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PROBIOTIC MICROORGANISMS IN BREAD SOURDOUGHS

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Abstract. The review allows for characterization and evaluation of the typical microbiota and probiotic properties of individual species isolated from various bread sourdoughs. It has been observed that an interest in using sourdoughs for bread making and studying their microbiota has been steadily increasing in recent years. However, an analysis of contemporary publications has revealed insufficient information regarding microorganisms characteristic of sourdoughs based on spelt, buckwheat, corn, rice, teff, amaranth, quinoa, barley, oats, chia, sorghum, beans, and peas. The most studied sourdoughs are those based on wheat and rye flour. A list of the most prevalent lactic acid bacteria (LAB) and yeasts isolated from sourdoughs has been established. It comprises *Companilactobacillus paralimentarius*, *Fructilactobacillus sanfranciscensis*, *Lactiplantibacillus plantarum*, *Latilactobacillus sakei*, *Leuconostoc citreum*, *Levilactobacillus brevis*, *Pediococcus pentosaceus*, *Weissella cibaria*, *Weissella confusa*, as well as *Kazachstania humilis*, *Kazachstania unispora*, *Pichia kudriavzevii*, *Pichia fermentans*, *Saccharomyces cerevisiae* and *Wickerhamomyces anomalus*. All typical mentions of the probiotic properties of microorganisms isolated from bread sourdoughs have been described. When isolating probiotics from bread sourdoughs, special attention should be paid to such species of LAB as *Lactiplantibacillus plantarum*, *Levilactobacillus brevis*, *Pediococcus pentosaceus*, *Enterococcus faecium*, as well as the yeasts *Saccharomyces cerevisiae* and *Kazachstania humilis*, as they are quite commonly found in sourdoughs from various types of flour and have the most conspicuous probiotic properties. According to the review, it has been established that stress tolerance and antimicrobial activity are typical probiotic properties for microorganisms isolated from sourdoughs, although antioxidant properties require further research. Advances in technology and increased economic accessibility will lead to increased demand for new probiotic strains and microorganisms from bread sourdoughs and may help meet new levels of consumer needs.

Key words: *Lactobacillaceae*, lactic acid bacteria, yeast, microbiota, stress tolerance, antimicrobial activity, sourdough bread, types of flour.

Introduction. Formulation of the problem

Bread has been and remains one of the staple foods all over the world, but now its role is especially great in poor and developing countries. It is a rich source of sugars, proteins, vitamins and minerals and is able to cover a significant part of a person's daily need for nutrients [1]. As a result of archaeological and genetic studies of various types of wheat (genus *Triticum*) and their wild relatives (genus *Aegilops*), it was established that bread was first baked more than 12,000 years ago [2]. Originally, it was made without yeast at all, but about 8,000 years ago, the Egyptians mixed water and flour and left it for a certain time, which led to fermentation and changed the taste and quality of the bread. In this way, the first version of

bread using sourdough was obtained. It is believed that such bread appeared in Europe about 5,000 years ago, although it did not immediately become widespread. Over time, the assortment and composition of sourdoughs expanded and, parallel to this, the use of sourdoughs in bread-making became increasingly important in society, and the product of such fermentation took a central role in the diet of peasants, since the production of sourdoughs did not require special efforts, but instead allowed to obtain a tastier and nutritious food [3].

Bread obtained with the use of sourdough is distinguished by improved organoleptic properties, especially taste and aroma, has a unique texture and a longer shelf life. Due to the reduction of phytic acid content in the finished product as a result of the

enzymatic activity of bacteria and yeast, the bioavailability of trace elements such as calcium, magnesium, iron and zinc increases, and the number of free amino acids rises, while the amount of fermented oligosaccharides, disaccharides, monosaccharides and polyols, which are poorly absorbed in the small intestine, as well as gluten, decreases [4, 5]. Sourdough starters can break down or inhibit the synthesis of various harmful substances, such as fungal toxins, acrylamide, and pesticide residues in flour [6]. The positive effect of sourdough bread on blood glucose levels, on gastrointestinal health, etc. has been described, although these hypotheses require proper standardized studies [4,5].

There are 3 types of sourdoughs: type I – obtained by spontaneous fermentation, that is, as a result of mixing flour of different types, water and salt [3] (sometimes other ingredients are also added, such as apples, grapes, honey, etc. [7]), and ready-made starters of this type can be added to new batches of flour to provide microorganisms with a new supply of nutrients; type II – obtained through the use of a starter culture (a mixture of microorganisms specifically selected by researchers and scientists to obtain high-quality bread – for example, acid-resistant strains of *Lactiplantibacillus plantarum*, *Limosilactobacillus fermentum*, *Limosilactobacillus reuteri*, and *Fructilactobacillus sanfranciscensis*, chosen for their ability to quickly lower the pH of the starter and form aromatic compounds, are often used); type III – obtained by drying type II sourdoughs. Sometimes type IV is also distinguished – sourdoughs obtained by a mixed method (combination of type I and type II) [3].

Since both saprophytic and pathogenic microorganisms develop on cereal plants [8], any flour derived from the grains of these crops will contain a certain amount of their native microbiota – bacteria, micromycetes, and yeasts, which can include both opportunistic and pathogenic species. For some time,

these representatives of the microbiota remain dormant, but given favorable conditions such as temperature, humidity, and the presence of nutrients, they become active and begin to develop. The process of making sourdough starters can provide such favorable conditions, creating an environment conducive to the development of LAB and acetic acid bacteria and yeasts, resulting in the production of carbon dioxide, the release of organic acids, and extracellular enzymes. These changes affect the composition of the flour and improve the organoleptic and rheological characteristics of the resulting bread [9].

The microorganisms that dominate in sourdoughs can be isolated for further use as intended. For example, various strains of LAB and yeasts are known as probiotics and are widely used in medicine and the food industry [10]. The isolation and subsequent evaluation of the probiotic properties of microorganisms from various sourdoughs will allow for the identification of their potential for use in medicine and other fields, as well as deepen the understanding of their impact on the quality characteristics of the finished bread.

There is a noticeable increase in scientific interest in the field of sourdoughs. The authors [11] indicate that the number of publications related to sourdoughs increased from 2010 to 2021, with articles published in 2020-2021 accounting for one-third of all publications during this period. It was found that research on this topic was conducted in 55 countries, mostly European, and the majority of them (58.8%) focused on the identification and selection of microorganisms isolated from sourdoughs, including those exhibiting probiotic properties. The authors also note an increase in the number of patents focused in this direction, with a maximum of 16 in 2020.

An analysis of publications in various scientometric databases over the past 35 years was conducted, as shown in Figure 1.

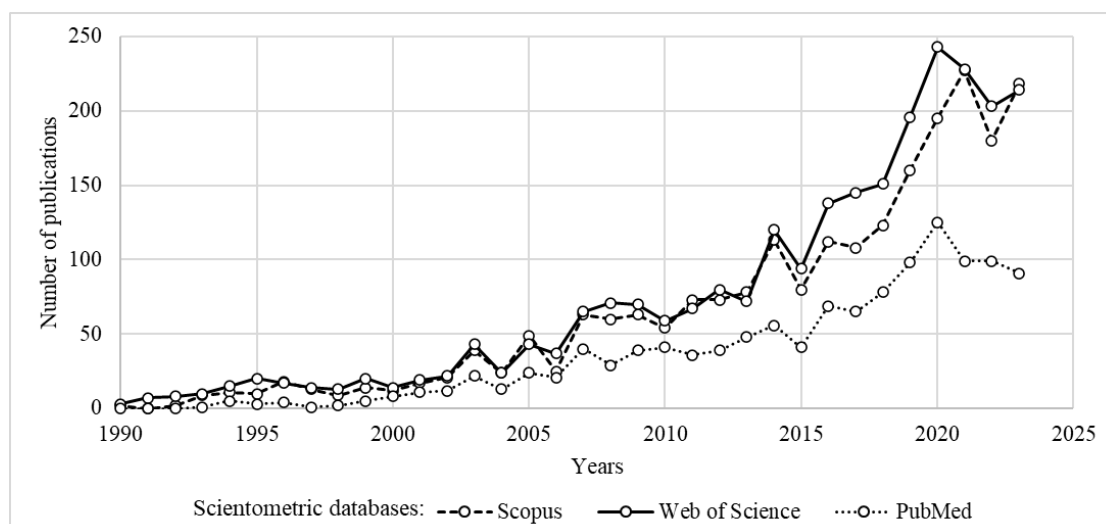


Fig. 1. Analysis of publications on the topic of «sourdough» (based on data from PubMed, Web of Science, Scopus)

The dynamics indicate an increase in the number of publications discussing sourdough. It can be observed that the highest number of publications is found in the «Web of Science» database, fewer in «Scopus» and the fewest in «PubMed».

The purpose of this review is to analyze the typical microorganisms present in Type I sourdoughs and to study experimental research concerning the probiotic properties of sourdough microbiota and their potential for further use.

1. Typical sourdough microbiota

Sourdoughs are complex ecosystems containing bacteria and yeast which proved to be the most adapted, survived natural selection and competition for limited resources within the sourdough and were able to completely colonize it. The number of colony-forming units (CFUs) of bacteria in mature and established sourdoughs can be about 100 times greater than the number of yeast CFUs [12]. The total number of bacterial genera encountered in sourdoughs at different stages of their development exceeds 52 (mostly various LAB genera), while the total number of genera of micromycetes and yeast is at least 22 [13-16].

In the microbiota of well-established sourdoughs, from which bread with high organoleptic characteristics is obtained, microorganisms can be conditionally divided into 3 groups: dominant, subdominant and satellite (that is, dependent or accompanying) groups. Dominant groups carry out a significant share of chemical transformations in carbohydrate and nitrogen metabolism and energy acquisition, while subdominant groups exert a synergistic effect due to the expression of additional genes and ensure the functioning of key metabolic pathways. Satellite groups do not produce critical substances for the existence of the starter as a system and usually include conditionally pathogenic microorganisms, for example, various types of *Staphylococcus*. This interaction of microorganisms ensures the stability of sourdough ecosystem in the event of a change in environmental conditions or the appearance of contaminants [17].

The microbiota of sourdoughs varies depending on the type and characteristics of the flour, the geographical origin of the grain, and the environment in the bakery, laboratory, or factory. Some microorganisms likely enter the starters from the skin of the people preparing them [18]. In the study [19], it was found that even the water added to the flour can influence the microbiota and introduce species that would not have developed under other conditions. Due to the diversity of possible sources of microorganisms, many questions still need to be resolved. For example, the results of the study by Landis et al. [9], who studied 500 sourdoughs from 4 continents, contradict the commonly accepted belief that geographic origin influences the microbiota of starters. In contrast, the study by L. von Gastrow et al. [20] indicates that the bacteria or yeast present in sourdoughs did not come from the flour. The conclusions of these studies do not align and thus require further investigation and clarification.

Although the microbial composition of sourdoughs is influenced by many different factors, it is conventionally believed that the types and quality of flour are among the most important and defining. The most studied is the microbial composition of sourdoughs based on wheat flour, less – on the basis of rye and spelt flour [7]. There are various (microbiological, chemical, etc.) studies on sourdoughs based on buckwheat flour [21], corn [22], rice [23], teff [24], amaranth [25], quinoa [26], barley [27], chia [28], sorghum [29], oats [30], and even legumes such as fava beans and peas [31]. Therefore, to understand the microbial diversity of sourdoughs it is worth considering microorganisms isolated from sourdoughs of different types of flour.

Despite the great diversity of the microbiota composition in sourdoughs and the significant number of other described factors that can influence it, it is known that sourdoughs are mainly composed of dominant and subdominant organisms, which mainly include representatives of the order *Lactobacillales* and yeasts. The inter-microbial and biochemical interactions of these microorganisms that occur during the fermentation of sourdoughs are presented in Figure 2.

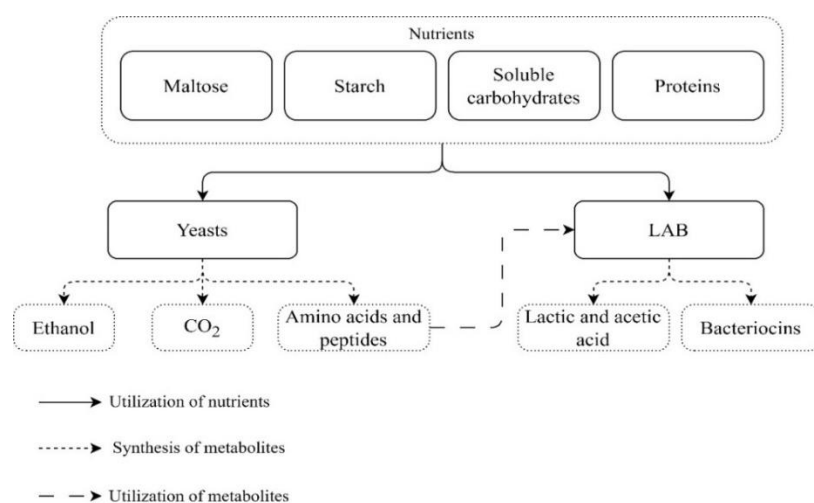


Fig. 2. Biochemical interactions between lactic acid bacteria and yeast in sourdoughs [17, 32, 33]

1.1. Lactic acid bacteria

The most common LAB isolated from wheat sourdoughs are *Companilactobacillus paralimentarius*, *Flb. sanfranciscensis*, *Lpb. plantarum*, *Latilactobacillus sakei*, *Leuconostoc citreum*, *Levilactobacillus brevis*, *Pediococcus pentosaceus*, *Weissella cibaria*, and *Weissella confusa*. *Lactocaseibacillus paracasei*, *Lactiplantibacillus pentosus*, *Lactococcus lactis*, *Latilactobacillus curvatus*, and *Leuconostoc mesenteroides* are also

frequently mentioned. Due to the high level of study of wheat sourdoughs, these microorganisms are also the most widespread among sourdoughs based on other types of flour. For instance, in rye sourdoughs, *Lpb. plantarum* and *Lv. brevis*, as well as *Com. paralimentarius*, are most commonly found; in spelt sourdoughs, *Lpb. plantarum*, *Lt. curvatus*, *Lv. brevis*, and *P. pentosaceus* are frequently present.

The LAB isolated from and identified in sourdoughs are presented in Table 1.

Table 1 – LAB isolated from sourdoughs

Flour types	Bacteria genera	Bacteria species	References
Wheat	<i>Agrilactobacillus</i>	<i>A. composti</i>	[34]
	<i>Companilactobacillus</i>	<i>Com. alimentarius</i> , <i>Com. crustorum</i> , <i>Com. farciminis</i> , <i>Com. futsaii</i> , <i>Com. kimchiensis</i> , <i>Com. kimchii</i> , <i>Com. mindensis</i> , <i>Com. nantensis</i> , <i>Com. nodensis</i> , <i>Com. nuruki</i> , <i>Com. paralimentarius</i> , <i>Com. tuceti</i>	[20, 34-42]
	<i>Enterococcus</i>	<i>Ec. devriesei</i> , <i>Ec. durans</i> , <i>Ec. faecalis</i> , <i>Ec. faecium</i> , <i>Ec. hermanniensiensis</i> , <i>Ec. hirae</i>	[38, 40, 43-45]
	<i>Fructilactobacillus</i>	<i>Flb. lindneri</i> , <i>Flb. sanfranciscensis</i>	[20, 40]
	<i>Fructobacillus</i>	<i>F. durionis</i> , <i>F. fructosus</i>	[46]
	<i>Furfurilactobacillus</i>	<i>Ffl. rossiae</i>	[45]
	<i>Holzapfelia</i>	<i>H. floricola</i>	[35, 36, 40, 44, 47]
	<i>Lactocaseibacillus</i>	<i>Lcb. brantae</i> , <i>Lcb. casei</i> , <i>Lcb. paracasei</i> , <i>Lcb. rhamnosus</i> , <i>Lcb. zeae</i>	
	<i>Lactiplantibacillus</i>	<i>Lpb. paraplantarum</i> , <i>Lpb. pentosus</i> , <i>Lpb. plantarum</i> , <i>Lpb. xiangfangensis</i>	[43, 48]
	<i>Lactobacillus</i>	<i>L. acetotolerans</i> , <i>L. acidophilus</i> , <i>L. amylolyticus</i> , <i>L. delbrueckii</i> , <i>L. gallinarum</i> , <i>L. quizhouensis</i> , <i>L. helveticus</i> , <i>L. japonicus</i> , <i>L. johnsonii</i> , <i>L. letivazi</i>	[12, 36, 40, 42, 44, 49-51]
	<i>Lactococcus</i>	<i>Lc. garvieae</i> , <i>Lc. lactis</i>	[38, 45]
	<i>Latilactobacillus</i>	<i>Lt. curvatus</i> , <i>Lt. graminis</i> , <i>Lt. sakei</i>	[34, 37, 45]
	<i>Lentilactobacillus</i>	<i>Ln. buchneri</i> , <i>Ln. diolivorans</i> , <i>Ln. farraginis</i> , <i>Ln. hilgardii</i> , <i>Ln. parabuchneri</i>	[48, 51]
	<i>Leuconostoc</i>	<i>Leu. carnosum</i> , <i>Leu. citreum</i> , <i>Leu. holzapfelii</i> , <i>Leu. kimchii</i> , <i>Leu. lactis</i> , <i>Leu. mesenteroides</i> , <i>Leu. palmae</i> , <i>Leu. pseudomesenteroides</i>	[36, 37, 40, 44, 52]
	<i>Levilactobacillus</i>	<i>Lv. brevis</i> , <i>Lv. hammesii</i> , <i>Lv. koreensis</i> , <i>Lv. namurensis</i> , <i>Lv. parabrevis</i> , <i>Lv. spicheri</i> , <i>Lv. zymae</i>	[20, 44, 48, 50, 53]
	<i>Ligilactobacillus</i>	<i>Lig. agilis</i> , <i>Lig. aviarius</i> , <i>Lig. salivarius</i>	[36, 42]
	<i>Limosilactobacillus</i>	<i>Lm. fermentum</i> , <i>Lm. frumenti</i> , <i>Lm. mucosae</i> , <i>Lm. panis</i> , <i>Lm. pontis</i> , <i>Lm. reuteri</i>	[12, 34, 36, 54]
	<i>Liquorilactobacillus</i>	<i>Liq. satsumensis</i>	[36]
	<i>Loigolactobacillus</i>	<i>Loig. coryniformis</i>	
	<i>Paucilactobacillus</i>	<i>Plb. oligofermentans</i> , <i>Plb. vaccinostercus</i>	[36, 55]
	<i>Pediococcus</i>	<i>P. acidilactici</i> , <i>P. argentinicus</i> , <i>P. inopinatus</i> , <i>P. parvulus</i> , <i>P. pentosaceus</i>	[36, 40, 43, 44]
	<i>Schleiferilactobacillus</i>	<i>Sch. perolens</i>	[36]
	<i>Secundilactobacillus</i>	<i>Sec. paracollinoides</i>	[34]
	<i>Weissella</i>	<i>W. cibaria</i> , <i>W. confusa</i> , <i>W. hellenica</i> , <i>W. paramesenteroides</i> , <i>W. salipiscis</i>	[34, 36, 40, 43, 50]
Rye	<i>Companilactobacillus</i>	<i>Com. crustorum</i> , <i>Com. farciminis</i> , <i>Com. futsaii</i> , <i>Com. heilongjiangensis</i> , <i>Com. kimchii</i> , <i>Com. mindensis</i> , <i>Com. nantensis</i> , <i>Com. paralimentarius</i>	[37]
	<i>Enterococcus</i>	<i>Ec. casseliflavus</i> , <i>Ec. faecalis</i> , <i>Ec. mundtii</i> , <i>Ec. pseudoavium</i>	[56-58]
	<i>Fructilactobacillus</i>	<i>Flb. sanfranciscensis</i>	[21]
	<i>Lactocaseibacillus</i>	<i>Lcb. casei</i> , <i>Lcb. paracasei</i>	[21, 56]

Flour types	Bacteria genera	Bacteria species	References
	<i>Lactiplantibacillus</i>	<i>Lpb. pentosus</i> , <i>Lpb. plantarum</i>	[37, 57]
	<i>Lactococcus</i>	<i>Lc. lactis</i>	[37]
	<i>Latilactobacillus</i>	<i>Lt. curvatus</i> , <i>Lt. graminis</i> , <i>Lt. sakei</i>	[56, 57]
	<i>Lentilactobacillus</i>	<i>Ln. farraginis</i>	[56]
	<i>Leuconostoc</i>	<i>Leu. citreum</i> , <i>Leu. holzapfelii</i> , <i>Leu. lactis</i> , <i>Leu. mesenteroides</i> , <i>Leu. pseudomesenteroides</i>	[37, 56-58]
	<i>Levilactobacillus</i>	<i>Lv. brevis</i> , <i>Lv. hammesii</i>	[21, 37]
	<i>Limosilactobacillus</i>	<i>Lm. pontis</i>	[48]
		<i>Lm. fermentum</i>	[58]
	<i>Liquorilactobacillus</i>	<i>Liq. uvarum</i>	[56]
	<i>Loigolactobacillus</i>	<i>Loig. coryniformis</i>	[37]
	<i>Pediococcus</i>	<i>P. acidilactici</i> , <i>P. parvulus</i> , <i>P. pentosaceus</i>	[21, 37, 56]
	<i>Weissella</i>	<i>W. cibaria</i> , <i>W. confusa</i> , <i>W. paramesenteroides</i>	[37, 57]
Wheat + rye	<i>Companilactobacillus</i>	<i>Com. alimentarius</i> , <i>Com. paralimentarius</i>	[51, 55]
	<i>Enterococcus</i>	<i>Ec. mundtii</i>	[51]
	<i>Fructilactobacillus</i>	<i>Flb. sanfranciscensis</i>	[21]
	<i>Furfurilactobacillus</i>	<i>Ffb. rossiae</i>	[51]
	<i>Lacticaseibacillus</i>	<i>Lcb. paracasei</i>	
	<i>Lactiplantibacillus</i>	<i>Lpb. pentosus</i> , <i>Lpb. plantarum</i>	[52]
	<i>Latilactobacillus</i>	<i>Lt. curvatus</i> , <i>Lt. sakei</i>	[21, 55]
	<i>Levilactobacillus</i>	<i>Lv. brevis</i> , <i>Lv. zymae</i>	[52]
	<i>Limosilactobacillus</i>	<i>Lm. fermentum</i> , <i>Lm. pontis</i>	[51]
	<i>Pediococcus</i>	<i>P. acidilactici</i> , <i>P. pentosaceus</i>	
	<i>Weissella</i>	<i>W. cibaria</i> , <i>W. confusa</i>	[51, 52]
Spelt	<i>Companilactobacillus</i>	<i>Com. kimchii</i> , <i>Com. nantensis</i> , <i>Com. paralimentarius</i>	[37, 51]
	<i>Enterococcus</i>	<i>Ec. faecium</i> , <i>Ec. hirae</i> , <i>Ec. mundtii</i>	[59, 60]
	<i>Fructilactobacillus</i>	<i>Flb. sanfranciscensis</i>	[52]
	<i>Furfurilactobacillus</i>	<i>Ffb. rossiae</i>	[51]
	<i>Lacticaseibacillus</i>	<i>Lcb. casei</i> , <i>Lcb. paracasei</i> , <i>Lcb. rhamnosus</i>	[37, 61]
	<i>Lactiplantibacillus</i>	<i>Lpb. paraplantarum</i> , <i>Lpb. pentosus</i> , <i>Lpb. plantarum</i> , <i>Lpb. xiangfangensis</i>	[21, 37, 61]
	<i>Lactobacillus</i>	<i>L. helveticus</i>	[60]
	<i>Lactococcus</i>	<i>Lc. lactis</i>	[37]
	<i>Latilactobacillus</i>	<i>Lt. curvatus</i> , <i>Lt. sakei</i>	[51]
	<i>Leuconostoc</i>	<i>Leu. citreum</i> , <i>Leu. holzapfelii</i> , <i>Leu. lactis</i> , <i>Leu. pseudomesenteroides</i>	[37, 60]
	<i>Levilactobacillus</i>	<i>Lv. brevis</i> , <i>Lv. hammesii</i>	[37]
	<i>Limosilactobacillus</i>	<i>Lm. fermentum</i> , <i>Lm. pontis</i> , <i>Lm. reuteri</i>	[37, 51, 59, 61]
	<i>Loigolactobacillus</i>	<i>Loig. coryniformis</i>	[37]
	<i>Pediococcus</i>	<i>P. acidilactici</i> , <i>P. pentosaceus</i>	[51]
	<i>Streptococcus</i>	<i>Sc. thermophilus</i>	[37]
	<i>Weissella</i>	<i>W. cibaria</i> , <i>W. confusa</i>	
Wheat + rye + spelt	<i>Companilactobacillus</i>	<i>Com. paralimentarius</i>	[51]
	<i>Lactiplantibacillus</i>	<i>Lpb. plantarum</i>	
	<i>Levilactobacillus</i>	<i>Lv. brevis</i> , <i>Lv. hammesii</i> , <i>Lv. namurensis</i>	
Buckwheat	<i>Fructilactobacillus</i>	<i>Flb. sanfranciscensis</i>	[21]
	<i>Lactiplantibacillus</i>	<i>Lpb. plantarum</i>	[62]
	<i>Lactobacillus</i>	<i>L. crispatus</i> , <i>L. gallinarum</i>	
	<i>Latilactobacillus</i>	<i>Lt. graminis</i> , <i>Lt. sakei</i>	
	<i>Leuconostoc</i>	<i>Leu. holzapfelii</i>	
	<i>Limosilactobacillus</i>	<i>Lm. fermentum</i> , <i>Lm. vaginalis</i>	
	<i>Pediococcus</i>	<i>P. pentosaceus</i>	
	<i>Weissella</i>	<i>W. cibaria</i>	
Corn	<i>Bifidobacterium</i>	<i>Bif. minimum</i>	[22]
	<i>Enterococcus</i>	<i>Ec. saccharolyticus</i>	
	<i>Lacticaseibacillus</i>	<i>Lcb. casei</i>	[63]
	<i>Lactiplantibacillus</i>	<i>Lpb. plantarum</i>	
	<i>Lactobacillus</i>	<i>L. acidophilus</i> , <i>L. delbrueckii</i>	[22, 63]
	<i>Leuconostoc</i>	<i>Leu. dextranicum</i> , <i>Leu. mesenteroides</i>	[63]
	<i>Levilactobacillus</i>	<i>Lv. brevis</i>	[23]

Flour types	Bacteria genera	Bacteria species	References
	<i>Limosilactobacillus</i>	<i>Lm. fermentum</i>	[63]
	<i>Pediococcus</i>	<i>P. acidilactici</i>	
	<i>Streptococcus</i>	<i>Sc. equinus</i>	[22]
Rice	<i>Companilactobacillus</i>	<i>Com. paralimentarius</i>	[64]
		<i>Com. kimchii</i>	
	<i>Lactocaseibacillus</i>	<i>Lcb. paracasei</i>	
	<i>Lactiplantibacillus</i>	<i>Lpb. plantarum, Lpb. paraplantarum</i>	[26, 65]
	<i>Lactobacillus</i>	<i>L. gallinarum</i>	[64]
	<i>Levilactobacillus</i>	<i>Lv. brevis, Lv. spicheri</i>	[23, 64]
	<i>Limosilactobacillus</i>	<i>Lm. fermentum, Lm. pontis</i>	[64, 65]
	<i>Schleiferilactobacillus</i>	<i>Sch. perolens</i>	[64]
Teff	<i>Weissella</i>	<i>W. confusa</i>	[23]
	<i>Fructilactobacillus</i>	<i>Flb. sanfranciscensis</i>	[24]
	<i>Lactiplantibacillus</i>	<i>Lpb. plantarum</i>	
	<i>Lactobacillus</i>	<i>L. gallinarum, L. helveticus</i>	[24, 62]
	<i>Lactococcus</i>	<i>Lc. lactis</i>	[24]
	<i>Latilactobacillus</i>	<i>Lt. sakei</i>	
	<i>Leuconostoc</i>	<i>Leu. citreum, Leu. holzapfelii, Leu. mesenteroides</i>	[24, 62]
	<i>Levilactobacillus</i>	<i>Lv. brevis</i>	
	<i>Limosilactobacillus</i>	<i>Lm. fermentum, Lm. pontis, Lm. vaginalis</i>	[62]
	<i>Loigolactobacillus</i>	<i>Loig. coryniformis</i>	[24]
	<i>Pediococcus</i>	<i>P. acidilactici, P. pentosaceus</i>	[24, 62]
	<i>Weissella</i>	<i>W. cibaria, W. confusa</i>	
Amaranth	<i>Enterococcus</i>	<i>Ec. casseliflavus, Ec. devriesei, Ec. faecium, Ec. mundtii</i>	[25]
	<i>Lactocaseibacillus</i>	<i>Lcb. rhamnosus</i>	
	<i>Lactiplantibacillus</i>	<i>Lpb. plantarum</i>	
	<i>Latilactobacillus</i>	<i>Lt. sakei</i>	[66]
	<i>Pediococcus</i>	<i>P. acidilactici, P. pentosaceus</i>	[25]
Quinoa	<i>Companilactobacillus</i>	<i>Com. kimchii</i>	[26]
	<i>Enterococcus</i>	<i>Ec. casseliflavus, Ec. devriesei, Ec. faecium, Ec. hermannienseis, Ec. mundtii</i>	[26, 67, 68]
	<i>Lactocaseibacillus</i>	<i>Lcb. rhamnosus</i>	[67]
	<i>Lactiplantibacillus</i>	<i>Lpb. paraplantarum, Lpb. plantarum</i>	[26]
	<i>Lactococcus</i>	<i>Lc. lactis</i>	
	<i>Latilactobacillus</i>	<i>Lt. graminis, Lt. sakei</i>	
	<i>Leuconostoc</i>	<i>Leu. citreum, Leu. mesenteroides</i>	[68]
	<i>Levilactobacillus</i>	<i>Lv. brevis</i>	
	<i>Pediococcus</i>	<i>P. pentosaceus</i>	[26]
Barley	<i>Weissella</i>	<i>W. cibaria</i>	[27]
	<i>Companilactobacillus</i>	<i>Com. musae, Com. paralimentarius</i>	
	<i>Enterococcus</i>	<i>Ec. faecium</i>	[69]
	<i>Lactiplantibacillus</i>	<i>Lpb. plantarum</i>	[27]
	<i>Lactococcus</i>	<i>Lc. lactis</i>	[69]
	<i>Latilactobacillus</i>	<i>Lt. curvatus</i>	[27]
	<i>Leuconostoc</i>	<i>Leu. citreum, Leu. mesenteroides, Leu. pseudomesenteroides</i>	[27, 70]
	<i>Levilactobacillus</i>	<i>Lv. brevis</i>	[27]
	<i>Limosilactobacillus</i>	<i>Lm. equigenerosi</i>	
		<i>Lm. fermentum</i>	[27, 69]
	<i>Pediococcus</i>	<i>P. acidilactici, P. pentosaceus</i>	
Chia	<i>Weissella</i>	<i>W. cibaria, W. confusa</i>	[28]
	<i>Enterococcus</i>	<i>Ec. asini, Ec. casseliflavus, Ec. devriesei, Ec. faecium, Ec. hermannienseis, Ec. hirae, Ec. italicus, Ec. mundtii</i>	
	<i>Lactocaseibacillus</i>	<i>Lcb. rhamnosus, Lcb. zeae</i>	
	<i>Lactiplantibacillus</i>	<i>Lpb. plantarum</i>	
	<i>Lactococcus</i>	<i>Lc. lactis</i>	
	<i>Latilactobacillus</i>	<i>Lt. sakei</i>	
	<i>Levilactobacillus</i>	<i>Lv. brevis</i>	
	<i>Limosilactobacillus</i>	<i>Lm. mucosae</i>	
	<i>Weissella</i>	<i>W. cibaria</i>	

Flour types	Bacteria genera	Bacteria species	References
Sorghum	<i>Enterococcus</i>	<i>Ec. faecalis</i>	[29]
	<i>Lactococcus</i>	<i>Lc. lactis</i>	
	<i>Limosilactobacillus</i>	<i>Lm. fermentum, Lm. reuteri</i>	
	<i>Pediococcus</i>	<i>P. pentosaceus</i>	[71]
	<i>Weissella</i>	<i>W. confusa</i>	
Faba bean	<i>Enterococcus</i>	<i>Ec. durans, Ec. mundtii</i>	[31]
	<i>Lactiplantibacillus</i>	<i>Lpb. fabifermentans, Lpb. paraplantarum, Lpb. pentosus, Lpb. plantarum</i>	
	<i>Lactococcus</i>	<i>Lc. cremoris, Lc. lactis</i>	
	<i>Latilactobacillus</i>	<i>Lt. sakei</i>	[72]
	<i>Leuconostoc</i>	<i>Leu. mesenteroides</i>	
	<i>Levilactobacillus</i>	<i>Lv. brevis</i>	[31]
	<i>Pediococcus</i>	<i>P. pentosaceus</i>	
Peas	<i>Weissella</i>	<i>W. cibaria, W. koreensis</i>	[72]
	<i>Enterococcus</i>	<i>Ec. durans, Ec. mundtii</i>	[31]
	<i>Lactocaseibacillus</i>	<i>Lcb. rhamnosus</i>	
	<i>Lactiplantibacillus</i>	<i>Lpb. fabifermentans, Lpb. paraplantarum, Lpb. pentosus, Lpb. plantarum</i>	
	<i>Lactococcus</i>	<i>Lc. cremoris, Lc. lactis</i>	
	<i>Leuconostoc</i>	<i>Leu. citreum, Leu. mesenteroides</i>	
	<i>Levilactobacillus</i>	<i>Lv. brevis</i>	
Oats	<i>Pediococcus</i>	<i>P. pentosaceus</i>	[30]
	<i>Leuconostoc</i>	<i>Leu. lactis</i>	
	<i>Loigolactobacillus</i>	<i>Loig. coryniformis</i>	
	<i>Pediococcus</i>	<i>P. pentosaceus</i>	
	<i>Weissella</i>	<i>W. cibaria</i>	

The prevalence of the listed microorganisms in carbohydrate- and protein-rich sourdoughs correlates with the characteristics of their metabolism and preferred living conditions: *Com. paralimentarius* actively grows in mediums rich in carbon sources, especially glucose and sucrose [73]; most strains of *Flb. sanfranciscensis* can metabolize fructose, maltose, and sucrose, and may be isolated from plant material [74]; *Lpb. plantarum* has a distinct ability to utilize a wide range of carbohydrates [75], including phenolic compounds, and is often used as a starter culture for initiating fermentation in the food industry [76]; *Lt. sakei* is characterized by metabolic plasticity and adaptability, which is manifested in its ability to obtain energy from various sources: hexoses and pentoses, aromatic compounds, amino acids, etc. [77]; *Leu. citreum* can metabolize a large number of diverse carbohydrate compounds, including glucose, fructose, sucrose, mannose, and others [78]; *Lv. brevis* can rapidly utilize sugars to produce organic acids, which promotes the fermentation of products, such as pickled radish [79]; *P. pentosaceus* has strain-dependent characteristics for using sugars as energy sources, but consistently retains the ability to metabolize major hexoses: galactose, fructose, mannose [80], and plays a significant proteolytic and oxidative role in fermentation [81]; *W. cibaria* and *W. confusa* exhibit high metabolic activity and the ability to utilize glucose, sucrose, xylose, and other sugars [82].

Microorganisms isolated exclusively from rye sourdoughs include *Com. heilongjiangensis*, *Ec. pseudoavium*, *Liq. uvarum*; from spelt sourdoughs – *Sc. thermophilus*; from buckwheat – *L. crispatus*; from corn – *Ec. saccharolyticus*, *Leu. dextranicum*, *Sc. equinus*; from barley – *Com. musae*, *Lm. equigenersi*; from chia – *Ec. asini*, *Ec. italicus*; from legumes – *W. koreensis*. For sourdoughs based on legumes (fava beans, peas), unique microorganisms were also *Lpb. fabifermentans* and *Lc. cremoris*. The presence of these microorganisms exclusively in sourdoughs from a single type of flour likely indicates a connection between their life cycle and the growth and development of the plants from which the flour was derived.

1.2. Yeasts

The diversity of yeast genera obtained from sourdoughs is significantly smaller than the diversity of LAB. This is due to a narrower range of adapted species and a greater interest from researchers in identifying LAB, which represent a more broadly distributed group of microorganisms. The yeasts that have been isolated from sourdoughs are presented in Table 2.

The most common yeasts found in both wheat sourdoughs and sourdoughs in general are *K. humilis*, *K. unispora*, *Pic. kudriavzevii*, *Pic. fermentans*, *S. cerevisiae*, and *Wic. anomalus*.

S. cerevisiae has been isolated from sourdoughs made with almost all types of flour, and references to its presence and relative abundance in sourdoughs are

significantly higher than for any other yeast species. These levels may be attributed to the large number of these microorganisms in the environment during sourdough preparation, especially within bakeries, as well as their high adaptability, which allows them to quickly dominate and colonize sourdoughs.

The prevalence of certain yeast species in sourdoughs can be explained similarly to the prevalence of LAB – through the adaptation of microorganisms and their metabolism to environmental conditions, including their ability to ferment compounds present in sourdoughs. For instance, *K. humilis* and *K. unispora* have limited metabolism (unable to utilize maltose), which allows them to form mutualistic relationships with LAB, unlike *S.*

cerevisiae, which must compete for nutrients. However, their resilience to pH, osmotic stress, and temperature is similar [93,94]. *Pic. kudriavzevii* and *Pic. fermentans* also exhibit high tolerance to increased acidity, temperature, and osmotic pressure, and can ferment glucose, fructose, etc. [95,96] Additionally, *Wic. anomalus* can catabolize specific cereal proteins, particularly wheat gliadins [97].

Yeasts are an important part of the sourdough microbiota because, together with LAB, they utilize different substrates, forming a complementary ecosystem [17]. This leads to softening and improvement of bread structure, produce precursors of aromatic compounds, such as free amino acids, which enhance flavor and aroma [7].

Table 2 – Yeasts isolated from sourdoughs

Flour types	Yeast genera	Yeast species	References
Wheat	<i>Brettanomyces</i>	<i>Brt. anomalus</i>	[21]
	<i>Buckleyzyma</i>	<i>Buc. aurantiaca</i>	[83]
	<i>Candida</i>	<i>C. boidinii</i> , <i>C. boleticola</i> , <i>C. diddensiae</i> , <i>C. saitoana</i> , <i>C. tropicalis</i>	[20, 43, 47, 84]
	<i>Debaryomyces</i>	<i>Deb. udonii</i>	[84]
	<i>Diutina</i>	<i>D. rugosa</i>	[34]
	<i>Geotrichum</i>	<i>Geo. candidum</i>	[43]
	<i>Hanseniaspora</i>	<i>Han. uvarum</i> , <i>Han. valbyensis</i>	[85, 86]
	<i>Hyphopichia</i>	<i>Hyp. pseudoburtonii</i>	[84]
	<i>Kazachstania</i>	<i>K. barnettii</i> , <i>K. bulderi</i> , <i>K. exigua</i> , <i>K. humilis</i> , <i>K. saulgeensis</i> , <i>K. servazzii</i> , <i>K. unispora</i>	[20, 43, 84]
	<i>Kluyveromyces</i>	<i>Kl. aestuarii</i> , <i>Kl. lactis</i> , <i>Kl. marxianus</i>	[43, 87]
	<i>Meyerozyma</i>	<i>M. carpophila</i> , <i>M. guilliermondii</i>	[83, 84]
	<i>Nakaseomyces</i>	<i>Nak. glabratus</i>	[43]
	<i>Naumovozyma</i>	<i>Nau. castellii</i>	[20]
	<i>Pichia</i>	<i>Pic. fermentans</i> , <i>Pic. kluyveri</i> , <i>Pic. kudriavzevii</i> , <i>Pic. membranifaciens</i>	[43, 47, 53]
	<i>Rhodotorula</i>	<i>R. mucilaginosa</i>	[38]
	<i>Saccharomyces</i>	<i>S. bayanus</i> , <i>S. cerevisiae</i> , <i>S. pastorianus</i> , <i>S. uvarum</i>	[20, 88]
	<i>Saccharomycopsis</i>	<i>Smc. fibuligera</i>	[23]
	<i>Saturnispora</i>	<i>Sat. silvae</i>	[89]
	<i>Torulaspora</i>	<i>T. delbrueckii</i>	[47]
	<i>Wickerhamomyces</i>	<i>Wic. anomalus</i>	[43]
	<i>Yarrowia</i>	<i>Y. lipolytica</i>	[90]
Rye	<i>Kazachstania</i>	<i>K. bulderi</i> , <i>K. humilis</i> , <i>K. unispora</i>	[21]
	<i>Kluyveromyces</i>	<i>Kl. marxianus</i>	[85]
	<i>Nakaseomyces</i>	<i>Nak. glabratus</i>	[57]
	<i>Pichia</i>	<i>Pic. fermentans</i> , <i>Pic. kudriavzevii</i>	[21, 57]
	<i>Saccharomyces</i>	<i>S. cerevisiae</i>	[21]
	<i>Saccharomycopsis</i>	<i>Smc. fibuligera</i>	[91]
	<i>Torulaspora</i>	<i>T. delbrueckii</i>	[85]
Wheat + rye	<i>Wickerhamomyces</i>	<i>Wic. anomalus</i>	[91]
	<i>Kazachstania</i>	<i>K. humilis</i>	[21]
Spelt	<i>Saccharomyces</i>	<i>S. cerevisiae</i>	[55]
	<i>Clavispora</i>	<i>Cl. lusitaniae</i>	[61]
	<i>Kazachstania</i>	<i>K. bulderi</i>	[21]
	<i>Pichia</i>	<i>Pic. fermentans</i>	[61]
	<i>Saccharomyces</i>	<i>S. cerevisiae</i>	[21]
Buckwheat	<i>Wickerhamomyces</i>	<i>Wic. anomalus</i>	[61]
	<i>Saccharomyces</i>	<i>S. cerevisiae</i>	[21]
Corn	<i>Kazachstania</i>	<i>K. barnettii</i>	[62]
	<i>Candida</i>	<i>C. albicans</i>	[63]

Flour types	Yeast genera	Yeast species	References
	<i>Saccharomyces</i>	<i>S. cerevisiae</i>	[23]
	<i>Schizosaccharomyces</i>	<i>Schm. pombe</i>	[63]
	<i>Wickerhamomyces</i>	<i>Wic. anomalus</i>	[23]
Rice	<i>Kluyveromyces</i>	<i>Kl. marxianus</i>	[64]
	<i>Pichia</i>	<i>Pic. kudriavzevii</i> , <i>Pic. membranifaciens</i>	
	<i>Saccharomyces</i>	<i>S. cerevisiae</i>	[23]
	<i>Wickerhamomyces</i>	<i>Wic. anomalus</i>	
Teff	<i>Nakaseomyces</i>	<i>Nak. glabratus</i>	[62]
	<i>Saccharomyces</i>	<i>S. cerevisiae</i>	
	<i>Kazachstania</i>	<i>K. humilis</i>	[92]
	<i>Pichia</i>	<i>Pic. kudriavzevii</i>	
Quinoa	<i>Kazachstania</i>	<i>K. servazzii</i>	[26]
	<i>Pichia</i>	<i>Pic. kudriavzevii</i>	
	<i>Saccharomyces</i>	<i>S. cerevisiae</i>	
	<i>Wickerhamomyces</i>	<i>Wic. anomalus</i>	
Barley	<i>Kluyveromyces</i>	<i>Kl. marxianus</i>	[85]
Sorghum	<i>Saccharomyces</i>	<i>S. cerevisiae</i>	[71]
Peas	<i>Saccharomyces</i>	<i>S. cerevisiae</i>	[31]
	<i>Wickerhamomyces</i>	<i>Wic. anomalus</i>	
Oats	<i>Kazachstania</i>	<i>K. unispora</i>	[91]
	<i>Nakaseomyces</i>	<i>Nak. glabratus</i>	
	<i>Saccharomyces</i>	<i>S. cerevisiae</i>	
	<i>Wickerhamomyces</i>	<i>Wic. anomalus</i>	

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Yeasts are an important part of the sourdough microbiota because, together with LAB, they utilize different substrates, forming a complementary ecosystem [17]. This leads to softening and improvement of bread structure, produce precursors of aromatic compounds, such as free amino acids, which enhance flavor and aroma [7].

1.3. Other representative microorganisms

In addition to LAB and yeasts, sourdoughs contain two other groups of bacteria, which are listed in Table 3.

Table 3 – Other bacteria isolated from sourdoughs

Flour types	Bacteria genera	Bacteria species	References
Wheat	<i>Acetobacter</i>	<i>Acet. cerevisiae</i> , <i>Acet. orleanensis</i> , <i>Acet. oryzafermentans</i> , <i>Acet. pasteurianus</i> , <i>Acet. senegalensis</i> , <i>Acet. sicerae</i> , <i>Acet. tropicalis</i>	[21, 34, 49, 98]
	<i>Acinetobacter</i>	<i>Acin. calcoaceticus</i> , <i>Acin. rhizosphaerae</i> , <i>Acin. ursingii</i>	[38, 40]
	<i>Aerococcus</i>	<i>Aerc. viridans</i>	[60]
	<i>Aeromonas</i>	<i>Aer. hydrophila</i>	[42]
	<i>Anaerobacillus</i>	<i>Anaer. alkalilacustris</i>	[40]
	<i>Asticcacaulis</i>	<i>Ast. excentricus</i>	[38]
	<i>Atlantibacter</i>	<i>Atl. hermannii</i>	

Flour types	Bacteria generas	Bacteria species	References
	<i>Bacillus</i>	<i>B. cereus</i> , <i>B. licheniformis</i> , <i>B. thuringiensis</i>	[37, 39, 99]
	<i>Caulobacter</i>	<i>Caul. tundrae</i>	[40]
	<i>Citrobacter</i>	<i>Cit. braakii</i>	[38]
		<i>Cit. freundii</i>	[42]
	<i>Clostridium</i>	<i>Clos. beijerinckii</i> , <i>Clos. butyricum</i> , <i>Clos. felsineum</i> , <i>Clos. intestinale</i> , <i>Clos. puniceum</i> , <i>Clos. saccharobutylicum</i>	[34, 38]
	<i>Cronobacter</i>	<i>Cron. dublinensis</i> , <i>Cron. sakazakii</i>	[38, 99]
	<i>Curtobacterium</i>	<i>Cur. flaccumfaciens</i>	[40]
	<i>Cutibacterium</i>	<i>Cut. acnes</i> , <i>Cut. modestum</i>	
	<i>Cyanobacterium</i>	<i>Cyan. aponinum</i>	
	<i>Enterobacter</i>	<i>Eb. asburiae</i> , <i>Eb. cloacae</i> , <i>Eb. hormaechei</i> , <i>Eb. kobei</i> , <i>Eb. nickellidurans</i>	[38, 40]
	<i>Erwinia</i>	<i>Er. billingiae</i> , <i>Er. mallotivora</i> , <i>Er. persicina</i> , <i>Er. rhapontici</i> , <i>Er. tasmaniensis</i>	[34, 38, 40]
	<i>Escherichia</i>	<i>E. coli</i>	[41]
	<i>Euzebya</i>	<i>Euz. tangerine</i>	[40]
	<i>Francisella</i>	<i>Fran. hispaniensis</i>	
	<i>Fusobacterium</i>	<i>Fus. nucleatum</i>	[38]
	<i>Gluconobacter</i>	<i>G. frateurii</i>	[34]
	<i>Hafnia</i>	<i>Haf. alvei</i>	[38]
	<i>Halorhodospira</i>	<i>Hal. halochloris</i>	[40]
	<i>Hymenobacter</i>	<i>Hym. xinjiangensis</i>	[42]
	<i>Klebsiella</i>	<i>Kleb. oxytoca</i> , <i>Kleb. variicola</i>	[40]
	<i>Kluyvera</i>	<i>Kluy. intermedia</i>	[38]
	<i>Kosakonia</i>	<i>Kos. cowanii</i>	
	<i>Lacrimispora</i>	<i>Lacr. xylanolytica</i>	
	<i>Lelliottia</i>	<i>Lell. amnigena</i>	
	<i>Leucothrix</i>	<i>Lth. mucor</i>	[40]
	<i>Methylobacterium</i>	<i>Meth. radiotolerans</i>	[42]
	<i>Microbacterium</i>	<i>Micrb. esteraromaticum</i>	
	<i>Micromonospora</i>	<i>Micrm. brunnescens</i> , <i>Micrm. rifamycinica</i>	[40]
	<i>Mixta</i>	<i>Mix. calida</i>	[38]
	<i>Nostoc</i>	<i>Nos. microscopicum</i>	[40]
	<i>Oerskovia</i>	<i>Oer. ginkgo</i>	[39]
	<i>Paenibacillus</i>	<i>Paen. polymyxa</i>	
	<i>Pantoea</i>	<i>Pan. agglomerans</i> , <i>Pan. ananatis</i> , <i>Pan. dispersa</i> , <i>Pan. stewartii</i> , <i>Pan. vagans</i>	[38]
	<i>Proteus</i>	<i>Pr. vulgaris</i>	[40]
	<i>Providencia</i>	<i>Prov. sneebia</i>	
	<i>Pseudomonas</i>	<i>Ps. aeruginosa</i> , <i>Ps. azotoformans</i> , <i>Ps. cedrina</i> , <i>Ps. fluorescens</i> , <i>Ps. fuscovaginae</i> , <i>Ps. psychrotolerans</i> , <i>Ps. putida</i> , <i>Ps. rhodesiae</i> , <i>Ps. tolaasii</i>	[38, 40]
	<i>Rickettsia</i>	<i>Ric. asiatica</i>	[40]
	<i>Rothia</i>	<i>Roth. kristinae</i>	[52]
	<i>Serratia</i>	<i>Ser. entomophila</i>	[40]
	<i>Shigella</i>	<i>Shig. sonnei</i>	[37]
	<i>Sodalis</i>	<i>Sod. glossinidius</i>	[40]
	<i>Sphingobium</i>	<i>Sphb. indicum</i>	
	<i>Sphingomonas</i>	<i>Sphm. roseiflava</i>	[38]
	<i>Staphylococcus</i>	<i>Staph. epidermidis</i> , <i>Staph. gallinarum</i> , <i>Staph. haemolyticus</i> , <i>Staph. hominis</i> , <i>Staph. kloosii</i> , <i>Staph. pasteurii</i> , <i>Staph. warneri</i>	[37, 40, 89]
	<i>Streptomyces</i>	<i>Str. rajshahiensis</i>	[40]
	<i>Thermovenabulum</i>	<i>Ther. ferriorganovorum</i>	
	<i>Thiohalorhabdus</i>	<i>Th. denitrificans</i>	
	<i>Variovorax</i>	<i>V. boronicumulans</i>	
	<i>Xanthomonas</i>	<i>Xan. albilineans</i> , <i>Xan. oryzae</i>	
Rye	<i>Acetobacter</i>	<i>Acet. cerevisiae</i> , <i>Acet. fabarum</i> , <i>Acet. oryzafermentans</i> , <i>Acet. pasteurianus</i>	[21]
	<i>Carnobacterium</i>	<i>Car. maltaromaticum</i>	[37]
	<i>Enterobacter</i>	<i>Eb. cloacae</i>	[57]

Flour types	Bacteria generas	Bacteria species	References
	<i>Komagataeibacter</i>	<i>Kom. sucrofermentans</i>	[21]
		<i>K. xylinus</i>	
	<i>Pantoea</i>	<i>Pan. agglomerans</i>	[57]
	<i>Staphylococcus</i>	<i>Staph. epidermidis</i>	[37]
Spelt	<i>Acetobacter</i>	<i>Acet. oryzipermentans</i> , <i>Acet. pasteurianus</i> , <i>Acet. senegalensis</i> , <i>Acet. sicerae</i>	[21]
	<i>Carnobacterium</i>	<i>Car. maltaromaticum</i>	[37]
	<i>Enterobacter</i>	<i>Eb. cloacae</i>	[60]
	<i>Escherichia</i>	<i>E. coli</i>	[37]
	<i>Staphylococcus</i>	<i>Staph. capitis</i> , <i>Staph. epidermidis</i>	
Corn	<i>Exiguobacterium</i>	<i>Ex. acetylicum</i> , <i>Ex. aurantiacum</i>	[22]
	<i>Oxalophagus</i>	<i>Ox. oxalicus</i>	
Quinoa	<i>Klebsiella</i>	<i>Kleb. oxytoca</i>	[68]
	<i>Pantoea</i>	<i>Pan. ananatis</i>	
Barley	<i>Pantoea</i>	<i>Pan. agglomerans</i>	[69]
Chia	<i>Asaccharospora</i>	<i>As. irregularis</i>	[28]
	<i>Bacillus</i>	<i>B. altitudinis</i> , <i>B. cereus</i> , <i>B. subtilis</i> , <i>B. vallismortis</i>	
	<i>Clostridium</i>	<i>Clos. acetobutylicum</i> , <i>Clos. baratii</i> , <i>Clos. beijerinckii</i> , <i>Clos. butyricum</i> , <i>Clos. diolis</i> , <i>Clos. felsineum</i> , <i>Clos. perfringens</i> , <i>Clos. puniceum</i> , <i>Clos. sardiniense</i> , <i>Clos. tyrobutyricum</i>	
	<i>Heyndrickxia</i>	<i>Heyn. acidiproducens</i>	
		<i>Heyn. coagulans</i>	
	<i>Priestia</i>	<i>Prs. flexa</i>	
	<i>Staphylococcus</i>	<i>Staph. capitis</i>	
		<i>Staph. epidermidis</i> , <i>Staph. hominis</i>	
Faba bean	<i>Cutibacterium</i>	<i>Cut. acnes</i>	[31]
	<i>Kosakonia</i>	<i>Kos. cowanii</i>	
	<i>Pantoea</i>	<i>Pan. agglomerans</i> , <i>Pan. vagans</i>	
Peas	<i>Cutibacterium</i>	<i>Cut. acnes</i>	
	<i>Kosakonia</i>	<i>Kos. cowanii</i>	
	<i>Pantoea</i>	<i>Pan. agglomerans</i> , <i>Pan. vagans</i>	

The first group consists of acetic acid bacteria (family *Acetobacteraceae*), represented in wheat sourdoughs by the genera *Acetobacter* and *Gluconobacter*, in rye sourdoughs by the genera *Acetobacter* and *Komagataeibacter*, and in spelt sourdoughs by the genus *Acetobacter*. These microorganisms are an integral part of the sourdough microbiota and contribute to producing higher quality bread (with a pronounced taste and aroma, and longer shelf life) by acidifying the environment through the production of acetic acid from ethanol, which is produced in large quantities by yeasts [100]. The second group includes bacteria that enter the sourdough from plants or humans but are present only at the beginning of fermentation and then disappear due to high acidity and overall unadaptability to fermentation conditions. For example, this group includes *E. coli* [37], *Clos. butyricum*, *Clos. puniceum*, *B. cereus* [38], *Pan. agglomerans*, *Eb. cloacae* [57], and others.

Among the representatives of the second group, pathogenic microorganisms predominate: *Pan. vagans*, *Er. persicina*, *Pan. stewartii*, *Cur. flaccumfaciens* are plant pathogens [101-104]; *Ps. aeruginosa*, *Eb. cloacae*, *Clos. perfringens* – human and animal pathogens [105-107]. Some pathogens may be opportunistic, or their impact on the organism may vary depending on the strain,

such as *Staph. epidermidis* and *E. coli* [108,109], and certain bacteria may be harmful to both plants and humans, such as *Kos. cowanii* [110,111].

In addition to various groups of bacteria and yeasts, sourdoughs can also contain micromycetes, which have been described in publications by several authors and are therefore also presented here in Table 4.

The analysis of Table 4 revealed that for all studied types of sourdoughs, only one genus and one species of micromycetes are common – *Clad. delicatulum*, which can be explained by its prevalence as an endophytic micromycete in many plant species [113]. Micromycetes of the genera *Alternaria*, *Aspergillus* and *Fusarium* have the most representatives in wheat sourdoughs, which also underscores their high level of dissemination.

Micromycetes are similar to the second group of bacteria and are mostly found in sourdoughs during the initial stages of their development, before the acidity of the environment increases and the fermentation conditions created by LAB and acetic acid bacteria and yeasts finally outcompete them for living space. Some of them are plant pathogens, such as *Fus. equiseti* and *Rhiz. Arrhizus* [114,115], while others are pathogens of animals and humans, like *Asp. flavus* and *Pap. Laurentii* [116,117].

2. Probiotic properties of sourdough microbiota representatives

The human intestine constantly harbors approximately 10^{14} cells (100 trillion) of various bacteria, with their content in the most colonized regions (i.e., the colon, due to the significantly slower transit compared to the small intestine) reaching up to 10^{11} CFU/g. The composition of the gut microbiome is closely linked to the host's health. Insufficient genera and species diversity of LAB, which are natural probiotics, can lead to the development of opportunistic and pathogenic bacteria, resulting in dysbiosis. Consequently, there will be an increased risk of gastrointestinal diseases (irritable bowel

syndrome, colorectal cancer, chronic liver diseases, or pancreatic disorders) [118, 119], cardiovascular diseases [120], and due to the close interconnection of different organs and systems of the body, even a negative impact on the central nervous system [121]. To address numerous potential problems associated with intestinal dysbiosis, as well as to prevent and preclude their occurrence, probiotics are used.

According to the WHO definition, probiotics are live microorganisms which, when administered in adequate amounts, confer a health benefit on the host. They can form a healthy gut microbiota, reducing disease incidence and improving overall human well-being [122].

Table 4 – Micromycetes isolated from sourdoughs

Flour types	Fungi genera	Fungi species	References
Wheat	<i>Alternaria</i>	<i>Alt. alternata</i> , <i>Alt. breviramosa</i> , <i>Alt. dactylidicola</i> , <i>Alt. tenuissima</i>	[34, 84, 112]
	<i>Anthracoecystis</i>	<i>Anth. panici-leucophaei</i>	[84]
	<i>Apiospora</i>	<i>Aps. sacchari</i>	
	<i>Aspergillus</i>	<i>Asp. caesiellus</i> , <i>Asp. cibarius</i> , <i>Asp. flavus</i> , <i>Asp. penicillioides</i> , <i>Asp. subversicolor</i>	[23, 84]
	<i>Aureobasidium</i>	<i>Aur. pullulans</i>	[84]
	<i>Bipolaris</i>	<i>Bip. maydis</i>	
	<i>Botrytis</i>	<i>Bot. caroliniana</i>	
	<i>Bullera</i>	<i>Bull. unica</i>	
	<i>Capnobotryella</i>	<i>Cap. sp. MA 4775</i>	
	<i>Cladosporium</i>	<i>Clad. delicatulum</i> , <i>Clad. herbarum</i>	[34, 84]
	<i>Claviceps</i>	<i>Clav. humidiphila</i>	[84]
	<i>Cryptococcus</i>	<i>Cryp. sp. SM13L02</i>	
	<i>Cutaneotrichosporon</i>	<i>Cts. cutaneum</i>	
	<i>Diaporthe</i>	<i>Diap. australafricana</i>	
		<i>D. citrichinensis</i>	
	<i>Didymella</i>	<i>Did. exigua</i>	
	<i>Dioszegia</i>	<i>Diosz. fristingensis</i> , <i>Diosz. hungarica</i>	[34]
	<i>Epicoccum</i>	<i>Ep. thailandicum</i>	
	<i>Filobasidium</i>	<i>Fil. wieringae</i>	[84]
	<i>Fusarium</i>	<i>Fus. culmorum</i> , <i>Fus. equiseti</i> , <i>Fus. graminearum</i> , <i>Fus. petersiae</i> , <i>Fus. poae</i> , <i>Fus. tricinctum</i>	[34, 84]
	<i>Gjaerumia</i>	<i>Gj. minor</i>	[84]
	<i>Itersonilia</i>	<i>It. pannonica</i> , <i>It. perplexans</i>	
	<i>Microdochium</i>	<i>Md. bolleyi</i> , <i>Md. seminicola</i>	[34, 84]
	<i>Monographella</i>	<i>Mg. nivalis</i>	[84]
	<i>Neosetophoma</i>	<i>Neos. rosarum</i>	[34]
	<i>Nigrospora</i>	<i>Nig. oryzae</i>	
	<i>Papiliotrema</i>	<i>Pap. laurentii</i>	[84]
	<i>Penicillium</i>	<i>Pen. polonicum</i>	
	<i>Phaeosphaeria</i>	<i>Ph. lunariae</i>	[34]
	<i>Phomopsis</i>	<i>Phom. sp. CLH1_10</i>	[84]
	<i>Plectosphaerella</i>	<i>Plec. sp. CCF3811</i>	
	<i>Pseudozyma</i>	<i>Pseud. flocculosa</i>	
	<i>Pyrenophora</i>	<i>Pyr. tritici-repentis</i>	
	<i>Rhizopus</i>	<i>Rhiz. arrhizus</i>	[83]
	<i>Rhodotorula</i>	<i>Rhod. mucilaginosus</i>	[84]
	<i>Rhynchogastrema</i>	<i>Rhyn. aquatica</i>	
	<i>Sarocladium</i>	<i>Sar. strictum</i>	
	<i>Septoriella</i>	<i>Sept. hubertusii</i>	
	<i>Sporobolomyces</i>	<i>Sbm. ruberrimus</i>	
	<i>Stemphylium</i>	<i>Stem. vesicarium</i>	
	<i>Tilletia</i>	<i>Till. controversa</i>	
	<i>Vishniacozyma</i>	<i>V. globispora</i> , <i>V. heimaeyensis</i> , <i>V. victoriae</i>	

Flour types	Fungi genera	Fungi species	References
	<i>Walleimia</i>	<i>Wall. sebi</i>	[34]
Rice	<i>Cladosporium</i>	<i>Clad. delicatulum</i>	[23]
	<i>Fusarium</i>	<i>Fus. equiseti</i>	
Barley	<i>Alternaria</i>	<i>Alt. metachromatica</i>	[69]
	<i>Cladosporium</i>	<i>Clad. delicatulum, Clad. herbarum</i>	
	<i>Sarocladium</i>	<i>Sar. bactrocephalum</i>	
	<i>Thyridium</i>	<i>Thyr. curvatum</i>	
	<i>Vishniacozyma</i>	<i>V. victoriae</i>	

As probiotics, LAB (*Lpb. plantarum*, *Lcb. rhamnosus*, *Lm. fermentum*, *Bif. longum*, etc.), yeasts (*S. cerevisiae*, *S. boulardii*, *Kl. marxianus*, etc.), as well as representatives of some other bacterial genera: *Bacillus* (*B. subtilis*, *B. licheniformis*, etc.), *Propionibacterium* (*Propionibacterium freudenreichii*), etc., are used [123]. Since LAB and yeasts form the basis of the microbiota of sourdoughs, microorganisms isolated from them can potentially be used as the basis for probiotic medicines or dietary supplements, further supported by the high resilience of strains that have become part of the sourdough ecosystem.

To determine whether microorganisms qualify as probiotics, it is necessary to establish the presence of probiotic properties: resistance to bile salts and acidic environments, hydrophobicity, ability to aggregate and adhere to biotic and abiotic surfaces (these properties ensure the cells' entry and survival in the intestine) [124], as well as antimicrobial, antioxidant, anti-inflammatory, and other desirable positive characteristics inherent to probiotic microorganisms [125].

2.1. Stress resistance and aggregation-adhesive properties of sourdough microorganisms

No matter how many beneficial properties certain microorganisms possess, they will be of no use if they cannot reach, survive, and establish themselves in the human intestine. Therefore, stress resistance and aggregation-adhesion properties are crucial for any probiotic strains [87]. To assess sourdoughs and the individual microorganisms they contain in terms of probiotics, it is necessary to consider existing references to the expression of relevant properties by bacteria and yeasts.

One of the first studies found was published in 2008 by Lavermicocca et al. [126], who investigated three strains of lactobacilli isolated from sourdough: *Lm. fermentum* ITM18B, *Lpb. plantarum* ITM21B, and *Com. alimentarius* ITM5Q. ITM21B and ITM5Q demonstrated high resistance to pH 2.5 and bile, with ITM5Q showing high adhesion to the surface of cultured human cells.

Since then, the frequency and complexity of studies in this direction have only increased, peaking in recent years. In 2019, a study [127] was published describing a step-by-step assessment of the resistance and characteristics of microorganisms, following the order of their manifestation upon entering the human

body. The authors, Doğan M. and Tekiner I.H., investigated 93 LAB isolates from 29 sourdoughs. The results of determining resistance to low pH levels, followed by bile salts, showed the survival of 41 and 31 isolates of LAB, respectively. An assessment of the hydrophobicity of potential probiotic microorganisms was carried out by calculating the adhesion of cells to xylene hydrocarbon. This study showed that only 4 strains out of 93 (4.3 %) exhibited a sufficiently high level of key probiotic properties: *Lv. brevis*, *Lpb. plantarum*, *Lpb. pentosus*, and *Ec. faecium*.

There are numerous studies that study not only LAB but also yeasts. Fekri A. et al studied the probiotic properties of microorganisms isolated from sourdough that demonstrated the ability to break down phytic acid, which reduces the nutritional value of food and inhibits the absorption of minerals by humans [87]. According to the results of the study, all strains (*Ec. faecium* AR-L02, *P. pentosaceus* AR-L04, *Leu. citreum* AR-L04, *Kl. marxianus* AR-Y01, *Kluyveromyces lactis* AR-Y02, *Kl. aestuarii* AR-Y04) showed resistance to artificial gastric juice and low pH, as well as to bile acids, with the yeasts performing slightly better compared to the LAB. The assessment of hydrophobicity and self-aggregation ability revealed similar results: all isolates showed moderate to very good results, with bacterial strains being slightly inferior to the yeast strains.

In the study [128], the authors established the ability of the strain *Ec. faecium* YF5, isolated from sourdough, to survive under low pH conditions (2.0-3.0), exposure to bile salts (0.3%), gastric and intestinal juices, and also observed the adhesion of the microorganism to a human colon cell line.

Bartkiene E. et al. [56] established the resistance of *P. pentosaceus*, *Lcb. casei*, *Lv. brevis*, *Liq. uvarum*, *Ln. farraginis*, *Lpb. plantarum*, and *Lcb. paracasei* isolates to pH levels of 2.5 for 2 hours.

In the study [27], the authors determined the resistance of *P. acidilactici*, *P. pentosaceus*, *Lt. curvatus*, *Leu. mesenteroides*, *Lm. equigenerosi*, *Lv. brevis*, *Lpb. plantarum*, *Com. paralimentarius*, and *Com. musae* isolates to low pH and bile.

Reviewing the presented works, it can be noted that mentions of certain species appear more frequently than others. For example, in the study [129], out of 88 isolates tested for potential probiotic properties, specifically resistance to artificial gastric juice, resistance to bile salts, and aggregation ability, none of

the strains survived for 24 hours at low pH, except for five strains belonging to one species: *Lpb. plantarum* ZJUFT34, *Lpb. plantarum* ZJUFT17, *Lpb. plantarum* ZJUFT32, *Lpb. plantarum* ZJUFHN9, and *Lpb. plantarum* ZJUFAH5. These strains withstood pH 2.5-3.0 and bile salts well, and also demonstrated high aggregation ability.

It is important to note that the manifestation of probiotic properties depends on the strains of microorganisms and is not a mandatory characteristic of the species. However, trends and the predominance of some species over others in terms of the frequency of these properties can be established. Among the LAB isolated from sourdoughs, *Lpb. plantarum*, *Lv. brevis*, *P. pentosaceus*, and *Ec. faecium* most often exhibit probiotic properties. These results partially align with the available information about these microorganisms: *Lpb. plantarum* strains are known for their stress resistance, adhesion capability, and various other properties such as antimicrobial or antioxidant effects [130], while *P. pentosaceus* strains also possess many probiotic properties [131] and are widely used in the food industry [81].

The rest of the analyzed studies on stress resistance mostly focus on yeast, with one exception. In the study [132], the probiotic properties of 30 isolates from the genus *Bacillus*, isolated from wheat sourdough, were tested. The authors found that 17 strains (species *B. subtilis* and *Bacillus amyloliquefaciens*) were able to grow in the presence of 5% bile in the medium and at pH 3.0. It was also determined that all strains were capable of forming biofilms. This study shows that even microorganisms that can be isolated only during the initial stages of sourdough development also present potential scientific and practical interest, although it is necessary to conduct safety studies on the investigated strains for human use.

Korcari D. et al., during their study [61], found that isolates of *Wic. anomalus*, obtained from spelt sourdough, exhibit high osmotolerance (30% carbon content in the medium) and the ability to grow at low pH values (2.5), while *S. cerevisiae* demonstrated only acid resistance, and *Pic. fermentans* were vulnerable to both stress factors. The authors also found that the osmotolerance levels of various *P. pentosaceus* strains varied significantly, but none could withstand prolonged exposure to low pH.

Muche N. et al. [92] studied yeast strains isolated from injera sourdough (a traditional Ethiopian dish made from teff flour and water). The authors determined the optimal growth temperature of the isolates (37 °C), their ability to actively grow at pH 2-3, resistance to bile salts at a concentration of 0.5 %, and the osmotolerance of most strains with glucose added to the medium up to a content of 40-50 %. This allowed them to identify that 5 out of 10 isolates (2 – *S. cerevisiae*, 2 – *K. humilis*, 1 – *Pic. kudriavzevii*) can

withstand the challenging conditions of the human gastrointestinal tract.

In the study [133], the authors tested the yeast isolates for resistance to pH 2.5, bile salts, hydrophobicity, and biofilm formation. Each of the 18 strains exhibited a good level of basic probiotic properties. However, 5 of them (belonging to the species *S. cerevisiae*, *K. humilis*, and *Wic. anomalus*) were identified as the most likely candidates for further study and potential application in the food and pharmaceutical industries due to their superior performance in all tests.

Vrancken G. et al. [134] found that 22 out of 23 *Wic. anomalus* isolates and 8 out of 17 *S. cerevisiae* isolates were able to grow at pH 2.5, while the only *T. delbrueckii* isolate they studied did not exhibit this property.

As can be seen from numerous articles, the yeasts most inclined to exhibit basic probiotic properties are predominantly *S. cerevisiae*, *K. humilis*, and *Wic. anomalus*. The presence of *S. cerevisiae* on this list is quite predictable, especially considering the probable presence of well-adapted industrial commercial strains in the sourdoughs, as mentioned earlier.

2.2. Antibacterial properties of sourdough microorganisms

LAB can exert an antagonistic effect on pathogenic microorganisms through the production of antimicrobial compounds: lactic and acetic acids, hydrogen peroxide, and specific peptides called bacteriocins [28]. The production of the latter has always been considered a desirable characteristic for probiotic microorganisms [135], as it helps regulate the microbial composition of the human gut and prevent dysbiosis [136]. Bacteriocins can not only have a direct negative impact on pathogens but also stimulate the host's nonspecific immunity [137]. Besides the health benefits for humans, bacteriocins play a significant role in the food industry by preserving products as natural preservatives [138].

Obviously, since the production of organic acids is inherent to all LAB, the basis of the antimicrobial effect of probiotic microorganisms is hydrogen peroxide and, most importantly, bacteriocins.

Bartkiene et al. [56] studied the antimicrobial activity of LAB isolates against pathogenic strains such as *Klebsiella pneumoniae*, *Salmonella enterica*, *Ps. aeruginosa*, *Acinetobacter baumannii*, *Proteus mirabilis*, methicillin-resistant *Staphylococcus aureus*, *Ec. faecalis*, *Ec. faecium*, *B. cereus*, *Streptococcus mutans*, *Eb. cloacae*, *Cit. freundii*, *S. epidermidis*, *Staph. haemolyticus*, and *Pasteurella multocida*. The strains of *Lpb. plantarum*, *Lcb. casei*, *Lcb. paracasei*, *Lt. curvatus*, and *Loig. coryniformis* demonstrated the ability to inhibit the growth of all test microorganisms, whereas *Ln. farraginis*, *P. pentosaceus*, *P. acidilactici*, *Liq. uvarum*, *Leu. mesenteroides*, and *Ec. pseudoavium* did not exhibit antimicrobial activity against 1-3

different pathogens. *Lv. brevis* were able to inhibit the growth of the fewest microorganisms (9 out of 15).

In the study [27], high antimicrobial activity was demonstrated by the strains of *P. acidilactici*, *Lt. curvatus*, *Leu. mesenteroides*, *Lm. equigenerosi*, *Lpb. plantarum*, and *Com. musae* against pathogenic *B. subtilis*, *B. cereus*, and *E. coli*. The authors [139] found that some strains of *Lpb. plantarum* and *Lt. curvatus* could inhibit the growth of *Lis. monocytogenes* and *Listeria innocua*.

Petkova et al. [140] identified high antagonistic activity of *P. pentosaceus*, *Lpb. plantarum*, *Lv. brevis*, *Ec. faecium*, and *Ec. durans* against pathogenic strains of *B. subtilis*, *Staph. aureus*, and *Salm. enterica*.

In the study [44], it was established that *Lpb. plantarum* has the ability to inhibit the growth of *B. subtilis*, *Bacillus licheniformis*, and *E. coli*, while *Flb. sanfranciscensis* inhibits only *B. subtilis*. Another study [141] demonstrated the antagonistic activity of *Lpb. plantarum* against *Pseudomonas syringae* and *Botrytis cinerea*.

Lavermicocca et al. [126] identified a high ability of the *Lpb. plantarum* ITM21B strain to inhibit the growth of the pathogenic bacterium *Yersinia enterocolitica*. Other strains studied (*Lm. fermentum* ITM18B and *Com. alimentarius* ITM5Q) showed low results.

Ruiz et al. in their study [25] noted the antimicrobial effect of *Lpb. plantarum* and *Ec. mundtii* against *Listeria monocytogenes*, as well as the antimicrobial effect of *Lpb. plantarum* and *P. pentosaceus* against *B. subtilis*.

Rodríguez et al. [68] established the activity of strains *Ec. mundtii* CRL1896 and *Ec. casseliflavus* CRL1899 against *Lis. monocytogenes*, and *Ec. mundtii* CRL1896, *Leu. citreum* CRL1904, *Leu. mesenteroides* CRL1907, *Lpb. plantarum* CRL1905 and CRL1906 against *B. subtilis*.

In the study [128], it was found that the strain *Ec. faecium* YF5 exhibits antagonistic effects on *Cron. sakazakii*, *E. coli*, *Salm. enterica* subsp. *enterica* serovar Typhimurium, *Shigella flexneri*, *Shig. sonnei*, and *Lis. monocytogenes*.

Sáez et al. [142] established the antagonistic effect of *Ec. faecium*, *Ec. durans*, and *W. cibaria* against *E. coli*, *B. cereus*, and *Lis. innocua*, noting the strain-specific nature of this characteristic in microorganisms. Maidana et al. [28] established the antagonistic activity of *W. cibaria* against *B. subtilis*.

A review of scientific literature on the antagonistic action of probiotic strains shows that not only LAB can exhibit antimicrobial properties. In the study [87], the activity of probiotic strains of microorganisms isolated from sourdoughs against pathogenic bacteria and fungi was examined. Antimicrobial properties were identified, but their effectiveness depended on the probiotic strain and the pathogenic microorganism. For instance, it was reported for the first time that *Leu. citreum*, *P.*

pentosaceus, and *Ec. faecium* could affect *Ec. faecalis*, *Kleb. pneumoniae*, and *Shigella dysenteriae*. *Kl. lactis* showed good results against *Kleb. pneumoniae*.

Muche et al. [92], who confirmed the potential use of yeast isolates as probiotics, also evaluated other properties, including antimicrobial activity. All five probiotic strains (*S. cerevisiae*, *K. humilis*, *Pic. kudriavzevii*) demonstrated the ability to inhibit the growth of pathogenic bacteria (*Salm. enterica* subsp. *enterica* serovar Typhi, *Staph. aureus*, *E. coli*).

In the study [133], yeasts of the species *S. cerevisiae*, *K. humilis*, and *Wic. anomalus* did not exhibit antimicrobial properties against *Lis. monocytogenes*, *Y. enterocolitica*, *E. coli*, and *Staph. aureus*.

Besides LAB and yeasts, other genera of bacteria can also exhibit inhibitory capabilities. For example, the study [132] found antagonistic properties in strains of *B. subtilis* and *B. amyloliquefaciens* against *Enterococcus cecorum*, as well as in strains of *B. amyloliquefaciens* against shiga-toxin-producing *E. coli*.

Antibacterial properties are most frequently observed and prominently displayed in *Lpb. plantarum* and *Lt. curvatus*, with fairly good results seen in *Leu. mesenteroides*, *P. pentosaceus*, *P. acidilactici*, and *Ec. faecium*. The impact of yeasts is insufficiently studied, and the existing research is contradictory.

Overall, it may be said that microorganisms from sourdoughs possess a wide range of antibacterial activity against various pathogenic and conditionally pathogenic bacteria. The presence of this characteristic indicates the potential of considering them as probiotics.

2.3. Antifungal properties of sourdough microorganisms

It is known that molds develop in bread, dairy products, sweets, meat, fish, fruits, vegetables, and more [143], leading to significant economic losses and food waste while posing health risks due to the production of mycotoxins [144]. Numerous probiotic microorganisms, especially LAB, can exhibit antifungal properties by producing a wide range of compounds, from the aforementioned lactic acid to fatty acids [145]. The exhibition of antifungal properties, like antibacterial ones, is a desirable characteristic of probiotics.

Bartkiene et al. [56] investigated the antifungal activity of LAB isolates. All species (*Lpb. plantarum*, *Lcb. casei*, *Lcb. paracasei*, *Lt. curvatus*, *Loig. coryniformis*, *Ln. farraginis*, *P. pentosaceus*, *P. acidilactici*, *Liq. uvarum*, *Leu. mesenteroides*, *Ec. pseudoavium*, and *Lv. brevis*) successfully inhibited the growth of *Aspergillus nidulans*, *Penicillium funiculosum*, and *Fus. poae*. A few species were unable to inhibit *Penicillium oxalicum* and *Pen. funiculosum*, while the greatest resistance to the effects of LAB isolates was shown by *Alt. alternata*, *Aspergillus fischeri*, and *Fus. graminearum*.

Rodríguez et al. [68] demonstrated the antifungal activity of LAB strains, showing the inhibition of *Asp. oryzae* and *Penicillium roqueforti* growth by strains *Ec. casseliflavus* CRL1899, *Leu. mesenteroides* CRL1907, *Leu. citreum* CRL1904, *Lv. brevis* CRL1959 and CRL1962. The strains *Ec. mundtii* CRL1896, *Leu. mesenteroides* CRL1901, *Lc. lactis* CRL1895, *Lpb. plantarum* CRL1905, CRL1906, and *Lv. brevis* CRL1961 sufficiently inhibited the growth of only *Asp. oryzae*.

In the study [27], the antifungal activity of isolates *P. acidilactici*, *Lpb. plantarum*, *Lv. brevis*, and *Com. paralimentarius* against *Aspergillus flavus*, *Aspergillus niger*, and *Penicillium carneum* was demonstrated.

Maidana et al. [28] showed the antagonistic activity of *Ec. casseliflavus*, *Ec. faecium*, *Lc. lactis*, and *W. cibaria* against *Asp. niger* and *Pen. roqueforti*. Additionally, the inhibitory effect on *Asp. niger* was also exhibited by the *Lcb. rhamnosus* strain.

The antifungal activity of LAB isolated from sourdoughs was demonstrated in the study by Hassan et al. [146]. The highest antagonistic activity was observed against *Fusarium proliferatum*, *Fus. graminearum*, and *Penicillium crustosum*, exhibited by the *Lcb. paracasei* subsp. *tolerans* strain. This strain also inhibited the growth of *Aspergillus candidus* and *Pen. roqueforti*.

Similarly high antagonistic activity of *P. pentosaceus*, *Lpb. plantarum*, *Lv. brevis*, *Ec. faecium*, and *Ec. durans* against *Penicillium chrysogenum*, *Fus. graminearum*, *Rhizopus stolonifer*, and *Asp. nidulans* was identified by Petkova et al. [140].

The antagonistic activity of *Lpb. plantarum* and *Lt. curvatus* strains against *Alt. alternata*, and the activity of *Lpb. plantarum* against *Cladosporium cladosporioides*, was demonstrated in the study [139].

Gunduz et al. [44] showed that *Lpb. plantarum* exhibits antagonistic properties against *Penicillium expansum*.

Unlike the previously discussed properties, no mentions were found regarding the antifungal properties of other bacteria besides LAB, with only one mention of the yeast's ability to inhibit fungal pathogens. In the study [87], *Kl. marxianus* and *Kl. aestuarii* were active against *C. albicans*.

Based on the gathered information, it can be concluded that *Lpb. plantarum* and *Lv. brevis* exhibit the most pronounced antifungal effects, followed by *Ec. faecium*. However, further research is desirable as this topic is not sufficiently covered in the current scientific literature. The antifungal effects of yeasts also require additional study and consideration.

2.4. Susceptibility to antibiotics of sourdough microorganisms

With the widespread use of antibiotics, the urgency and consequences of the problem of antibiotic-resistant microorganisms are increasing. Since probiotics can contribute to the spread of antibiotic

resistance through horizontal gene transfer, it is crucial for them to lack antibiotic resistance. The presence of such resistance can lead to the successful development of pathogenic microorganisms in the host body [147] or the spread of multidrug-resistant pathogens in the environment, given that 40 % of unused probiotics are discarded in household waste and, consequently, end up in the environment [148]. There is no microorganism that fully meets all requirements, or an ideal probiotic – most probiotic strains of LAB are resistant to numerous antibiotics such as streptomycin, vancomycin, norfloxacin, metronidazole, etc. However, probiotics should have resistance to a minimal number of compounds to ensure their successful use and prevent the spread of antibiotic resistance [147]. Therefore, understanding the antibiotic sensitivity of microorganisms isolated from sourdough is essential.

Rodríguez et al. [68] studied the sensitivity of various LAB strains isolated from sourdough to the antibiotics ampicillin, vancomycin, chloramphenicol, streptomycin, gentamicin, kanamycin, clindamycin, tetracycline, and erythromycin. They found that different strains of *Enterococcus hermanniensis* showed resistance to clindamycin and tetracycline, *Ec. casseliflavus* to streptomycin, gentamicin, and clindamycin, *Ec. mundtii* to erythromycin, streptomycin, gentamicin, and clindamycin, *Leu. mesenteroides* to chloramphenicol and kanamycin, *Leu. citreum* and *Lv. brevis* to ampicillin.

In the study [128], the strain *Ec. faecium* YF5 was shown to be sensitive to vancomycin, amoxicillin, and chloramphenicol, and resistant to streptomycin, gentamicin, kanamycin, rifampin, ciprofloxacin, clarithromycin, erythromycin, mupirocin, spectinomycin, and polymyxin B.

A team of authors led by Maidana S. D. [28] also established a wide range of resistances in LAB isolated from sourdough: different strains of *Ec. casseliflavus*, *Ec. faecium*, and *Ec. mundtii* were resistant to ampicillin, chloramphenicol, clindamycin, streptomycin, gentamicin, and erythromycin; *Lc. lactis* to clindamycin, erythromycin, gentamicin, and vancomycin; *Lcb. rhamnosus* and *W. cibaria* to erythromycin. However, all studied strains were sensitive to tetracycline and kanamycin.

In the study [87], the resistance of a wide range of probiotic strains of LAB and yeasts (*Ec. faecium* AR-L02, *P. pentosaceus* AR-L04, *Leu. citreum* AR-L04, *Kl. marxianus* AR-Y01, *Kl. lactis* AR-Y02, *Kl. aestuarii* AR-Y04) to 19 different antibiotics was investigated. It was found that *Ec. faecium* is resistant to a large number of antibiotics and easily acquires new resistance (it was vulnerable only to penicillin, ampicillin, and chloramphenicol), while other isolates were resistant to 2-4 antibiotics (*Leu. citreum* to gentamicin and ciprofloxacin, *P. pentosaceus* to ampicillin and gentamicin, *Kl. lactis* and *Kl. aestuarii* to amphotericin and flucytosine, *Kl. marxianus* to

flucytosine, itraconazole, ketoconazole, and voriconazole).

Muhce et al. evaluated the sensitivity of 5 yeast isolates (*S. cerevisiae*, *K. humilis*, *Pic. kudriavzevii*) to antibiotics [92]. The results showed that none of the strains were sensitive to any of the selected antibiotics – gentamicin, chloramphenicol, tetracycline, and ampicillin.

Yeasts of the species *S. cerevisiae*, *K. humilis*, and *Wic. anomalus* were found to be indifferent to streptomycin, gentamicin, erythromycin, tetracycline, and chloramphenicol [133].

Available data indicate a lack of sensitivity in a significant number of yeasts to most antibiotics, which is corroborated by the limited number of antifungal agents and the spread of resistance among fungal microorganisms [149]. There is insufficient information on LAB to draw definitive conclusions; however, it can be noted that members of the genus *Enterococcus* are more prone to exhibiting and developing antibiotic resistance, making them less suitable for use as probiotics. Overall, it should be noted that the study of the sensitivity of potential probiotic microorganisms to various antibiotic substances is conducted individually in each specific case. However, the available information suggests that, despite the significant prevalence of antibiotic resistance among the studied bacteria, strains suitable for further use in medicine and other fields can be selected.

2.5. Antioxidant activity of sourdough microorganisms

Antioxidants play a crucial role in protecting the body from reactive oxygen species (H_2O_2 , $OH^\bullet$, etc.), which can negatively impact food products and human health [150]. LAB are known for their antioxidant properties, which are considered one of the main sources of health benefits provided by probiotics [151].

The antioxidant properties of metabolites produced by microorganisms isolated from sourdoughs are largely unexplored. However, in a study [142], the authors discovered the production of significant amounts of antioxidant compounds by strains *W. paramesenteroides* CRL 2182 and *Ec. durans* CRL 2178.

To fully understand the antioxidant – and consequently, probiotic – potential of microorganisms isolated from sourdoughs, it is important to conduct comprehensive studies and determine the extent to which these microorganisms exhibit antioxidant properties.

3. Prospects for further research and industrial application of sourdough microorganisms

Despite the significant number of articles dedicated to the isolation, identification, and genetic, molecular, technological, and functional research of microorganisms that colonize type I sourdoughs, much work remains unfinished, and many questions lack

definitive answers. The microbiota of sourdoughs based on wheat and rye flour is the only one that can be considered fully studied. For spelt sourdoughs, an adequate list of yeast species that can develop in them has not been established, and there are too few studies covering sourdoughs based on other types of flour – buckwheat, corn, rice, teff, amaranth, quinoa, barley, oats, chia, sorghum, faba beans, and peas. Additionally, the main issue is determining the origin of the sourdough microorganisms, conducting a systematic analysis, and finding relationships that would allow for the understanding and prediction of the appearance of specific strains in the studied samples. Such knowledge would significantly ease the work of researchers and expedite the acquisition of potentially industrially viable strains for further use.

At the same time, there are enough studies showing the promising application of probiotic microorganisms isolated from sourdoughs based on various types of flour. Isolates of LAB and yeasts demonstrate stress resistance, such as the ability to withstand low pH values and bile salts for a considerable time (not less than 2 hours), the aggregation ability, antimicrobial activity against pathogenic strains, and sensitivity to some common antibiotic compounds. The combination of these qualities makes them potential candidates for use by people to meet their needs.

The scope of probiotic applications is quite broad, which is related to the range of properties they exhibit and the numerous health benefits resulting from their intake. They can have antioxidant, antimutagenic [152], immunomodulatory, anticancer [153], and many other characteristics, such as the synthesis of digestive enzymes (lipases, proteases), amino acids, vitamins, and more [154]. The combination of unique features of probiotic microorganisms leads to a whole spectrum of sometimes non-obvious effects on the human body. For example, there is evidence that various bacteria and viruses that enter the central nervous system via the gut-brain axis, overcoming the blood-brain barrier, can be risk factors for the development of neurodegenerative diseases [155]. There is a possibility that a healthy, highly functional gut microbiome can prevent the entry of disease-causing pathogens [156]. Moreover, studies indicate that taking probiotic supplements helps alleviate neurodegeneration symptoms in Parkinson's disease [157], Alzheimer's disease, or even mild cognitive impairments [158]. Additionally, due to nonspecific therapeutic effects, probiotics help patients with mild to moderate depression [159].

A completely different but more obvious example of the positive impact of probiotics can be the reduction of cholesterol levels due to their effect on residual lipoprotein particles in the blood and on lipid metabolism in general [154]. Changes in energy

metabolism also manifest in weight loss in obese individuals [160].

Due to their multifunctionality and benefits, probiotics have found applications in the food industry (production of dairy products, beverages, baked goods, etc.), where they contribute to extended shelf life, taste, and nutritional properties of products, as well as their overall positive impact on the body [161]. Probiotics are also used in medicine [162] and many other fields, such as the perfumery and cosmetics industry, where probiotic microorganism lysates are primarily used [163]. It has been proven that they provide skin care products with rejuvenating, whitening, anti-inflammatory, and photoprotective effects [164].

The role and use of probiotics are constantly increasing across all sectors, and new trends are emerging that help the market and technologies develop. Recently, there has been growing consumer interest and, consequently, manufacturer investment in functional food products – products that, with regular consumption, have a positive impact on human health. Among the most noticeable and beneficial of these are probiotic-containing products: dairy products, desserts, and a wide range of other non-dairy products [165].

Despite the widespread use of probiotics, insufficient attention is currently given to the individual effects and impacts of different microorganisms, considering the composition of the human gut microbiome and the potential risks associated with their uncontrolled use. The advancement of science and technology, the implementation of high-throughput sequencing, and various experimental methodologies will facilitate the optimal use of probiotics according to the specific

advantages of particular strains and the needs of patients [166].

An individualized approach to the use of probiotics in medicine, as well as the increase in their use in other fields, will necessitate a growing collection of probiotic microorganisms with a wide range of properties, activities, and resistances. Strains isolated from sourdoughs, especially those based on less studied types of flour, could prove to be invaluable assets for human needs.

Conclusion

Probiotics have carved out a niche in various industries and medicine due to their unique combination of characteristic properties. Isolating microorganisms from type I sourdough starters is a promising avenue for obtaining new probiotic strains, with the most significant potential found in studying starters made from less researched types of flour.

Comparing the most common types of microorganisms found in sourdoughs with their potential as probiotics, *Lpb. plantarum*, *Lv. brevis*, *P. pentosaceus*, *S. cerevisiae*, and *K. humilis* emerge as the most likely candidates for further isolation and use. Additionally, *Ec. faecium* is of considerable interest, although this microorganism is relatively rare in sourdoughs.

Microorganisms that frequently occur in sourdoughs do not necessarily exhibit probiotic properties. Conversely, species that are rarely found may hold significant potential for further study and use.

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МІКРООРГАНІЗМИ-ПРОБІОТИКИ В ХЛІБНИХ ЗАКВАСКАХ

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Анотація. Огляд літератури дозволяє охарактеризувати і оцінити типову мікробіоту та пробіотичні властивості окремих видів, виділених з різних заквасок для хліба. Встановлено, що в останні роки інтерес до використання заквасок для отримання хліба та до вивчення їхньої мікробіоти поступово зростає. Однак, проведений аналіз сучасних публікацій показав недостатню кількість інформації, яка би стосувалася мікроорганізмів, характерних для заквасок на основі борошна спельти, гречки, кукурудзи, рису, тефу, амаранта, кіноа, ячменю, вівса, чіа, сорго, бобів та гороху. Найбільш вивченими є закваски на основі борошна пшениці та жита. Встановлено перелік найрозповсюдженіших молочнокислих бактерій та дріжджів, які виділяють із заквасок: *Companilactobacillus paralimentarius*, *Fructilactobacillus sanfranciscensis*, *Lactiplantibacillus plantarum*, *Latilactobacillus sakei*, *Leuconostoc citreum*, *Levilactobacillus brevis*, *Pediococcus pentosaceus*, *Weissella cibaria*, *Weissella confusa*, а також *Kazachstania humilis*, *Kazachstania unispora*, *Pichia kudriavzevii*, *Pichia fermentans*, *Saccharomyces cerevisiae* та *Wickerhamomyces anomalus*. Описано всі типові згадки пробіотичних властивостей мікроорганізмів, виділених із хлібних заквасок. При виділенні пробіотиків із хлібних заквасок варто особливо звертати увагу на такі види молочнокислих бактерій як: *Lactiplantibacillus plantarum*, *Levilactobacillus brevis*, *Pediococcus pentosaceus*, *Enterococcus faecium*, а також дріжджів *Saccharomyces cerevisiae* та *Kazachstania humilis*, оскільки вони досить часто зустрічаються у хлібних заквасках з різних видів борошна, та мають найбільш яскраво виражені пробіотичні властивості. За проведеним оглядом встановлено, що типовими пробіотичними властивостями для мікроорганізмів, виділених з заквасок є стресостійкість та антимікробна активність, проте антиоксидантні властивості потребують подальших досліджень. Поширення технологій та збільшення їхньої економічної доступності означатиме зростання попиту на нові пробіотичні штами й мікроорганізми хлібних заквасок і можуть допомогти задовольнити нові рівні споживчих потреб.

Ключові слова: *Lactobacillaceae*, молочнокислі бактерії, дріжджі, мікробіота, стресостійкість, антимікробна активність, хлібні закваски, види борошна.