety of exopolysaccharides (EPS) and oligosaccharides during the lactic acid fermentation of sourdoughs. These compounds have been shown to have the ability to function as hydrocolloids and thus improve the texture properties of bread during storage [3]. Torrieri et al. [46] recorded that adding EPS-producing LAB to sourdough significantly improved the texture during bread storage, further to gluten proteolysis. Besides, they observed that bread had a higher moisture content and better mechanical properties during storage, which may be an alternative to reducing the aging process of bread [46].

3.2. Flavor

Sourdough bread has a complex flavor profile influenced by the compounds generated during microbial fermentation [48–50]. Odors and flavors are generated in the sourdough mainly due to enzymatic and microbial processes during the fermentation of these doughs. These compounds belong to different chemical classes: aldehydes, acids, alcohols, ketones, esters, and pyrazines. The flavors and odors from the raw materials are insignificant compared to those generated during fermentation. However, other aromatic and flavor compounds are produced from lipid oxidation processes and Maillard reactions [39].

Two categories of flavor (taste and aroma) compounds are produced during the lactic acid fermentation of sourdoughs. The first of them includes non-volatile compounds, such as organic acids (lactic, acetic, phenyllactic, and phenylacetic acid) that LAB produce and volatile compounds that include alcohols, aldehydes, ketones, esters, and sulfur compounds, which are formed during the fermentation and baking stages of bread [3,39]. The generation of aromatic and flavor compounds is closely related to LAB type, temperature, pH, and moisture content since they directly influence the metabolic activity of the microorganisms [3]. Mantzourani et al. [50] reported that sourdough (fermented *with Lb. paracasei* K5) improved bread's sensory properties related to the detected aroma volatiles and consumer preference. Warburton et al. [48] characterized the volatile organic compounds in the crumb of 12 sourdough breads. The authors attributed the observed differences to the culture identified if the fermentation activity was dominated by yeast or the different classes of LAB. The authors associated the profiles in three clusters. In Cluster 1, volatile organic compounds (ethanol, 3-methyl-1-butanol, phenylethanol, 2-methyl-1-propanol, acetaldehyde, and 2,3-butanedione) predominated, along with increased production of lactic acid, indicating the activity of yeast and homofermentative or facultative heterofermentative LAB. Cluster 2 was associated with acetic acid, acetate esters, and acidity, revealing that obligate heterofermentative LAB predominates. Fermentation of lipids (production of aldehydes and lactones) related to yeast fermentation activity was classified in Cluster 3.

Siepmann et al. [40] observed sourdoughs made with *Lb brevis* and *Lb. plantarum* and with the fermentation temperature changed from 28 to 35 °C. They reported the formation of furfurals, compounds associated with almond aromas in pieces of bread incorporating doughs fermented at 35 °C. On the other hand, pieces of bread made with sourdough fermented at 28 °C did not show the formation of these compounds, demonstrating that the fermentation temperature in the sourdough is important for forming volatile compounds that affect the bread's flavor. Also, they verified that the type of LAB significantly influences the generation of final flavors in the bread. These researchers observed that sourdoughs fermented with *Lb. reuteri*, *Lb. plantarum*, and *Lb. amylovorus* generated a greater diversity of flavor and aroma compounds in the bread than in loaves of bread to which sourdoughs fermented with *Lb. brevis* and *Lb. plantarum* had been added. Xu et al. [51] investigated the influence of different starter cultures (*Kazachstania humilis*, *S. cerevisiae*, *Wickerhamomyces anomalus*, *Lb. sanfranciscensis* DSM20451T and *Lactobacillus sakei* LS8, in various combinations) on sourdough wheat bread volatiles. Using headspace solid-phase microextraction and gas chromatography/mass spectrometry analysis (SPME-GC/MS) established that sourdough bread fermented with a combination of lactobacilli and yeast had a more complex profile of volatiles (particularly concerning esters). Finally, Siepmann et al. [40] determined that both the starter culture and the sourdough fermentation temperature significantly affect the final aroma and flavor of bread.

Various investigations have reported different sensory analyses to determine the acceptability of breads formulated with sourdoughs. Sourdough fermentation is known for its ability to produce complex and desirable flavors [32]. Understanding sourdough fermentation's microbial dynamics and metabolic pathways [52] can lead to new and unique bread flavors and aromatic profiles. Adding 20 to 30% sourdough to the bread formulation has increased the acceptability of both texture and flavor compared with bread made exclusively with yeast. These results demonstrate that the aromatic compounds formed during the fermentation process of sourdoughs help to improve the sensory acceptability of bakery products [8,13,45,50,53].

4. Sourdough Effect on the Bread's Shelf Life

It has been shown that LAB produce bioactive compounds with antimicrobial capacity during the lactic acid fermentation process. Substances such as short-chain fatty acids, peptides, diacetyl, hydrogen peroxide, and organic acids have been reported with the potential for inhibiting both pathogenic bacteria and important molds in foods [26,54–60]. Some of these compounds have been identified and isolated from sourdoughs, which are also related to the antifungal activity in bread when sourdough is used as an ingredient. In addition, an increase in the bread's shelf life was observed.

Various investigations have been carried out on the ability of sourdough, as an additive, to extend the useful life of bakery products [14,15,26,37,50,61,62]. Table 2 presents some examples of these investigations carried out in recent years. According to Table 2, adding 20% (*w*/*w*) of sourdough to the bread formulation increases the product's shelf life by an average of six days. Garofalo et al. [10] observed that the addition of 30% (*w*/*w*) sourdough in the bread formulation considerably increased the shelf life of the product, achieving improvements of 19 to 21 days (Table 2). The type of LAB used for the fermentation of the sourdough affects the effectiveness in increasing the shelf life of the bread. Hernández-Figueroa et al. [15] reported that bread incorporating sourdoughs fermented with *Lactobacillus* (*Lactobacillus acidophilus* NRRL B-4495 or *L. casei* 21/1) had a longer shelf life compared to a traditional one. The addition of a poolish-type sourdough (fermented with *Lactiplantibacillus plantarum* NRRL B-4496) inhibited fungal growth in bread for ten days [14]. As can be seen in Table 2, the sourdoughs fermented with *Lb. amylovorus*, *Lb rossiae,* and a mixture of *Lb. rossiae* and *Lb. paralimentarius* presented a significant ability to increase the final product's shelf life.

In addition to mold growth, bread aging (retrogradation of starch and loss of moisture) is one of the determining factors for the shelf life of baking products. Torrieri et al. [46] observed that adding 30% sourdough fermented with exopolysaccharide-forming LAB to the bread formulation reduced the moisture loss rate and affected starch retrogradation kinetics. The results were attributed mainly to the production of organic acids, bacterial hydrolysis (by LAB) of starch molecules, and proteolysis of gluten subunits. Finally, they concluded that adding sourdoughs to the bread formulation could be an alternative to produce bakery products free of synthetic additives.

Table 2. Results of improvement in the shelf life of bread with the addition of sourdoughs fermented by different types of lactic acid bacteria (LAB).

LAB in Sourdough	% Sourdough Addition (*w*/*w*)	Improvement in Shelf Life *	Reference
Lb. plantarum	20	2 days	[12,63]
Lb. sanfrancisencis	20	2 days	
Lb. amylovorus	20	9 days	
Lb. sakei, Pediococcus acidilactici y *Pediococcus pentosaceus*	20	6 days	[53]
Lb. plantarum	20	1 day	[11]
Lb. bulgaricus	20	2 days	
Lb. plantarum, L. reuteri and *Lb. brevis*	30	6 days	[64]
Lb. rossiae	30	21 days	[10]
Lb. paralimentarius		8 days	
Lb. rossiae and *Lb. paralimentarius*		19 days	
Lactiplantibacillus plantarum NRRL B-4496	28	9 days	[14]
Lb. acidophilus NRRL B-4495 *Lb. casei 21/1*	38	14 days	[15]
Lb. sanfranciscensis	30	>25 days	[61]

* In comparison to control bread that did not have any antimicrobial agent added to it.

5. Properties of Sourdough Bioactive Compound Extracts

LAB are distinguished by their ability to produce lactic acid, among other interesting metabolites with antimicrobial activity [60,65]. Also, cell-free supernatants' antibacterial and antifungal activity in vitro has been widely studied, particularly in members of the *Lactobacillus* genus. Studies of extracts obtained from sourdoughs focus on analyzing the bioactive capacity presented mainly by peptides and organic acids formed from the fermentation of LAB in the doughs [26]. These extracts and their different fractions are obtained using the Osborne method (1907) and a physical separation employing centrifugation. The compounds' separation and identification in these extracts are commonly obtained through different instrumental techniques based on chromatography [11,15,52,57].

For peptide compounds, the peptidases of the lactic acid bacteria in the sourdough participate in secondary proteolysis (Figure 2), releasing free amino acids, which in turn are subjected to various catabolic reactions by the same microorganisms. These peptide compounds, which generally increase during lactic acid fermentation, are native protein fragments with amino acid sequences that can have a positive impact as antimicrobial, antioxidant, and anti-inflammatory agents [21,54,66–68].

Similarly, the organic acids identified and isolated in the sourdough extracts show bioactive properties, mainly functioning as antimicrobial agents against important pathogenic bacteria in food and mold spoilage of bakery products. This property means that the extracts can be used as "natural" preservatives in the development of products free of synthetic additives or clean labels, and in this way, satisfy consumers' demand [14,15,53,55,58,69].

5.1. Bioactive Compounds from Sourdoughs with Antimicrobial Properties

As mentioned previously, organic acids and peptide compounds formed during the lactic acid fermentation of sourdoughs have been shown to have antimicrobial activity when used as pure compounds, individually or together, in in vitro studies [53,56,59,63,70]. For this reason, various investigations assess the antifungal capacity of the pure compounds and the aqueous extracts obtained from sourdoughs against the bread's spoilage molds [14,15]. Table 3 presents the bioactive compounds in the sourdough extracts that have shown antifungal activity in vitro against selected molds.

According to Table 3, organic acids such as lactic, acetic, and phenyllactic acids are identified in sourdoughs fermented with *Lb. reuteri*, *Lb. plantarum*, and *Lb. brevis* presented significant antifungal activity, reducing the radial growth of molds such as

Fusarium graminearum and *A. niger*. When these sourdoughs were incorporated into the bread formulation, they increased the product's shelf life by seven days compared with control bread [64]. Similarly, Axel et al. [71] and Luz et al. [11] identified another type of organic acid, which inhibited the growth of molds on the surface of the bread and, in this way, increased the shelf life of the product (Table 3).

Table 3. Bioactive compounds identified in sourdoughs fermented with different lactic acid bacteria (LAB) and their effect against bread's spoilage molds.

LAB	Identified Bioactive Compounds	Antimicrobial Effect Against	Main Findings	Reference
Lb. reuteri, *Lb. plantarum* and *Lb. brevis*	Organic acids: Lactic acid, acetic acid, and phenyllactic acid	*Fusarium graminearum* and *Aspergillus niger*	Inhibition in radial growth (>70%) of *F. graminearum* and decrease (>40%) in radial growth of *A. niger*. Increased shelf life in breads incorporating sourdough of 2–3 days compared to control bread	[64]
Lb. plantarum	Peptides sequence: SAFEFADEHKGAYS, AAIIFGSIFWNV GMKR, AEGEVILEDVQPSSVQS, and PPDVLTKL-TAVPAAQQLDEADGHPR	*Penicillium roqueforti*, *Aspergillus parasiticus* and *Penicillium polonicum*	Increased shelf life of bread by 7 days compared with control Inhibition of radial growth of molds between 50–60% in in vitro tests	[72]
Lb. plantarum and *Lb. rossiae LB*	Peptide compounds: Temporiina-Sha Temporina-1Gc Expansin-B4 (Q94LR4) Organic acids: Lactic, formic, acetic, and phenyllactic acid	*Penicillium roqueforti*, *Penicillium paneum*, and *Aspergillus parasiticus*	Increased bread shelf life by 7–14 days compared with control. Inhibitory activity of 40–45% against the molds *P. roqueforti*, *P. paneum*, and *A. parasiticus*.	[57]
Lb. reuteri	4-hydroxyphenyllactic acid, 2-hydroxy-isocaproic acid, vanillinic acid and 3-phenyllactic acid	Environmental molds	Increased shelf life in bread slices by 7–8 days compared with control.	[71]
Lb. brevis	2-hydroxy-isocaproic acid and vanillinic acid	Environmental molds	Increased shelf life in bread slices by 5–6 days compared with control.	
Lb. plantarum	Gallic acid, chlorogenic acid, caffeic acid, and syringic acid	*Penicillium expansum*, *Penicillium roqueforti* and *Fusarium moniliformis*	Increased shelf life in bread slices by 3–4 days compared with control.	[11]
Lb. bulgaricus	Sinapinic acid and DL-3-phenyllactic acid	*Fusarium monoliformis* and *Penicillium expansum*	Increased shelf life in bread slices by 4–5 days compared with control.	
Lb. paracasei K5	Lactic and acetic acid	Environmental molds	Increased shelf life in pieces by bread 15–16 days (5 days more than the control bread)	[50]
Lactiplantibacillus plantarum S4.2 and *Lentilactobacillus parabuchneri S2.9*	Organic acids	*Fusarium graminearum*, *Aspergillus fumigatus*, *A. flavus* *A. brasiliensis*, and *Penicillium roqueforti*	Inhibition in mold growth	[62]

Fraberger et al. [62] isolated (*Lactiplantibacillus plantarum* S4.2 and *Lentilactobacillus parabuchneri* S2.9) from sourdoughs and reported antifungal growth suppression against *F. graminearum* MUCL43764, *Aspergillus fumigatus*, *A. flavus* MUCL11945, *A. brasiliensis* DSM1988, and *P. roqueforti* DSM1079. They also found antibacterial activity against *Bacillus cereus* DSM31, *B. licheniformis* DSM13, *B. subtilis* LMG7135, and *B. subtilis* S15.20. Hernández-Figueroa et al. [14] found that aqueous extracts from poolish-type sourdoughs fermented with *Lactiplantibacillus plantarum* NRRL B-4496 presented fungistatic capacity primarily attributed to lactic and acetic acids and probably antifungal peptides. Hernández-Figueroa et al. [15] identified lactic acid in concentrations between 1 and 2% in sourdoughs fermented with *L. acidophilus*, while in those fermented by *L. casei*, lactic acid (1–2%) and acetic acid (0.1–0.2%) were identified.

Table 3 shows some peptide compounds identified in sourdoughs fermented with LAB. These compounds have shown the ability to inhibit the growth of molds such as *P. roqueforti*, *Aspergillus parasiticus*, *P. polonicum*, and *P. paneum* in slices of bread. Likewise, the ability of peptide compounds to increase the shelf life of bakery products by up to seven days has been demonstrated [14,54,57].

In addition, bacteriocins produced by LAB have been isolated from the aqueous extracts of sourdoughs. One of the bacteriocins identified in these doughs is reutericycline produced by *Lb. reuteri* LTH2584. This compound has significant antibacterial capacity against *Listeria monocytogenes*, *B. subtilis*, and *Staphylococcus aureus* [73]. Other bacteriocins isolated from aqueous extracts of sourdoughs with antibacterial capacity are bavaricin A produced by *Lb. bavaricus* MI401, plantaricin ST31 produced by *Lb. plantarum*, and BLIS C57 produced by *Lb. sanfranciscensis* C57. Although these bacteriocins have not been approved as antimicrobials or antifungals, studying their antimicrobial capacity and food safety may generate alternatives that can replace synthetic antimicrobials as preservatives [3].

5.2. Effects of Bioactive Compounds on the Shelf Life of Bread

Despite the existence of various investigations on the in vitro antifungal capacity of bioactive compounds formed by LAB isolated from sourdoughs, tested in specific culture broths at the laboratory level, studies of this capacity, obtained from sourdough extracts and incorporated into bread for the study of the shelf life of the product, are scarce [14,15,53,55,58,69,74].

Coda et al. [72] demonstrated the addition of aqueous extracts of fermented sourdoughs with *Lb. plantarum* caused an increase in mold appearance time in bread inoculated with *P. roqueforti* and without inoculation, of 7 and 21 days, respectively. In another study, Rizello et al. [57] evaluated the addition of 4% (w/w) of a lyophilized extract from sourdough fermented with *Lb. rossiaie* and *Lb. plantarum* to the bread formulation, finding that it inhibited mold growth for around 28 days of storage at room temperature. These researchers concluded that the antifungal activity of the extract was due to the synergistic and complex activity between organic acids and peptide compounds formed during lactic acid fermentation. These results open the possibility of obtaining antifungal compounds from fermented sourdough extracts, which can be made with accessible and lower-cost raw materials and be used as natural antimicrobials in a wide range of food products.

5.3. Other Possible Beneficial Effects

Functional LAB as starter cultures used in sourdough fermentation have been researched for years [32,75]. Acidification caused by LAB in sourdough is a central aspect in activating several cereal enzymes and synthesizing microbial active metabolites, positively influencing the derived products' nutritional/functional and health-promoting benefits [1]. Akamine et al. [5] stated that proper management of sourdough fermentation allows gluten levels to be adjusted, delaying starch digestibility and increasing the bioaccessibility of vitamins and minerals. The nutritional quality and the biotransformation observed in the flour during the fermentation process impact the nutrients' bioaccessibility, and the beneficial effects from this process influence the final product and consumers' health [76,77]. Perri et al. [78] reported that fermentation of sprouted barley with selected lactic acid bacteria enhanced its nutritional features through increases in free amino acids (35%) and γ-aminobutyric acid concentrations (57%), and a decrease in phytic acid content. The fermentation process strongly mitigated the adverse effects (on dough rheology and baking) related to sprouted barley flour enzymatic activities.

Utilizing food production byproducts back into food production within a circular food economy is one of the driving methods used to improve sustainability within the food industry [7,23,79]. Sourdough production can benefit from various byproducts from other industries if they are safe and suitable for consumption. Some examples are fruit and vegetable peelings (apple skins or potato peels) [80], spent grains, yeast slurry byproducts from breweries [5], coffee grounds, and leftovers from grinding nuts and seeds [81].

According to D'Amico et al. [82], certain cereal components, particularly in wheat and rye, which are known to trigger adverse reactions in a small subset of the population, may undergo partial modification or degradation during sourdough fermentation. This process can potentially decrease their harmful effects, depending upon the composition of sourdough microbiota, processing conditions, and the resultant acidification. Nissen et al. [83] investigated the impact of gluten-free bread enriched with spirulina on the colon microbiota of non-celiac volunteers. These authors indicate that sourdough fermentation and algae enrichment can mitigate the negative effect of gluten-free bread on the gut microbiota of non-celiac consumers. To make gluten-free sourdough bread, a gluten-free starter can be produced by fermenting flours, such as brown rice, white rice, sorghum, tapioca, or a blend of gluten-free flours to replace wheat flour [84–86], and proper selection of the starter is important [87,88]. Gluten-free doughs lack the structure provided by gluten; thus, many formulations incorporate hydrocolloids (such as xanthan gum) to improve the texture and elasticity. These ingredients trap gas produced during fermentation and improve the overall structure of the bread.

Foods with high daily intake, such as cereal-based products, are good vehicles for supplementary probiotics [4,5]. The addition of probiotics is challenging for cereal-based baked foods due to the high temperatures applied during baking [5]. The use of microencapsulated probiotics, edible films containing probiotics, spore-forming probiotics, and probiotic addition after baking are the main strategies used to formulate probiotic cereal-based baked products [89]. Spore-forming probiotics represent the best approach to supplementing foods before baking [89]. Da Ros et al. [90] studied industrially made baker's yeast and sourdough bread, which were used to feed for two weeks the gastrointestinal simulator Twin Mucosal-SHIME, and found that only the consumption of sourdough bread has the potential to enhance the synthesis of short-chain fatty acids and free amino acids at the colon level. Akamine et al. [5] identified probiotics (*Bacillus licheniformis*) isolated from sourdough and analyzed hydrolases that presented the capacity to hydrolyze gluten from *Limosilactobacillus fermentum*, *Pediococcus pentosaceus*, and *Saccharomyces cerevisiae*.

Müller et al. [75] evaluated *Leuconostoc citreum* DCM65 and *Lactiplantibacillus plantarum* subsp. *plantarum* MA418 selected for producing mannitol, exopolysaccharides, and amylolytic and antifungal activity) and their potential as single or co-culture starters in sourdough fermented buns containing different levels of sugar (control 9% and reduced 0, 3, 6%). The authors reported that sourdough buns started with *Lactiplantibacillus plantarum* had higher volume, larger slice area, and softer crumb; this was in contrast to buns fermented with *Leuconostoc citreum*. Both starter cultures showed high potential for producing sourdough buns with reduced sugar content.

Sourdough fermentation can partially break down gluten proteins, potentially making bread more tolerable for individuals with mild gluten sensitivities. Also, it can increase the bioavailability of certain nutrients in grains, making them more digestible and nutritious. For example, phytic acid reduction through fermentation can improve mineral absorption. The study of sourdough can lead to healthier and more nutritious bread products.

6. Final Remarks

Although it remains a traditional process, adding sourdoughs to the formulations of bakery products represents an effective option to enhance the properties of those products. These improvements are primarily attributed to the compounds formed during the sourdough lactic acid fermentation, such as organic acids, peptide compounds, and/or exopolysaccharides.

This review highlights sourdough's significant role in enhancing bread's quality and shelf life. Decades of research has consistently demonstrated that incorporating sourdough into bread formulations positively influences their organoleptic attributes, imparting distinct and desirable flavors and textures. The bioactive compounds generated through sourdough fermentation, especially by lactic acid bacteria, possess antimicrobial properties that play a crucial role in prolonging bread shelf life. These compounds effectively combat spoilage, particularly inhibiting the growth of molds. Selected studies about using extracts from sourdoughs containing these bioactives to extend the shelf life of bread have shown favorable results. This emphasizes the importance of continuing to study and integrate sourdough or its extracts into bread production processes as it can improve the quality and diversity of products and align with broader objectives of improving sustainability.

Author Contributions: Conceptualization, R.H.H.-F. and A.L.-M.; methodology, R.H.H.-F.; formal analysis, R.H.H.-F. and A.L.-M.; investigation, R.H.H.-F., E.M.-L. and A.L.-M.; data curation, R.H.H.-F., E.M.-L., E.P. and A.L.-M.; writing—original draft preparation, R.H.H.-F., E.M.-L., E.P. and A.L.-M.; writing—review and editing, R.H.H.-F., E.M.-L., E.P. and A.L.-M. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by [Universidad de las Américas Puebla] grant numbers [2478 and 3555]. The APC was funded by [MDPI].

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data sharing is not applicable to this article.

Acknowledgments: Author Hernández-Figueroa acknowledges financial support for his Ph.D. studies in Food Science from the National Council for Humanities, Sciences, and Technologies (CONAHCyT) and Universidad de las Américas Puebla (UDLAP).

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Graça, C.; Lima, A.; Raymundo, A.; Sousa, I. Sourdough Fermentation as a Tool to Improve the Nutritional and Health-Promoting Properties of Its Derived-Products. *Fermentation* **2021**, *7*, 246. [CrossRef]
2. Cauvain, S.P.; Young, L.S. Water Control in Baking. In *Bread Making: Improving Quality*; CAB International: Wallingford, UK, 2003; pp. 447–466.
3. Chavan, R.S.; Chavan, S.R. Sourdough Technology-A Traditional Way for Wholesome Foods: A Review. *Compr. Rev. Food Sci. Food Saf.* **2011**, *10*, 169–182. [CrossRef]
4. Fraberger, V.; Özülkü, G.; Petrova, P.; Nada, K.; Petrov, K.; Johann, D.K.; Rocha, J.M.F. Sourdough as a Source of Technological, Antimicrobial, and Probiotic Microorganisms. In *Sourdough Innovations*; CRC Press: Boca Raton, FL, USA, 2023; pp. 265–310. [CrossRef]
5. Akamine, I.T.; Mansoldo, F.R.P.; Vermelho, A.B. Probiotics in the Sourdough Bread Fermentation: Current Status. *Fermentation* **2023**, *9*, 90. [CrossRef]
6. Gänzle, M.G.; Qiao, N.; Bechtner, J. The Quest for the Perfect Loaf of Sourdough Bread Continues: Novel Developments for Selection of Sourdough Starter Cultures. *Int. J. Food Microbiol.* **2023**, *407*, 110421. [CrossRef] [PubMed]
7. Vriesekoop, F.; Haynes, A.; Van Der Heijden, N.; Liang, H.; Paximada, P.; Zuidberg, A. Incorporation of Fermented Brewers Spent Grain in the Production of Sourdough Bread. *Fermentation* **2021**, *7*, 96. [CrossRef]
8. Park, Y.-H.; Jung, L.-H.; Jeon, E.-R. Quality Characteristics of Bread Using Sour Dough. *Prev. Nutr. Food Sci.* **2006**, *11*, 323–327. [CrossRef]
9. Corsetti, A.; Settanni, L. Lactobacilli in Sourdough Fermentation. *Food Res. Int.* **2007**, *40*, 539–558. [CrossRef]
10. Garofalo, C.; Zannini, E.; Aquilanti, L.; Silvestri, G.; Fierro, O.; Picariello, G.; Clementi, F. Selection of Sourdough Lactobacilli with Antifungal Activity for Use as Biopreservatives in Bakery Products. *J. Agric. Food Chem.* **2012**, *60*, 7719–7728. [CrossRef]
11. Luz, C.; D'Opazo, V.; Mañes, J.; Meca, G. Antifungal Activity and Shelf Life Extension of Loaf Bread Produced with Sourdough Fermented by *Lactobacillus* Strains. *J. Food Process. Preserv.* **2019**, *43*, e14126. [CrossRef]
12. Ryan, L.A.M.; Zannini, E.; Dal Bello, F.; Pawlowska, A.; Koehler, P.; Arendt, E.K. *Lactobacillus Amylovorus* DSM 19280 as a Novel Food-Grade Antifungal Agent for Bakery Products. *Int. J. Food Microbiol.* **2011**, *146*, 276–283. [CrossRef]
13. Samapundo, S.; Devlieghere, F.; Vroman, A.; Eeckhout, M. Antifungal Activity of Fermentates and Their Potential to Replace Propionate in Bread. *LWT—Food Sci. Technol.* **2017**, *76*, 101–107. [CrossRef]
14. Hernández-Figueroa, R.H.; Mani-López, E.; López-Malo, A. Antifungal Capacity of Poolish-Type Sourdough Supplemented with *Lactiplantibacillus Plantarum* and Its Aqueous Extracts In Vitro and Bread. *Antibiotics* **2022**, *11*, 1813. [CrossRef] [PubMed]
15. Hernández-Figueroa, R.H.; Mani-López, E.; López-Malo, A. Antifungal Activity of Wheat-Flour Sourdough (Type II) from Two Different *Lactobacillus* In Vitro and Bread. *Appl. Food Res.* **2023**, *3*, 100319. [CrossRef]
16. Garcia, M.V.; Bernardi, A.O.; Copetti, M.V. The Fungal Problem in Bread Production: Insights of Causes, Consequences, and Control Methods. *Curr. Opin. Food Sci.* **2019**, *29*, 1–6. [CrossRef]
17. Magan, N.; Arroyo, M.; Aldred, D. Mould Prevention in Bread. In *Bread Making: Improving Quality*; CAB International: Wallingford, UK, 2003; pp. 500–514.
18. Jay, J.M.; Loessner, M.J.; Golden, D.A. *Modern Food Microbiology*, 7th ed.; Food Science Text Series; Springer: New York, NY, USA, 2005.

19. Catzeddu, P. Sourdough Breads. In *Flour and Breads and Their Fortification in Health and Disease Prevention*; Elsevier: Berlin/Heidelberg, Germany, 2019; pp. 177–188. [CrossRef]
20. Gänzle, M.; Ripari, V. Composition and Function of Sourdough Microbiota: From Ecological Theory to Bread Quality. *Int. J. Food Microbiol.* **2016**, *239*, 19–25. [CrossRef]
21. Zou, T.B.; He, T.P.; Li, H.B.; Tang, H.W.; Xia, E.Q. The Structure-Activity Relationship of the Antioxidant Peptides from Natural Proteins. *Molecules* **2016**, *21*, 72. [CrossRef]
22. Fu, W.; Wang, S.; Xue, W. Mechanism of Carbohydrate and Protein Conversion during Sourdough Fermentation: An Analysis Based on Representative Chinese Sourdough Microbiota. *Int. J. Food Microbiol.* **2023**, *410*, 110487. [CrossRef]
23. Arora, K.; Ameur, H.; Polo, A.; Di Cagno, R.; Rizzello, C.G.; Gobbetti, M. Thirty Years of Knowledge on Sourdough Fermentation: A Systematic Review. *Trends Food Sci. Technol.* **2021**, *108*, 71–83. [CrossRef]
24. Gänzle, M.G.; Zheng, J. Lifestyles of Sourdough Lactobacilli—Do They Matter for Microbial Ecology and Bread Quality? *Int. J. Food Microbiol.* **2019**, *302*, 15–23. [CrossRef]
25. De Vuyst, L.; Neysens, P. The Sourdough Microflora: Biodiversity and Metabolic Interactions. *Trends Food Sci. Technol.* **2005**, *16*, 43–56. [CrossRef]
26. Sakandar, H.A.; Hussain, R.; Kubow, S.; Sadiq, F.A.; Huang, W.; Imran, M. Sourdough Bread: A Contemporary Cereal Fermented Product. *J. Food Process. Preserv.* **2019**, *43*, e13883. [CrossRef]
27. De Vuyst, L.; González-Alonso, V.; Wardhana, Y.R.; Pradal, I. Taxonomy and Species Diversity of Sourdough Lactic Acid Bacteria. In *Handbook on Sourdough Biotechnology*; Gobbetti, M., Gänzle, M., Eds.; Springer International Publishing: Cham, Switzerland, 2023; pp. 97–160. [CrossRef]
28. Lima, T.T.M.; Hosken, B.D.O.; De Dea Lindner, J.; Menezes, L.A.A.; Pirozi, M.R.; Martin, J.G.P. How to Deliver Sourdough with Appropriate Characteristics for the Bakery Industry? The Answer May Be Provided by Microbiota. *Food Biosci.* **2023**, *56*, 103072. [CrossRef]
29. De Vuyst, L.; Comasio, A.; Kerrebroeck, S.V. Sourdough Production: Fermentation Strategies, Microbial Ecology, and Use of Non-Flour Ingredients. *Crit. Rev. Food Sci. Nutr.* **2023**, *63*, 2447–2479. [CrossRef] [PubMed]
30. Siepmann, F.B.; Ripari, V.; Waszczynskyj, N.; Spier, M.R. Overview of Sourdough Technology: From Production to Marketing. *Food Bioprocess Technol.* **2018**, *11*, 242–270. [CrossRef]
31. Lai, H.M.; Lin, T.C. *Bakery Products: Science and Technology*; Wiley Blackwell: Hoboken, NJ, USA, 2007. [CrossRef]
32. Plessas, S. Innovations in Sourdough Bread Making. *Fermentation* **2021**, *7*, 29. [CrossRef]
33. Lau, S.W.; Chong, A.Q.; Chin, N.L.; Talib, R.A.; Basha, R.K. Sourdough Microbiome Comparison and Benefits. *Microorganisms* **2021**, *9*, 1355. [CrossRef] [PubMed]
34. Minervini, F.; Lattanzi, A.; De Angelis, M.; Di Cagno, R.; Gobbetti, M. Influence of Artisan Bakery- or Laboratory-Propagated Sourdoughs on the Diversity of Lactic Acid Bacterium and Yeast Microbiotas. *Appl. Environ. Microbiol.* **2012**, *78*, 5328–5340. [CrossRef] [PubMed]
35. Lin, X.B.; Gänzle, M.G. Quantitative High-Resolution Melting PCR Analysis for Monitoring of Fermentation Microbiota in Sourdough. *Int. J. Food Microbiol.* **2014**, *186*, 42–48. [CrossRef]
36. Manini, F.; Casiraghi, M.C.; Poutanen, K.; Brasca, M.; Erba, D.; Plumed-Ferrer, C. Characterization of Lactic Acid Bacteria Isolated from Wheat Bran Sourdough. *LWT—Food Sci. Technol.* **2016**, *66*, 275–283. [CrossRef]
37. Arena, M.P.; Russo, P.; Spano, G.; Capozzi, V. Exploration of the Microbial Biodiversity Associated with North Apulian Sourdoughs and the Effect of the Increasing Number of Inoculated Lactic Acid Bacteria Strains on the Biocontrol against Fungal Spoilage. *Fermentation* **2019**, *5*, 97. [CrossRef]
38. Gobbetti, M.; Rizzello, C.G.; Di Cagno, R.; De Angelis, M. How the Sourdough May Affect the Functional Features of Leavened Baked Goods. *Food Microbiol.* **2014**, *37*, 30–40. [CrossRef] [PubMed]
39. Pétel, C.; Onno, B.; Prost, C. Sourdough Volatile Compounds and Their Contribution to Bread: A Review. *Trends Food Sci. Technol.* **2017**, *59*, 105–123. [CrossRef]
40. Siepmann, F.B.; Sousa de Almeida, B.; Waszczynskyj, N.; Spier, M.R. Influence of Temperature and of Starter Culture on Biochemical Characteristics and the Aromatic Compounds Evolution on Type II Sourdough and Wheat Bread. *LWT* **2019**, *108*, 199–206. [CrossRef]
41. Gänzle, M.G.; Vermeulen, N.; Vogel, R.F. Carbohydrate, Peptide and Lipid Metabolism of Lactic Acid Bacteria in Sourdough. *Food Microbiol.* **2007**, *24*, 128–138. [CrossRef] [PubMed]
42. Di Cagno, R.; De Angelis, M.; Lavermicocca, P.; De Vincenzi, M.; Giovannini, C.; Faccia, M.; Gobbetti, M. Proteolysis by Sourdough Lactic Acid Bacteria: Effects on Wheat Flour Protein Fractions and Gliadin Peptides Involved in Human Cereal Intolerance. *Appl. Environ. Microbiol.* **2002**, *68*, 623–633. [CrossRef] [PubMed]
43. Jekle, M.; Becker, T. Effects of Acidification, Sodium Chloride, and Moisture Levels on Wheat Dough: II. Modeling of Bread Texture and Staling Kinetics. *Food Biophys.* **2012**, *7*, 200–208. [CrossRef]
44. Nutter, J.; Saiz, A.I.; Iurlina, M.O. Microstructural and Conformational Changes of Gluten Proteins in Wheat-Rye Sourdough. *J. Cereal Sci.* **2019**, *87*, 91–97. [CrossRef]
45. Rizzello, C.G.; Nionelli, L.; Coda, R.; Di Cagno, R.; Gobbetti, M. Use of Sourdough Fermented Wheat Germ for Enhancing the Nutritional, Texture and Sensory Characteristics of the White Bread. *Eur. Food Res. Technol.* **2010**, *230*, 645–654. [CrossRef]

46. Torrieri, E.; Pepe, O.; Ventorino, V.; Masi, P.; Cavella, S. Effect of Sourdough at Different Concentrations on Quality and Shelf Life of Bread. *LWT—Food Sci. Technol.* **2014**, *56*, 508–516. [CrossRef]
47. Zhao, Y.; Zhang, J.; Wei, Y.; Ai, L.; Ying, D.; Xiao, X. Improvement of Bread Quality by Adding Wheat Germ Fermented with *Lactobacillus Plantarum* Dy-1. *J. Food Qual.* **2020**, *2020*, 9348951. [CrossRef]
48. Warburton, A.; Silcock, P.; Eyres, G.T. Impact of Sourdough Culture on the Volatile Compounds in Wholemeal Sourdough Bread. *Food Res. Int.* **2022**, *161*, 111885. [CrossRef] [PubMed]
49. Gonzalez Viejo, C.; Harris, N.M.; Fuentes, S. Quality Traits of Sourdough Bread Obtained by Novel Digital Technologies and Machine Learning Modelling. *Fermentation* **2022**, *8*, 516. [CrossRef]
50. Mantzourani, I.; Plessas, S.; Odatzidou, M.; Alexopoulos, A.; Galanis, A.; Bezirtzoglou, E.; Bekatorou, A. Effect of a Novel *Lactobacillus Paracasei* Starter on Sourdough Bread Quality. *Food Chem.* **2019**, *271*, 259–265. [CrossRef] [PubMed]
51. Xu, D.; Zhang, Y.; Tang, K.; Hu, Y.; Xu, X.; Gänzle, M.G. Effect of Mixed Cultures of Yeast and Lactobacilli on the Quality of Wheat Sourdough Bread. *Front. Microbiol.* **2019**, *10*, 2113. [CrossRef] [PubMed]
52. Soto-Reyes, N.; Dávila-Rodríguez, M.; Lorenzo-Leal, A.C.; Reyes-Jurado, F.; Mani-López, E.; Hernández-Figueroa, R.; Morales-Camacho, J.I.; López-Malo, A. Prospects for Food Applications of Products from Microorganisms. In *Research and Technological Advances in Food Science*; Elsevier: Amsterdam, The Netherlands, 2022; pp. 195–229. [CrossRef]
53. Cizeikiene, D.; Juodeikiene, G.; Paskevicius, A.; Bartkiene, E. Antimicrobial Activity of Lactic Acid Bacteria against Pathogenic and Spoilage Microorganism Isolated from Food and Their Control in Wheat Bread. *Food Control* **2013**, *31*, 539–545. [CrossRef]
54. Coda, R.; Rizzello, C.G.; Nigro, F.; De Angelis, M.; Arnault, P.; Gobbetti, M. Long-Term Fungal Inhibitory Activity of Water-Soluble Extracts of *Phaseolus Vulgaris* Cv. Pinto and Sourdough Lactic Acid Bacteria during Bread Storage. *Appl. Environ. Microbiol.* **2008**, *74*, 7391–7398. [CrossRef] [PubMed]
55. Luz, C.; Saladino, F.; Luciano, F.B.; Mañes, J.; Meca, G. In Vitro Antifungal Activity of Bioactive Peptides Produced by *Lactobacillus Plantarum* against Aspergillus Parasiticus and Penicillium Expansum. *LWT—Food Sci. Technol.* **2017**, *81*, 128–135. [CrossRef]
56. Muhialdin, B.J.; Hassan, Z.; Saari, N. In Vitro Antifungal Activity of Lactic Acid Bacteria Low Molecular Peptides against Spoilage Fungi of Bakery Products. *Ann. Microbiol.* **2018**, *68*, 557–567. [CrossRef]
57. Rizzello, C.G.; Cassone, A.; Coda, R.; Gobbetti, M. Antifungal Activity of Sourdough Fermented Wheat Germ Used as an Ingredient for Bread Making. *Food Chem.* **2011**, *127*, 952–959. [CrossRef]
58. Schmidt, M.; Lynch, K.M.; Zannini, E.; Arendt, E.K. Fundamental Study on the Improvement of the Antifungal Activity of *Lactobacillus Reuteri* R29 through Increased Production of Phenyllactic Acid and Reuterin. *Food Control* **2018**, *88*, 139–148. [CrossRef]
59. Shehata, M.G.; Badr, A.N.; El Sohaimy, S.A.; Asker, D.; Awad, T.S. Characterization of Antifungal Metabolites Produced by Novel Lactic Acid Bacterium and Their Potential Application as Food Biopreservatives. *Ann. Agric. Sci.* **2019**, *64*, 71–78. [CrossRef]
60. Arrioja-Bretón, D.; Mani-López, E.; Palou, E.; López-Malo, A. Antimicrobial Activity and Storage Stability of Cell-Free Supernatants from Lactic Acid Bacteria and Their Applications with Fresh Beef. *Food Control* **2020**, *115*, 107286. [CrossRef]
61. Debonne, E.; Vermeulen, A.; Bouboutiefski, N.; Ruyssen, T.; Van Bockstaele, F.; Eeckhout, M.; Devlieghere, F. Modelling and Validation of the Antifungal Activity of DL-3-Phenyllactic Acid and Acetic Acid on Bread Spoilage Moulds. *Food Microbiol.* **2020**, *88*, 103407. [CrossRef] [PubMed]
62. Fraberger, V.; Ammer, C.; Domig, K.J. Functional Properties and Sustainability Improvement of Sourdough Bread by Lactic Acid Bacteria. *Microorganisms* **2020**, *8*, 1895. [CrossRef] [PubMed]
63. Ryan, L.A.M.; Dal Bello, F.; Arendt, E.K. The Use of Sourdough Fermented by Antifungal LAB to Reduce the Amount of Calcium Propionate in Bread. *Int. J. Food Microbiol.* **2008**, *125*, 274–278. [CrossRef] [PubMed]
64. Gerez, C.L.; Torino, M.I.; Rollán, G.; Font de Valdez, G. Prevention of Bread Mould Spoilage by Using Lactic Acid Bacteria with Antifungal Properties. *Food Control* **2009**, *20*, 144–148. [CrossRef]
65. Mani-López, E.; Arrioja-Bretón, D.; López-Malo, A. The Impacts of Antimicrobial and Antifungal Activity of Cell-Free Supernatants from Lactic Acid Bacteria In Vitro and Foods. *Compr. Rev. Food Sci. Food Saf.* **2021**, *21*, 604–641. [CrossRef]
66. Malaguti, M.; Dinelli, G.; Leoncini, E.; Bregola, V.; Bosi, S.; Cicero, A.F.G.; Hrelia, S. Bioactive Peptides in Cereals and Legumes: Agronomical, Biochemical and Clinical Aspects. *Int. J. Mol. Sci.* **2014**, *15*, 21120–21135. [CrossRef]
67. Li, Y.; Yu, J. Research Progress in Structure-Activity Relationship of Bioactive Peptides. *J. Med. Food* **2015**, *18*, 147–156. [CrossRef]
68. Galli, V.; Mazzoli, L.; Luti, S.; Venturi, M.; Guerrini, S.; Paoli, P.; Vincenzini, M.; Granchi, L.; Pazzagli, L. Effect of Selected Strains of Lactobacilli on the Antioxidant and Anti-Inflammatory Properties of Sourdough. *Int. J. Food Microbiol.* **2018**, *286*, 55–65. [CrossRef]
69. Demirbaş, F.; İspirli, H.; Kurnaz, A.A.; Yilmaz, M.T.; Dertli, E. Antimicrobial and Functional Properties of Lactic Acid Bacteria Isolated from Sourdoughs. *LWT—Food Sci. Technol.* **2017**, *79*, 361–366. [CrossRef]
70. Garnier, L.; Penland, M.; Thierry, A.; Maillard, M.-B.; Jardin, J.; Coton, M.; Leyva Salas, M.; Coton, E.; Valence, F.; Mounier, J. Antifungal Activity of Fermented Dairy Ingredients: Identification of Antifungal Compounds. *Int. J. Food Microbiol.* **2020**, *322*, 108574. [CrossRef] [PubMed]
71. Axel, C.; Brosnan, B.; Zannini, E.; Furey, A.; Coffey, A.; Arendt, E.K. Antifungal Sourdough Lactic Acid Bacteria as Biopreservation Tool in Quinoa and Rice Bread. *Int. J. Food Microbiol.* **2016**, *239*, 86–94. [CrossRef] [PubMed]

72. Coda, R.; Cassone, A.; Rizzello, C.G.; Nionelli, L.; Cardinali, G.; Gobbetti, M. Antifungal Activity of *Wickerhamomyces Anomalus* and *Lactobacillus Plantarum* during Sourdough Fermentation: Identification of Novel Compounds and Long-Term Effect during Storage of Wheat Bread. *Appl. Environ. Microbiol.* **2011**, *77*, 3484–3492. [CrossRef] [PubMed]
73. Höltzel, A.; Gänzle, M.G.; Nicholson, G.J.; Hammes, W.P.; Jung, G. The First Low Molecular Weight Antibiotic from Lactic Acid Bacteria: Reutericyclin, a New Tetramic Acid. *Angew. Chem. Int. Ed.* **2000**, *39*, 2766–2768. [CrossRef]
74. Valerio, F.; Di Biase, M.; Lattanzio, V.M.T.; Lavermicocca, P. Improvement of the Antifungal Activity of Lactic Acid Bacteria by Addition to the Growth Medium of Phenylpyruvic Acid, a Precursor of Phenyllactic Acid. *Int. J. Food Microbiol.* **2016**, *222*, 1–7. [CrossRef] [PubMed]
75. Müller, D.C.; Schipali, S.; Näf, P.; Kinner, M.; Miescher Schwenninger, S.; Schönlechner, R. Potential of a Techno-Functional Sourdough and Its Application in Sugar-Reduced Soft Buns. *Fermentation* **2022**, *8*, 42. [CrossRef]
76. Canesin, M.R.; Cazarin, C.B.B. Nutritional Quality and Nutrient Bioaccessibility in Sourdough Bread. *Curr. Opin. Food Sci.* **2021**, *40*, 81–86. [CrossRef]
77. Kulathunga, J.; Whitney, K.; Simsek, S. Impact of Starter Culture on Biochemical Properties of Sourdough Bread Related to Composition and Macronutrient Digestibility. *Food Biosci.* **2023**, *53*, 102640. [CrossRef]
78. Perri, G.; Minisci, A.; Montemurro, M.; Pontonio, E.; Verni, M.; Rizzello, C.G. Exploitation of Sprouted Barley Grains and Flour through Sourdough Fermentation. *LWT* **2023**, *187*, 115326. [CrossRef]
79. Gobbetti, M.; De Angelis, M.; Di Cagno, R.; Polo, A.; Rizzello, C.G. The Sourdough Fermentation Is the Powerful Process to Exploit the Potential of Legumes, Pseudo-Cereals and Milling by-Products in Baking Industry. *Crit. Rev. Food Sci. Nutr.* **2020**, *60*, 2158–2173. [CrossRef] [PubMed]
80. Litwinek, D.; Gumul, D.; Łukasiewicz, M.; Zięba, T.; Kowalski, S. The Effect of Red Potato Pulp Preparation and Stage of Its Incorporation into Sourdough or Dough on the Quality and Health-Promoting Value of Bread. *Appl. Sci.* **2023**, *13*, 7670. [CrossRef]
81. Melini, V.; Melini, F.; Luziatelli, F.; Ruzzi, M. Functional Ingredients from Agri-Food Waste: Effect of Inclusion Thereof on Phenolic Compound Content and Bioaccessibility in Bakery Products. *Antioxidants* **2020**, *9*, 1216. [CrossRef]
82. D'Amico, V.; Gänzle, M.; Call, L.; Zwirzitz, B.; Grausgruber, H.; D'Amico, S.; Brouns, F. Does Sourdough Bread Provide Clinically Relevant Health Benefits? *Front. Nutr.* **2023**, *10*, 1230043. [CrossRef] [PubMed]
83. Nissen, L.; Casciano, F.; Chiarello, E.; Di Nunzio, M.; Bordoni, A.; Gianotti, A. Sourdough Process and Spirulina-Enrichment Can Mitigate the Limitations of Colon Fermentation Performances of Gluten-Free Breads in Non-Celiac Gut Model. *Food Chem.* **2024**, *436*, 137633. [CrossRef] [PubMed]
84. Bender, D.; Fraberger, V.; Szepasvári, P.; D'Amico, S.; Tömösközi, S.; Cavazzi, G.; Jäger, H.; Domig, K.J.; Schoenlechner, R. Effects of Selected Lactobacilli on the Functional Properties and Stability of Gluten-Free Sourdough Bread. *Eur. Food Res. Technol.* **2018**, *244*, 1037–1046. [CrossRef] [PubMed]
85. Nissen, L.; Samaei, S.P.; Babini, E.; Gianotti, A. Gluten Free Sourdough Bread Enriched with Cricket Flour for Protein Fortification: Antioxidant Improvement and Volatilome Characterization. *Food Chem.* **2020**, *333*, 127410. [CrossRef]
86. Adepehin, J.O.; Enujiugha, V.N.; Badejo, A.A.; Young, G.M.; Odeny, D.A. Physicochemical and Sensory Attributes of Gluten-free Sourdough Breads Produced from Underutilised African Cereal Flours and Flour Blends. *Int. J. Food Sci. Technol.* **2023**, *58*, 493–501. [CrossRef]
87. Olojede, A.O.; Sanni, A.I.; Banwo, K. Rheological, Textural and Nutritional Properties of Gluten-Free Sourdough Made with Functionally Important Lactic Acid Bacteria and Yeast from Nigerian Sorghum. *LWT* **2020**, *120*, 108875. [CrossRef]
88. Olojede, A.O.; Sanni, A.I.; Banwo, K.; Adesulu-Dahunsi, A.T. Sensory and Antioxidant Properties and In-Vitro Digestibility of Gluten-Free Sourdough Made with Selected Starter Cultures. *LWT* **2020**, *129*, 109576. [CrossRef]
89. Mani-López, E.; Ramírez-Corona, N.; López-Malo, A. Advances in Probiotic Incorporation into Cereal-Based Baked Foods: Strategies, Viability, and Effects–A Review. *Appl. Food Res.* **2023**, *3*, 100330. [CrossRef]
90. Da Ros, A.; Polo, A.; Rizzello, C.G.; Acin-Albiac, M.; Montemurro, M.; Di Cagno, R.; Gobbetti, M. Feeding with Sustainably Sourdough Bread Has the Potential to Promote the Healthy Microbiota Metabolism at the Colon Level. *Microbiol. Spectr.* **2021**, *9*, e00494-21. [CrossRef] [PubMed]