Chapter 6

Sourdough Fermentation And Microbiome

Ayşe Sevgili[1]

Abstract

The history of sourdough bread production dates back to ancient times. This bread, which has a high nutritional value, has been replaced by breads produced with baker's yeast over time. In recent years, demand for sourdough bread, which is rich in nutrients, has a low glycemic index and has high mineral absorption, has increased. Sourdough generally contains lactic acid bacteria and yeast microbial groups. *Lactobacillus, Pediococcus* and *Leuconostoc* species are common. These bacteria reduce pH through acid production, increase microbial safety and contribute to aroma formation. Yeast species such as *Saccharomyces cerevisiae, Candida milleri, Kazachstania exigua, Pichia kudriavzevii* ferment carbohydrates and produce CO_2 and ethanol. This gas production allows the dough to rise. In this context, fermentation and microbiota of sourdough were examined.

1. Introduction

Sourdough (SD) represents one of the oldest methods for producing cereal-based foods, with its origins dating back to ancient civilizations (Islam and Islam, 2024; De Vuyst and Neysens, 2005). The application of the SD process in its role as a leavening agent is considered one of the oldest biotechnological methods used in the processing of food (Arendt et al., 2007). When we look at the Egyptians, we see that they were the first to use beer foam as a leavening agent in bread making, and SD has become a traditional method for baking bread. In the bread production, SD was employed as a leavening agent until the introduction of baking yeast species (baker's yeast) in the early 1900s, when it was replaced by baker's yeast, after which time its use declined and it became associated mainly with handmade and rye bread (Carnevali et al., 2007; Corsetti and Settanni, 2007). SD bread has gained popularity in recent years due to its health and nutritional

1 Lecturer Dr., Gaziantep University, Naci Topcuoglu Vocational School, aysesevgili@gantep.edu.tr, ORCID ID: 0000-0002-9579-5074

https://doi.org/10.58830/ozgur.pub722.c3039

benefits. This reveals the importance of SD microbiota for production SD bread.

The SD ecosystem is characterized by a mixture of flour and water that is exposed to the process of fermentation by yeasts and lactic acid bacteria (LAB) (De Vuyst et al., 2014). The purpose of the SD fermentation was to facilitate the growth of yeasts and heterofermentative lactobacilli, thereby ensuring that enough CO_2 is produced for effective dough leavening (Brandt, 2007). The item originates from a SD 'starter culture' that is carefully maintained, portioned, and shared with bread bakers worldwide. A starter culture is composed of a diverse range of microorganisms, specifically bacteria and yeasts, which engage in the fermentation of flour's carbohydrates, resulting in the production of CO_2 that facilitates the rising of the bread dough before it is baked (Landis et al., 2021).

Yeasts act as the main leavening agent in bread-making by generating CO_2 as a metabolic by-product. Bacteria play a significant role in determining starter acidity through the production of organic acids as metabolic by-products, as well as influencing volatile organic compounds and various other attributes (Calvert et al., 2021). The process of preparing SD involves combining water and flour, followed by fermentation using both homofermentative and heterofermentative LAB. This fermentation leads to an rise in the concentrations of acetic and lactic acids, ultimately resulting in a product with a sour flavor (Sakandar et al., 2019). Yeast growth is restricted due to the acidic conditions that are predominantly established by LAB. As a result, LAB counts ($\geq 10^8$ CFU/g) are significantly greater than those of yeast ($\leq 10^7$ CFU/g), leading to a common ratio of LAB to yeast of approximately 10:1 to 100:1 (Fekri et al., 2024). As a traditional and natural process, lactic acid fermentation serves as a sustainable and efficient means of promoting hygiene, improving rheological characteristics, enhancing sensory qualities, and extending shelf life, in addition to elevating the functional and nutritional value of numerous animal and plant foods and drinks (Gobbetti et al., 2019).

2. SD Types and SD Fermentation

The classification of SD fermentation can be based on the type of inoculum, which includes types I, II, and III, as well as the technological processes, categorized into types 0, I, II, and III (Akamine et al., 2023). Based on production methods and processes, SD is categorized into four distinct types: Type I (traditional SD), Type II (starter culture-initiated SD), Type III (dried SD), and Type IV (mixed dried). Both industrial and

traditional approaches utilize these four types of SD production. Traditional SD is classified into type I and type II, depending on the procedures utilized in its production (Akamine et al., 2023; Fekri et al., 2024). The basic type 0 fermentation process initiates with a combination of flour and water, which is allowed to ferment for a brief period. The LAB naturally occurring in the flour exhibit faster growth rates and greater abundance compared to yeast (Akamine et al., 2023).

2.1. SD Types

The classification of SD into four categories is determined by the fermentation method and the technological strategy that is implemented (Akamine et al., 2023; Islam and Islam, 2024):

Type I SD; Type I SD's are made through traditional techniques and are noted for their continuous daily feedings that keep the microorganisms in a state of activity. This is demonstrated by a high level of metabolic activity, particularly in terms of leavening, which refers to the production of gas (Vuyst and Neysens, 2005).

Type II SD; the liquid SD could serve as an effective means to customize bread quality, enabling the production of an industrial product with unique characteristics (Carnevali et al., 2007).

Type III SD; SD can be dehydrated. This variety of SD is commonly employed by industrial bakeries because it offers a stable quality, thereby preventing inconsistencies in the end product that may occur with freshly prepared SD (Decock and Cappelle, 2005).

Type IV SD; type IV represents a laboratory-scale combination of type I and type II SD. In comparison to freshly made SD, type III SD is more user-friendly and provides enhanced storage convenience. This feature supports standardized industrial production and reduces the need for maintaining SD starters (Islam and Islam, 2024).

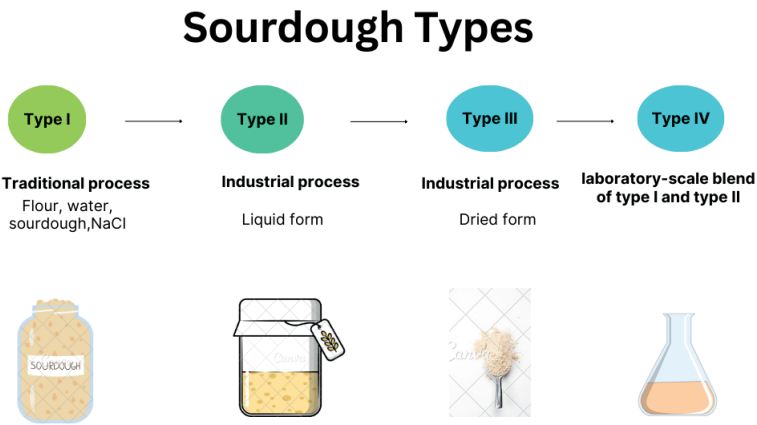

Figure 1 Scheme of SD production processes

2.2. SD Fermentation

During the SD fermentation process, the predominant byproducts include alcohols, acids, esters, aldehydes, and ketones, which represent the principal means of producing volatile organic compounds. The complexity of SD bread's profile is largely determined by the compounds created during fermentation, which are influenced by a wide range of microorganisms, predominantly yeasts and LAB (Akamine et al., 2023). The primary component of wheat flour is starch, which accounts for approximately 70–75% of its composition. Additionally, it contains around 14% water and 10–12% proteins. Minor constituents, such as non-starch polysaccharides (about 2–3%), particularly arabinoxylans, and lipids (approximately 2%), also have a crucial impact on the production and bread quality (Goesaert et al., 2005). The effects of SD fermentation are linked to the production of organic acids, the stimulation of endogenous enzymes in flour, and the activity of microbial secondary metabolism (Graça et al., 2021). SD fermentation typically takes place in conditions of restricted aeration and is characterized by a sequence of LAB and yeast activity (Hernández-Parada et al., 2022). SD consists of a diverse array of fermentation organisms. Nevertheless, when a specific area is colonized repeatedly (more than 10 times) over an extended duration, it typically develops a stable microbial community structure (Ma et al., 2021). SD is crucial in the field of baking technology, contributing to improvements in aroma, texture, shelf life, and the availability of minerals for absorption (Galle and Arendt, 2014). The diversity of microbial species in SD, especially in terms of phylogenetic variety, is restricted. This includes yeasts from the Ascomycota phylum, LAB primarily from the Firmicutes

group, particularly the Lactobacillaceae family, and occasionally acetic acid bacteria belonging to the α-proteobacteria class (De Vuyst et al., 2023).

During the fermentation process, the concentration of glucose rises as LAB and yeasts metabolize various complex carbohydrates (Akamine et al., 2023). In addition to maltose, the SD matrix comprises sucrose, glucose—produced by the action of endogenous amylase in flour and the breakdown of glucofructans by yeast—and fructose, which is generated from glucofructans through yeast activity. It is well-established that numerous LAB isolates from SD exhibit facultative heterofermentative characteristics (Weckx et al., 2019). Amino acids play a role as substrates for microbial conversions or are converted into flavor compounds in the baking process; therefore, a limited degree of proteolysis during fermentation can enhance the flavor of the bread (Gänzle et al., 2008).

The assessment of SD fermentation typically involves the analysis of various parameters, including acidity, pH levels, and the composition of microflora (Wick et al., 2003). Additionally, temperature is a crucial factor affecting the microflora in SD. For instance, when fermentation occurs at temperatures exceeding 30°C, homofermentative and facultative heterofermentative lactobacilli, such as *Lactobacillus fermentum* (*L. fermentum*) and *L. plantarum*, are more prevalent. Conversely, at temperatures below 30°C, heterofermentative lactobacilli like *L. sanfranciscensis* become dominant. It is important to note that, alongside temperature, dough hydration is also a key parameter that influences the fermentation process of SD (Casado et al., 2017).

In SD, a complex community of microorganisms is invariably present, and the dynamics between LAB and yeast significantly influence the qualities of the final product (Fu et al., 2024). Different types of yeasts and LAB, including both homofermentative and heterofermentative strains, have varying effects on the attributes of SD (Gianotti et al., 1997). The production of diverse aromatic compounds by yeasts plays a crucial role in creating balanced flavors in bread, particularly when paired with acids. In contrast, yeasts in SD demonstrate a capacity to thrive in stressful environments marked by low pH, high carbohydrate levels, and a significant presence of LAB (Hernández-Parada et al., 2022). In SD bread, LAB generates lower levels of volatile compounds compared to yeast. The activity of microbial or wheat proteases during lactic fermentation leads to the release of amino acids (Meignen et al., 2001). The fermentation of cereal SD involves the release of oligopeptides primarily due to the activity of cereal endoproteases during the primary stage of proteolysis. Conversely, the generation of

smaller peptides and free amino acids is a result of the secondary metabolic activity of microbial peptidases, particularly from LAB (Graça et al., 2021). Fermentation occurs through two principal pathways: alcoholic fermentation and lactic fermentation. In the case of lactic fermentation, pyruvate molecules produced from glucose oxidation via the Embden–Meyerhof–Parnas (EMP) or glycolytic pathway are reduced to lactic acid, a process termed homolactic fermentation. This pathway is employed by bacteria such as *Streptococcus, Lactobacillus*, and *Enterococcus*. Alternatively, pyruvate can be derived from a combination of lactate, ethanol, and/or acetic acid, which is facilitated by the oxidation of coenzymes NADH + and H+ by lactate dehydrogenase, along with the release of CO_2 from glucose until it reaches ribulose 5-phosphate, known as heterolactic fermentation (Akamine et al., 2023).

Homofermentative LAB are capable of nearly entirely converting hexoses into lactic acid, achieving rates greater than 85%. Conversely, heterofermentative LAB process hexoses into a combination of acetic acid or ethanol, lactic acid, and carbon dioxide. The ratio of acetic acid to lactic acid is influenced not only by the choice of starter culture but also by the fermentation temperature. Moreover, heterofermentative LAB can synthesize both lactic and acetic acid from pentose sugars (Hansen and Schieberle, 2005). SD fermentation involves the action of LAB, which moderately hydrolyze starch, conduct proteolysis, and acidify the dough. These processes yield a soft and flavorful crumb, improve the bioavailability of minerals through the degradation of phytates, and prevent the growth of microorganisms that lead to spoilage (Hernández-Parada et al., 2022). The generation of exopolysaccharides (EPS) by LAB during SD fermentation contributes to improved bread volume and texture, in addition to elevating the dietary fiber levels (Gänzle, 2014).

Research on the function of LAB in protein metabolism during fermentation has predominantly focused on two specific profiles:

(1) improving the solubility of insoluble components by means of acidification and the regeneration of glutathione;

(2) the process of hydrolyzing native proteins in flour using proteinase and peptidase enzymes (Fu et al., 2024).

Initially, maltose is preferentially fermented through the action of a constitutively expressed and energy-efficient maltose phosphorylase. This fermentation process is not inhibited by glucose and does not prevent growth of yeast. This is attributed to the synergistic relationship between maltose phosphorylase-positive heterofermentative LAB species, such

as *Frul. sanfranciscensis*, *Liml. fermentum*, and *Liml. reuteri*, and maltose-negative yeasts, particularly *K. humilis*, within the SD environment (De Vuyst et al., 2023).

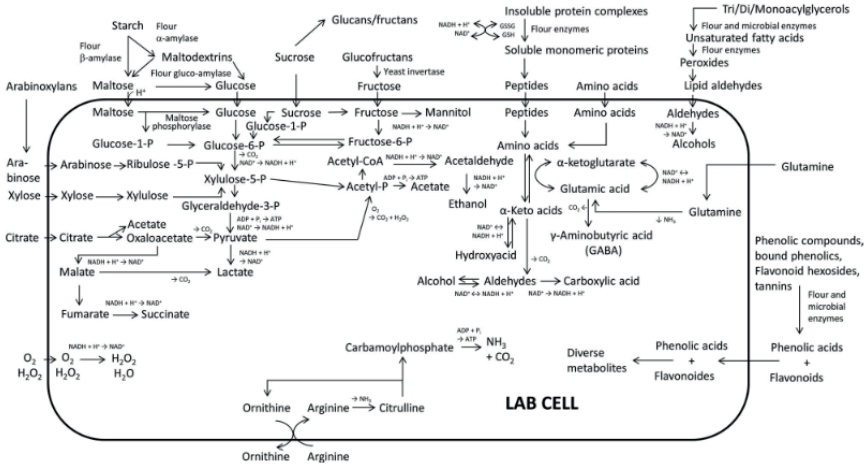

Figure 2 Overview of the metabolic activities of LAB species in the context of a SD matrix (De Vuyst et al., 2023)

SD yeasts metabolize the saccharides present in flour, including maltose, glucose, sucrose, and fructose, through the EMP pathway, resulting in the production of pyruvate. This process generates adenosine triphosphate and reducing equivalents in the form of NADH and H+. Subsequently, pyruvate is transformed into ethanol and CO_2 during alcoholic fermentation, which also replenishes the NAD+ cofactor that was utilized earlier in the EMP pathway (De Vuyst et al., 2023). Homofermentative LAB primarily convert glucose into lactic acid via glycolysis, a process known as homolactic fermentation. In contrast, heterofermentative LAB not only generate lactic acid but also produce CO_2, acetic acid, and/or ethanol, contingent upon the availability of supplementary substrates that serve as electron acceptors, particularly in the case of *Lactobacillus sanfranciscensis*. This occurs through the 6-phosphogluconate/phosphoketolase (6-PG/PK) pathway, which characterizes heterolactic fermentation (Corsetti and Settanni, 2007). By producing metabolites such as esters, aldehydes, and acetoin, yeasts play an important role in enhancing the flavor profile of bread (Hernández-Parada et al., 2022).

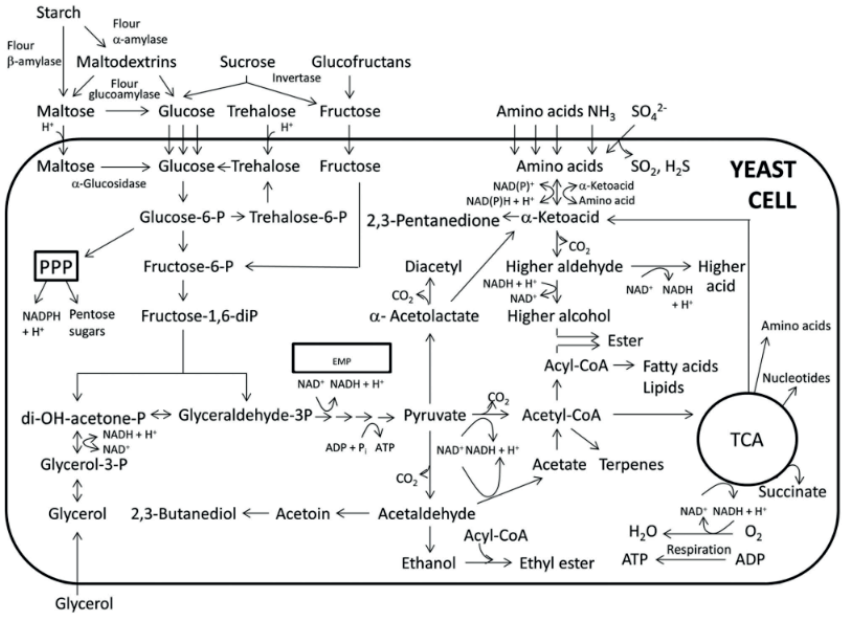

Figure 3 Overview of the metabolic activities of yeasts species in the context of a SD matrix (De Vuyst et al., 2023)

The presence and significance of various microorganisms in SD:

- The principal carbon sources utilized by *Pediococcus acidilactici* were glucose and fructose (Fu et al., 2024).
- The presence of *L. plantarum* is commonly observed in conjunction with *Lactobacillus fermentum* in the spontaneous fermentation processes of cereal products (Coda et al., 2014).
- Previous research indicates that *L. plantarum* is frequently present in the ecosystems of SD's (De Vuyst and Neysens, 2005).
- Isolated from SD fermentation, the strains *L. plantarum* ES137 and *P. acidilactici* ES22 exhibited a remarkable ability to break down proteins (Akamine et al., 2023).
- In SD's with a high pH level (exceeding 4.0), heterofermentative *Leuconostoc* and *Weissella* are commonly present, particularly when fermentation occurs at low temperatures (below 30 °C) and with a low dough yield (less than 200) (De Vuyst et al., 2023).

- It has been established that *L. brevis* subsp. *lindneri* and *L. plantarum* exhibit the most appropriate flavor component profiles (Paterson and Piggott, 2006).

Enzymes: The enzymatic processes of LAB and yeast during SD fermentation are increasingly understood. Hydrolases play a crucial role in the production of SD bread. Additionally, other classes of enzymes, such as transferases and oxidoreductases, contribute to the characteristics of SD fermentation (Akamine et al., 2023). Transferases, oxidoreductases, lyases and hydrolases are enzymes involved in SD production.

EPS: The EPS synthesized by LAB have the potential to enhance both the rheological behavior of dough and the quality of bread texture. This indicates that EPS from LAB could be utilized to substitute or diminish the reliance on pricier hydrocolloids that are typically used to improve bread texture. Furthermore, some LAB-produced EPS are known to possess prebiotic properties (Arendt et al., 2007). EPS like β-glucan, dextran, and inulin are metabolites produced by LAB during the fermentation of SD. β-glucan, in particular, is a prebiotic homopolysaccharide composed of glucose, which offers significant health advantages, including the regulation of cholesterol levels, anti-inflammatory properties, and support for probiotic microorganisms (Akamine et al, 2023).

Gluten: Gluten is a crucial protein complex that plays a significant role in determining the quality and structural integrity of products made from wheat (Nionelli and Rizzello, 2016). According to Poutanen et al., (2009), the breakdown of cereal proteins during the fermentation of wheat and rye SD is closely linked to acidity, significantly influencing both the flavor and texture of the resulting bread. The acidification process and the reduction of disulfide bonds in gluten, mediated by heterofermentative lactobacilli, result in increased cereal protease activity and enhanced substrate accessibility. Moreover, strain-specific intracellular peptidases from lactobacilli play a crucial role in the accumulation of amino acids. Germinated cereals and specific proteases promote a thorough degradation of proteins in SD's throughout fermentation protocols, potentially leading to the development of innovative products for individuals suffering from gluten intolerance.

Aroma and taste: SD fermentation generates two types of flavor compounds. The first category consists of non-volatile compounds, such as organic acids, which are produced by both homofermentative and heterofermentative bacteria. These compounds play a crucial role in acidifying the dough, lowering its pH, and enhancing its aroma (Paterson and Piggott, 2006). In SD bread, flavor-active compounds are generated both by LAB

and yeasts, as well as through their interactions. Heterofermentative LAB primarily generate ethyl acetate along with various alcohols and aldehydes, while homofermentative LAB are responsible for the production of diacetyl and other carbonyl compounds. Conversely, iso-alcohols arise from yeast fermentation, although they contribute minimally to the overall flavor of the finished bread (Paterson et al.,2006).

3. SD Microbiome

The group of SD lactobacilli, comprising obligate and facultative heterofermentative species alongside obligate homofermentative species (see Table 1), is associated with type I, type II, and type III SD's, in addition to type 0 dough. Type 0 dough, characterized by the use of baker's yeast as the main fermenting agent, is not created using SD processes (Corsetti and Settanni, 2007). Table 1 outlines the LAB and yeasts that are typically found in SD. The yeasts identified in SD represent a diversity of over 20 species (Corsetti and Settanni, 2007). The frequently dominant *Saccharomyces cerevisiae (S. cerevisiae) (Corsetti and Settanni, 2007)*. In a systematic examination spanning from 1990 to 2020, Arora et al. (2021) identified the following article counts by geographic area using "sourdough" as a keyword: North America (13), South America (6), Africa (31), Europe (175), Asia (54), China (20), and Oceania (1, specifically New Zealand). In Latin America and America, very few studies have been published. *Lactobacillus plantarum* and *Saccharomyces cerevisiae* appeared in several SD microbiota characterizations (Arora et al., 2021). Additionally, the timeline for the literature review in this research commenced with the initial isolation of yeasts from SD sourced from various regions in Türkiye. This was achieved through the use of keywords including "sourdough," "yeast isolation from sourdough," "sourdough microbiota," and "yeast from sourdough," as indicated by Sevgili and Erkmen in 2024. The findings of their research indicate that the literature reveals the greatest diversity of species was identified in the Central Anatolia Region, the Mediterranean Sea, and the Aegean Region. In all these areas, *S. cerevisiae* emerged as the most frequently isolated yeast, followed by *Torulaspora delbrueckii* and *Pichia guilliermondii* as the next most commonly isolated species.

In particular, the microorganisms *L. plantarum, L. sanfranciscensis, L. pontis*, and *L. panis* are considered fundamental to the SD fermentation process (Arendt et al., 2007). According to (Van Kerrebroeck et al., 2017) study, in general, the most prevalent LAB species are *L. sanfranciscensis* (belonging to the *Lactobacillus fructivorans* group), *L. plantarum* (*Lb. plantarum* group), *L. brevis* (*Lb. brevis* group), *P. pentosaceus* (pediococci),

L. paralimentarius (*Lactobacillus alimentarius* group), and *L. fermentum* (*Lactobacillus reuteri* group). Some varieties of SD are known to include *Leuconostoc* and *Weissella* species. The most common yeast species present are *Candida humilis*, now reclassified as *Kazachstania humilis*, alongside other members of the *Kazachstania* clade, in addition to *S. cerevisiae* from the *Saccharomyces* clade (Van Kerrebroeck et al., 2017).

The research conducted by Gänzle and Zheng (2019) indicates that the literature on the 227 SD's categorized as type I primarily comprises samples from Italy, France, Germany, Belgium, the United States, and Canada. Since 2015, information has also emerged regarding the use of Chinese SD's in the production of steamed bread. Notably, over 95% of these SD's were found to contain heterofermentative LAB, either exclusively or in combination with homofermentative lactobacilli. *L. sanfranciscensis* was the most commonly found species, present in 178 out of 227 SD samples. Other notable species included *L. plantarum* and *L. brevis*, as well as several members of the *L. alimentarius* group, such as *L. paralimentarius, L. crustorum, L. mindensis*, and *L. nantensis*. Additionally, *Leuconostoc* spp. and *Weissella* spp. were also identified. Among the SD samples, five were kept at the household level, where the fermentation process was temporarily halted due to refrigeration for periods ranging from several days to weeks. Each of these SD's contained a mixture of *L. plantarum* and *L. brevis*. The literature pertaining to the 32 SD's categorized as type II primarily featured rye SD's from Finland, Estonia, Denmark, and Germany, with some data also available for a limited number of wheat SD's from the United States, China, and France. Type II SD's were found to contain heterofermentative microorganisms, either independently or in combination with homofermentative lactobacilli. Notable species from the *L. reuteri* group, such as *L. pontis, L. panis, L. frumenti*, and *L. reuteri*, along with members of the *L. delbrueckii* group, including *L. amylovorus, L. crispatus*, and *L. acidophilus*, were commonly detected in these type II SD's. Additionally, *L. sanfranciscensis* was identified in three Chinese SD's utilized for dough acidification alongside baker's yeast (Gänzle and Zheng, 2019).

Sevgili et al. (2021) worked on isolation of SD from collected Gaziantep, Konya and Mardin. They are identified as *L. brevis, L. plantarum, P. acidilactici, L. paraplantarum, L. pentosus, Enterococcus faecalis, L. paralimentarius, Weissella confusa, Leuconostoc mesenteroides* subsp. *mesenteroides, Leuconostoc mesenteroides* subsp. *cremoris* and *Enterococcus hirae* in LAB. They are identified as *Pichia kudriavzevii, Kluyveromyces marxianus, S. cerevisiae, Wickerhamomyces anomalus*, *Kazachstania humilis, Candida glabrata, Geotrichum candidum, Kazachstania unispora, Galactomyces candidum, Candida kefyr* and *Candida tropicalis* in yeasts.

According to Weckx et al., (2019) study, the dominant species of LAB are primarily heterofermentative, including *L. sanfranciscensis, L. plantarum* (which is facultatively heterofermentative), *L. brevis*, and *P. pentosaceus* (which is homofermentative). Additionally, *L. paralimentarius* (facultatively heterofermentative) and *L. fermentum* are also notable. In contrast, the most common yeast species are *Kazachstania humilis* (previously known as *Candida humilis* and *Candida milleri*) and *S. cerevisiae*. The composition of minor communities consists of different *Lactobacillus* species, like *L. reuteri* and *L. rossiae*, in conjunction with species from the LAB genera *Leuconostoc* and *Weissella*, as well as various yeast species from the *Kazachstania* clade (Weckx et al., 2019).

Table 1 Some microbiome as Type I, II and III (yeasts and bacteria) of different SD types (Gänzle and Zheng., (2019); De Marco et al., (2022); Teixeira et al., (2024))

Type I	Type II	Type III*
L. sanfranciscensis	*L. reuteri*	*S. cerevisiae*
L. plantarum	*L. pontis*	*A. penicillioides*
L. brevis	*L. panis*	*Al. tenuissima*
L. paralimentarius	*L. frumenti*	*X. bisporus*
L. crustorum	*L. reuteri*	*Al. dactytidicola*
L. mindensis	*L. delbrueckii*	*X. dermatitidis*
L. nantensis	*L. amylovorus*	*V. victoriae*
Leuconostoc spp.	*L. crispatus*	*A. montevidensis*
Weissella spp.	*L. acidophilus*	*Cl. delicatutum*
P. pentosaceus	*L. sanfranciscensis*	*Monilia* spp.
Limosilactobacillus fermentum		
Lacticaseibacillus casei		

- *A. penicillioides* (*Aspergillus penicillioides*), *Al. tenuissima* (*Alternaria tenuissima*), *X. bisporus* (*Xeromyces bisporus*), *Al. dactytidicola* (*Alternaria dactytidicola*), *X. dermatitidis* (*Xerochrysium dermatitidis*), *V. victoriae* (*Vishniacozyma victoriae*), *A. montevidensis* (*Aspergillus montevidensis*), *Cl. delicatutum* (*Cladosporium delicatutum*)

4. Conclusion

SD has a rich historical, with various reports emphasizing its efficacy in improving the quality of bread and prolonging its shelf life. The microbiota of isolated traditional SD is primarily composed of heterofermentative species. Key members of this microbiota include *L. brevis, P. acidilactici*, and *L. plantarum*. The predominant yeasts found in this environment are *S. cerevisiae, Pichia kudriavzevii*, and *Kluyveromyces marxianus*. When fermentation

occurs at temperatures above 30°C, the dominant microorganisms shift to homofermentative and facultative heterofermentative lactobacilli, such as *L. fermentum* and *L. plantarum*. In contrast, when temperatures drop below 30°C, the microbiota is dominated by heterofermentative lactobacilli, including *L. sanfranciscensis*.

Table 2 Current scientific name and bases of some microorganisms in the text accepted at the National Center for Biotechnology Information (NCBI, 2025)

Current scientific name	**Basioynm**
Lactiplantibacillus plantarum	*Lactobacillus plantarum*
Limosilactobacillus fermentum	*Lactobacillus fermentum*
Fructilactobacillus sanfranciscensis	*Lactobacillus sanfranciscensis*
Torulaspora delbrueckii	*Saccharomyces delbrueckii*
Meyerozyma guilliermondii	*Pichia guilliermondii*
Limosilactobacillus pontis	*Lactobacillus pontis*
Limosilactobacillus panis	*Lactobacillus panis*
Companilactobacillus paralimentarius	*Lactobacillus paralimentarius*
Companilactobacillus alimentarius	*Lactobacillus alimentarius*
Companilactobacillus crustorum	*Lactobacillus crustorum*
Companilactobacillus mindensis	*Lactobacillus mindensis*
Companilactobacillus nantensis	*Lactobacillus nantensis*
Limosilactobacillus frumenti	*Lactobacillus frumenti*
Limosilactobacillus reuteri	*Lactobacillus reuteri*
Lactobacillus crispatus	*Eubacterium crispatum*
Lactiplantibacillus paraplantarum	*Lactobacillus paraplantarum*
Lactiplantibacillus pentosus	*Lactobacillus pentosus*
Companilactobacillus paralimentarius	*Lactobacillus paralimentarius*
Leuconostoc mesenteroides	*Ascococcus mesenteroides*
Kluyveromyces marxianus	*Saccharomyces marxianus*
Wickerhamomyces anomalus	*Saccharomyces anomalus*
Lacticaseibacillus casei	*Lactobacillus casei*

References

Akamine, I. T., Mansoldo, F. R., & Vermelho, A. B. (2023). Probiotics in the sourdough bread fermentation: current status. *Fermentation*, *9*(2), 90. https://doi.org/10.3390/fermentation9020090.

Arendt, E. K., Ryan, L. A., & Dal Bello, F. (2007). Impact of sourdough on the texture of bread. *Food microbiology*, *24*(2), 165-174. https://doi.org/10.1016/j.fm.2006.07.011.

Arora, K., Ameur, H., Polo, A., Di Cagno, R., Rizzello, C. G., & Gobbetti, M. (2021). Thirty years of knowledge on sourdough fermentation: A systematic review. *Trends in Food Science & Technology*, *108*, 71-83. https://doi.org/10.1016/j.tifs.2020.12.008.

Brandt, M. J. (2007). Sourdough products for convenient use in baking. *Food microbiology*, *24*(2), 161-164. https://doi.org/10.1016/j.fm.2006.07.010.

Calvert, M. D., Madden, A. A., Nichols, L. M., Haddad, N. M., Lahne, J., Dunn, R. R., & McKenney, E. A. (2021). A review of sourdough starters: Ecology, practices, and sensory quality with applications for baking and recommendations for future research. *PeerJ*, *9*, e11389. https://doi.org/10.7717/peerj.11389.

Carnevali, P., Ciati, R., Leporati, A., & Paese, M. (2007). Liquid sourdough fermentation: Industrial application perspectives. *Food microbiology*, *24*(2), 150-154. https://doi.org/10.1016/j.fm.2006.07.009.

Casado, A., Álvarez, A., González, L., Fernández, D., Marcos, J. L., & Tornadijo, M. E. (2017). Effect of fermentation on microbiological, physicochemical and physical characteristics of sourdough and impact of its use on bread quality. *Czech Journal of Food Sciences*, *35*(6). https://doi: 10.17221/68/2017-CJFS.

Coda, R., Di Cagno, R., Gobbetti, M., & Rizzello, C. G. (2014). Sourdough lactic acid bacteria: Exploration of non-wheat cereal-based fermentation. *Food microbiology*, *37*, 51-58. https://doi.org/10.1016/j.fm.2013.06.018.

Corsetti, A., & Settanni, L. (2007). Lactobacilli in sourdough fermentation. *Food research international*, *40*(5), 539-558. https://doi.org/10.1016/j.foodres.2006.11.001.

De Marco, I., da Silva, C. M., de Moraes, J. O., Menezes, L. A. A., Miotto, M., Laurindo, J. B., & Lindner, J. D. D. (2022). A systematic review of drying methods and their impact on technological characteristics of sourdough type III. *Biotechnology Research and Innovation Journal*, *6*(1), 0-0. http://dx.doi.org/10.4322/biori.202203.

De Vuyst, L., & Neysens, P. (2005). The sourdough microflora: biodiversity and metabolic interactions. *Trends in Food Science & Technology*, *16*(1-3), 43-56. https://doi.org/10.1016/j.tifs.2004.02.012.

De Vuyst, L., Comasio, A., & Kerrebroeck, S. V. (2023). Sourdough production: fermentation strategies, microbial ecology, and use of non-flour ingredients. *Critical reviews in food science and nutrition*, *63*(15), 2447-2479. https://doi.org/10.1080/10408398.2021.1976100.

De Vuyst, L., Van Kerrebroeck, S., Harth, H., Huys, G., Daniel, H. M., & Weckx, S. (2014). Microbial ecology of sourdough fermentations: diverse or uniform?. *Food microbiology*, *37*, 11-29. https://doi.org/10.1016/j.fm.2013.06.002.

Decock, P., & Cappelle, S. (2005). Bread technology and sourdough technology. *Trends in Food Science & Technology*, *16*(1-3), 113-120. https://doi.org/10.1016/j.tifs.2004.04.012.

Fekri, A., Abedinzadeh, S., Torbati, M., Azadmard-Damirchi, S., & Savage, G. P. (2024). Considering sourdough from a biochemical, organoleptic, and nutritional perspective. *Journal of Food Composition and Analysis*, *125*, 105853. https://doi.org/10.1016/j.jfca.2023.105853.

Fu, W., Wang, S., & Xue, W. (2024). Mechanism of carbohydrate and protein conversion during sourdough fermentation: An analysis based on representative Chinese sourdough microbiota. *International Journal of Food Microbiology*, *410*, 110487. https://doi.org/10.1016/j.ijfoodmicro.2023.110487.

Galle, S., & Arendt, E. K. (2014). Exopolysaccharides from sourdough lactic acid bacteria. *Critical reviews in food science and nutrition*, *54*(7), 891-901. https://doi.org/10.1080/10408398.2011.617474.

Gänzle, M. G. (2014). Enzymatic and bacterial conversions during sourdough fermentation. *Food microbiology*, *37*, 2-10. https://doi.org/10.1016/j.fm.2013.04.007.

Gänzle, M. G., & Zheng, J. (2019). Lifestyles of sourdough lactobacilli–Do they matter for microbial ecology and bread quality?. *International Journal of Food Microbiology*, *302*, 15-23. https://doi.org/10.1016/j.ijfoodmicro.2018.08.019.

Gänzle, M. G., Loponen, J., & Gobbetti, M. (2008). Proteolysis in sourdough fermentations: mechanisms and potential for improved bread quality. *Trends in food science & technology*, *19*(10), 513-521. https://doi.org/10.1016/j.tifs.2008.04.002.

Gianotti, A., Vannini, L., Gobbetti, M., Corsetti, A., Gardini, F., & Guerzoni, M. E. (1997). Modelling of the activity of selected starters during sourdough fermentation. *Food microbiology*, *14*(4), 327-337. https://doi.org/10.1006/fmic.1997.0099.

Gobbetti, M., De Angelis, M., Di Cagno, R., Calasso, M., Archetti, G., & Rizzello, C. G. (2019). Novel insights on the functional/nutritional featu-

res of the sourdough fermentation. *International journal of food microbiology*, *302*, 103-113. https://doi.org/10.1016/j.ijfoodmicro.2018.05.018.

Goesaert, H., Brijs, K., Veraverbeke, W. S., Courtin, C. M., Gebruers, K., & Delcour, J. A. (2005). Wheat flour constituents: how they impact bread quality, and how to impact their functionality. *Trends in food science & technology*, *16*(1-3), 12-30. doi:10.1016/j.tifs.2004.02.011.

Graça, C., Lima, A., Raymundo, A., & Sousa, I. (2021). Sourdough fermentation as a tool to improve the nutritional and health-promoting properties of its derived-products. *Fermentation*, *7*(4), 246. https://doi.org/10.3390/fermentation7040246.

Hansen, A., & Schieberle, P. (2005). Generation of aroma compounds during sourdough fermentation: applied and fundamental aspects. *Trends in Food Science & Technology*, *16*(1-3), 85-94. https://doi.org/10.1016/j.tifs.2004.03.007.

Hernández-Parada, N., González-Ríos, O., Suárez-Quiroz, M. L., Hernández-Estrada, Z. J., Figueroa-Hernández, C. Y., Figueroa-Cárdenas, J. D. D., ... & Figueroa-Espinoza, M. C. (2022). Exploiting the native microorganisms from different food matrices to formulate starter cultures for sourdough bread production. *Microorganisms*, *11*(1), 109. https://doi.org/10.3390/microorganisms11010109.

Islam, M. A., & Islam, S. (2024). Sourdough bread quality: Facts and Factors. *Foods*, *13*(13), 2132. https://doi.org/10.3390/foods13132132.

Landis, E. A., Oliverio, A. M., McKenney, E. A., Nichols, L. M., Kfoury, N., Biango-Daniels, M., ... & Wolfe, B. E. (2021). The diversity and function of sourdough starter microbiomes. *elife*, *10*, e61644. https://doi.org/10.7554/eLife.61644.

Ma, S., Wang, Z., Guo, X., Wang, F., Huang, J., Sun, B., & Wang, X. (2021). Sourdough improves the quality of whole-wheat flour products: Mechanisms and challenges—A review. *Food Chemistry*, *360*, 130038. https://doi.org/10.1016/j.foodchem.2021.130038.

Meignen, B., Onno, B., Gélinas, P., Infantes, M., Guilois, S., & Cahagnier, B. (2001). Optimization of sourdough fermentation with *Lactobacillus brevis* and baker's yeast. *Food microbiology*, *18*(3), 239-245. https://doi.org/10.1006/fmic.2000.0395.

National Center for Biotechnology Information (NCBI). (2025). NCBI Genome & Taxonomy Databases. https://www.ncbi.nlm.nih.gov/.

Nionelli, L., & Rizzello, C. G. (2016). Sourdough-based biotechnologies for the production of gluten-free foods. *Foods*, *5*(3), 65. https://doi.org/10.3390/foods5030065.

Paterson, A., & Piggott, J. R. (2006). Flavour in sourdough breads: a review. *Trends in Food Science & Technology*, *17*(10), 557-566. doi:10.1016/j.tifs.2006.03.006.

Sakandar, H. A., Hussain, R., Kubow, S., Sadiq, F. A., Huang, W., & Imran, M. (2019). Sourdough bread: A contemporary cereal fermented product. *Journal of Food Processing and Preservation*, *43*(3), e13883. https://doi.org/10.1111/jfpp.13883.

Sevgili, A., Erkmen, O., & Koçaslan, S. (2021). Identification of lactic acid bacteria and yeasts from traditional sourdoughs and sourdough production by enrichment. *Czech Journal of Food Sciences*, *39*(4). https://doi.org/10.17221/56/2021-CJFS.

Teixeira, L. B., Campos, J. Z., Kothe, C. I., Welke, J. E., Rodrigues, E., Frazzon, J., & Thys, R. C. S. (2024). Type III sourdough: Evaluation of biopreservative potential in bakery products with enhanced antifungal activity. *Food Research International*, *189*, 114482. https://doi.org/10.1016/j.foodres.2024.114482.

Van Kerrebroeck, S., Maes, D., & De Vuyst, L. (2017). Sourdoughs as a function of their species diversity and process conditions, a meta-analysis. *Trends in Food Science & Technology*, *68*, 152-159. https://doi.org/10.1016/j.tifs.2017.08.016.

Weckx, S., Van Kerrebroeck, S., & De Vuyst, L. (2019). Omics approaches to understand sourdough fermentation processes. *International Journal of Food Microbiology*, *302*, 90-102. https://doi.org/10.1016/j.ijfoodmicro.2018.05.029.

Wick, M., Stolz, P., Böcker, G., & Lebeault, J. M. (2003). Influence of several process parameters on sourdough fermentation. *Acta biotechnologica*, *23*(1), 51-61. https://doi.org/10.1002/abio.200390008.