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Omics approaches to understand sourdough fermentation processes

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ABSTRACT

The application of omics methodologies helps to further unravel sourdough fermentation processes. Of all methodologies applied, metagenetics is the most used one to analyse sourdoughs, allowing to elucidate their microbial structure, albeit that it is based on the sequencing of a very small part of whole-community DNA. Although shotgun metagenomics, metatranscriptomics, metaproteomics, and meta-metabolomics are very promising to analyse sourdough fermentations and the terminology is often used in a confusing way, they have not been fully used *sensu stricto* yet. For instance, up to now, metatranscriptomics is restricted to the use of a functional gene microarray for lactic acid bacteria. Further, meta-metabolomics often deals with metabolite target analysis of sourdough fermentation samples to determine the actual concentrations of residual substrates and metabolites produced as well as to list their volatilome solely. In contrast, genomics has been applied several times, albeit that the whole-genome sequence of only one yeast strain and of 41 lactic acid bacterial strains, originally isolated from sourdoughs, is available. However, the genomics data accessible in public databases should be considered with caution because of inaccurate gene annotations, due to automated annotation pipelines, thereby possibly overruling original, high-quality, well-curated gene annotations.

1. Introduction

The last decade knows an increasing trend of the use of omics technologies to dissect food fermentation processes and functional starter cultures (Bigot et al., 2015; Ercolini, 2013; Kergourlay et al., 2015; O'Flaherty and Klaenhammer, 2011). Also in the area of sourdough fermentations, several studies have dealt with metagenetics, metagenomics, metatranscriptomics, or metaproteomics (Cocolin and Ercolini, 2015; De Filippis et al., 2017b; Gobbetti et al., 2016). Furthermore, genomics has been applied to unravel the whole-genome sequences of several microbial strains derived from spontaneous sourdough fermentation processes (De Vuyst et al., 2017; Martino et al., 2016; Sun et al., 2015; Zheng et al., 2015a, 2015c).

This review deals with a state-of-the-art overview of omics studies applied on sourdough fermentation processes and further examines the relationship between certain genetic properties, unravelled through whole-genome sequencing, and phenotypic traits such as adaptation to and competitiveness in the sourdough fermentation ecosystem of strains isolated thereof.

2. Sourdoughs

Sourdoughs are obtained through fermentation of mixtures of water and flour (fractions), the latter being derived from cereals and/or pseudocereals, by a consortium of microorganisms involving yeasts and lactic acid bacteria (LAB) (De Vuyst et al., 2014, 2016, 2017; Gobbetti and Gänzle, 2013; Gobbetti et al., 2016; Minervini et al., 2014, 2016). Sourdough can be used as leavening agent, acidifier, or flavour carrier in the production of breads and other baked goods. Both spontaneous and starter culture-initiated sourdough fermentation processes are in use, mainly by artisan bakeries and industrial bakery companies, respectively. In the case of spontaneous fermentation, the microorganisms are derived from the flour and other ingredients used and/or from the environment. Whereas the yeasts mainly contribute to leavening and extensive aroma formation in sourdoughs, LAB mainly perform acidification and contribute to a lesser extent to flavour formation. Typically, the number of prevalent LAB species in sourdoughs is higher than the number of prevalent yeast species (Van Kerrebroeck et al., 2017). The most prevalent LAB species are heterofermentative and encompass *Lactobacillus sanfranciscensis*, *Lactobacillus plantarum* (facultatively heterofermentative), *Lactobacillus brevis*, *Pediococcus pentosaceus* (homofermentative), *Lactobacillus paralimentarius* (facultatively heterofermentative), and *Lactobacillus fermentum*, whereas the most prevalent yeast species are *Kazachstania humilis* (formerly *Candida humilis* and *Candida milleri*) and *Saccharomyces cerevisiae*. Minor communities encompass other *Lactobacillus* species (*e.g.*, *Lactobacillus reuteri* and *Lactobacillus rossiae*) and species of the LAB genera *Leuconostoc* and *Weissella* as well as other yeast species of the *Kazachstania* clade. Thanks

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to the availability of improved methodologies for species identification, the presence of acetic acid bacteria in sourdough fermentation processes has been reported (De Vuyst et al., 2017; Gänzle and Ripari, 2016). Their possible contribution to the sourdough fermentation process is not well understood yet and therefore needs further investigation.

In general, firm sourdoughs that are daily backslopped at ambient temperature in artisan bakeries (Type I) have a lower number of prevalent LAB and yeast species compared to liquid sourdoughs produced in one fermentation stage at elevated temperature in industrial settings (Type II), which is attributed to the prevalence of *Lb. sanfranciscensis* in Type I sourdoughs (Van Kerrebroeck et al., 2017). Further, process conditions have an impact on the microbial species diversity of sourdoughs, as differences are found in relation with fermentation temperature, dough yield, and fermentation time (De Vuyst et al., 2017; Minervini et al., 2014; Van Kerrebroeck et al., 2017). No influence has been found concerning the region of origin, as the technologies and practices applied are of decisive impact (De Vuyst et al., 2014, 2017; Van Kerrebroeck et al., 2017; Vrancken et al., 2010).

3. Metagenetics

3.1. Culture-independent microbiological analysis

For many years, denaturing gradient gel electrophoresis of polymerase chain reaction amplicons (PCR-DGGE) was the technology of choice for the elucidation of the microbial composition of ecosystems in a culture-independent way (Cocolin et al., 2013). With the availability of high-throughput DNA sequencing technologies, PCR-DGGE is getting replaced by metagenetics, which involves PCR-based amplification of a specific genomic region using whole-community DNA, followed by high-throughput sequencing of the amplicons obtained. In the case of bacteria, one or several hypervariable regions of the 16S ribosomal RNA (rRNA) gene is/are targeted, whereas for fungi, the internal transcribed spacer (ITS) regions of the rRNA operon or the 18S or 26S rRNA genes are targeted. In fact, metagenetics is an etymologically more correct naming of what is often called 16S metagenomics or related wordings (Esposito and Kirschberg, 2014).

Given the parallels with PCR-DGGE, similar experimental biases, including inadequate whole-community DNA extraction and PCR biases, need to be considered when interpreting metagenetic results obtained. Also, biases linked to the study design need to be considered. Given the fact that different hypervariable regions of the 16S rRNA gene (Parente et al., 2016) or different parts of the ITS regions (Bokulich and Mills, 2013), both resulting in amplicons of different lengths, are targeted across different metagenetic studies, this not only introduces biases within a study but also obstructs proper comparison of different studies. Moreover, the length differences of the sequenced regions, which is intangibly linked to the sequencing platform used, can influence the taxonomic resolution (Parente et al., 2016). Even the procedures applied in sequencing facilities might introduce additional biases (Hiergeist et al., 2016). Overall, the elucidation of microbial ecosystems to species level is not guaranteed, especially when closely related species are involved (Ercolini, 2013).

3.2. LAB composition of sourdoughs

In recent years, several microbiological studies on sourdough have applied metagenetics, including studies dealing with backslopped or traditional bakery sourdoughs and studies on the source tracking of microorganisms involved in sourdough fermentation processes. Most of these studies only focus on the bacterial communities of sourdough ecosystems, whether or not in combination with other techniques for their further identification. For several of these studies, the results (previously) obtained with other identification techniques are confirmed with the application of metagenetics, such as the dominance of *Lactobacillus*, *Leuconostoc*, and *Weissella* during backslopping of wheat sourdoughs for steamed bread production (Zhang and He, 2013), or the dominance of *Firmicutes* (in particular LAB species) in backslopped wheat and rye sourdoughs after one day of fermentation (Bessmeltseva et al., 2014; Celano et al., 2016; Ercolini et al., 2013). Nevertheless, the application of metagenetics could reveal the presence of persisting subpopulations, mainly *Enterobacteriaceae* (Bessmeltseva et al., 2014; Ercolini et al., 2013), or the presence of *Acetobacter* as the most prevalent genus in a *Jiaozi* starter for Chinese steamed bread, due to the specific preparations of this starter (Li et al., 2017). Several metagenetics-based studies have confirmed the presence of *Lb. sanfranciscensis* as prevalent LAB species in traditional bakery sourdoughs (Cavallo et al., 2017; Lattanzi et al., 2013; Lhomme et al., 2015a, 2015b; Liu et al., 2016; Minervini et al., 2015a; Raimondi et al., 2017). However, differences between metagenetic analysis and selective plating have been noted, especially for those LAB species that are in general difficult to cultivate, for instance in the case of *Lb. sanfranciscensis*, indicating that the abundance of this sourdough-characteristic LAB species might have been underestimated before (Bessmeltseva et al., 2014; Lattanzi et al., 2013; Lhomme et al., 2015a; Viiard et al., 2016). Nevertheless, *Lb. sanfranciscensis* shows a high prevalence in French bakery sourdoughs based on studies combining selective plating and incubation, metagenetics, and quantitative PCR analysis (Lhomme et al., 2015a, 2015b; Michel et al., 2016). In addition, two studies on the bacterial community composition of Estonian rye sourdoughs that combine selective plating and incubation, metagenetic analysis targeting the combined V2 and V3 regions of the 16S rRNA gene, and PCR-DGGE analysis targeting the V3 region of the 16S rRNA gene, have shown good agreement between the techniques as well (Bessmeltseva et al., 2014; Viiard et al., 2016). Alternatively, the combination of several techniques in a study on (organic) French bakery sourdoughs has shown a relatively high LAB species diversity, encompassing *Lb. brevis*, *Lactobacillus curvatus*, *Lactobacillus heilongjiangensis*, *Lactobacillus koreensis*, *Lactobacillus xiangfangensis*, *P. pentosaceus*, and *Weissella* spp., some of which are not frequently isolated from sourdoughs (Michel et al., 2016). Furthermore, for some of these sourdoughs, discrepancies have been found between the results obtained by metagenetic analysis and isolate identification, whereby metagenetics tends to suggest a greater bacterial diversity (Michel et al., 2016). Metagenetic analysis even tends to suggest a greater bacterial diversity than PCR-DGGE community profiling (Viiard et al., 2016). All these results indicate that, although metagenetics has the potential of giving a more detailed view on the microbial community composition of a microbial ecosystem, it likely suffers from several biases that are introduced during the workflow applied.

3.3. Microbial source tracking

Given the low detection limit, metagenetic analysis is of utmost interest in source tracking of microorganisms. For instance, metagenetic analysis of durum wheat plant parts and flour derived from the harvested wheat kernels has demonstrated that *Firmicutes*, among which the genus *Lactobacillus*, are endophytic components of the plant during its life cycle, indicating that the plant is a source of the sourdough microbiota (Minervini et al., 2015b). Furthermore, the distribution of the genera *Lactobacillus*, *Leuconostoc*, and *Pediococcus* in the flours is influenced by the agricultural practices (Rizzello et al., 2015). Similarly, metagenetics of insect frass has indicated that various insects, including fruit flies and weevils, could be carriers of *Lb. sanfranciscensis* (Boiocchi et al., 2017). In addition, the common prevalence of *Lb. sanfranciscensis* in Italian bakery sourdoughs is reflected by its presence in the house microbiota, albeit that other LAB species can be retrieved as well, including *Weissella* spp. and *Streptococcus* spp. (Minervini et al., 2015a).

3.4. RNA-based metagenetics

A criticism of metagenetics, and in general of all techniques based on whole-community DNA analysis, is that it cannot distinguish between metabolically active cells and cells that are not metabolically active anymore but are still present in an intact status. To have a better view on the microorganisms that are actively involved in the fermentation process at a given moment in time, total RNA can be used for sequencing, which needs to be converted to cDNA first (Ercolini et al., 2013). Comparing DNA- with RNA-based metagenetic analysis for backslopped wheat and rye sourdoughs, both approaches have revealed a similar prevalence of *Firmicutes* after several backslopping steps during sourdough production (Ercolini et al., 2013). However, the RNA-based approach reveals a higher diversity in the initial stages of fermentation, in which Proteobacteria are strongly represented (Rizzello et al., 2015). This is also the case for faba bean-based sourdoughs (Coda et al., 2017).

3.5. Yeast composition of sourdoughs

Only few metagenetic studies have attempted to characterise the fungal microbiota of sourdoughs and/or the bakery environment (Coda et al., 2017; Minervini et al., 2015a; Raimondi et al., 2017). Concerning the fungal microbiota, Ascomycota are the dominant phylum in sourdoughs, but not in the flours assessed. The species *S. cerevisiae* and *Kazachstania exigua* are prevalent in sourdoughs and on the bakery equipment. Thus, metagenetics illustrates the reduction of a broad microbial diversity in the initial flour/water mixture toward an ecosystem that is dominated by a few species, for the yeasts as well as for the bacteria present (Minervini et al., 2015a). Presumably, the lack of metagenetic studies on fungal communities in sourdoughs is due to a more non-standard workflow that is associated with yeast metagenetic analysis, including the selection of the most optimal region to be amplified (Bokulich and Mills, 2013; De Filippis et al., 2017a), or to an overall lower interest in the yeast composition by the research teams. Indeed, up to now, only few fungal community studies are available, such as those targeting sake (Bokulich et al., 2014), coffee (De Bruyn et al., 2017), olives (Zaragoza et al., 2017), and wine (Sternes et al., 2017).

4. Metagenomics

Metagenomics based on high-throughput shotgun sequencing of whole-community DNA samples obtained from sourdough fermentation processes allows not only the elucidation of their taxonomic composition but also of the functional potential of the microbial ecosystem. Shotgun metagenomics is more expensive and data processing is more difficult than metagenetics, probably explaining why it is carried out less. As far as the authors are aware, no metagenomic study of sourdoughs has been published yet. Actually, only few other fermented foods have been investigated through shotgun metagenomics, more precisely kimchi (Jung et al., 2011), cocoa beans (Illeghems et al., 2012, 2015), puer tea (Lyu et al., 2013), various cheeses (Dugat-Bony et al., 2015; Escobar-Zepeda et al., 2016; Wolfe et al., 2014), milk kefir (Nalbantoglu et al., 2014), withered Corvina grapes (Salvetti et al., 2016), cereal vinegar (Wu et al., 2017), and wines (Bora et al., 2016; Sternes et al., 2017).

Based on searches in the Genomes, BioProject, and BioSamples databases of the National Center for Biotechnology Information (NCBI, Bethesda, MA, USA) for sourdough-related metagenomes (accessed in December 2017), three entries in the BioProjects database were found (PRJNA254750, PRJNA284752, and PRJNA318402) that comprised in total 37 BioSamples. However, all sequence data submitted to the NCBI's Short Read Archive (SRA) database are only partial 16S rRNA gene sequences, illustrating the confusion between metagenomics and metagenetics and the need for a correct usage of these terms.

5. Metatranscriptomics

Metatranscriptomics of sourdough fermentation processes involves the elucidation of the microbial ecosystems' gene expressions based on whole-community RNA samples. Initially, microarray-based metatranscriptomics has been applied (Weckx et al., 2009, 2010b, 2011). The use of a functional LAB gene microarray has been of great help to understand the microbial dynamics and functional behaviour of sourdoughs. First, it has confirmed the three-phased microbial evolution of backslopped wheat and rye sourdough fermentation processes, namely the prevalence of *Enterococcus* spp., *Lactococcus lactis*, and *Leuconostoc mesenteroides* in a first phase of the backslopping process, that of *P. pentosaceus* in a second phase, and finally stable microbial communities of *Lb. fermentum* and *Lb. plantarum* in a third phase. Second, it has revealed the activation of different key metabolic pathways, the ability to use carbohydrates other than glucose (*e.g.*, starch and maltose), and the conversion of amino acids as a contribution to redox equilibrium and flavour compound generation during sourdough fermentation. The lack of information regarding prevalent LAB species such as *Lb. reuteri*, *Lb. rossiae*, and *Lb. sanfranciscensis* can be ascribed to the lack of genome information of these species at the moment the LAB gene microarray was designed, indicating one of the pitfalls of microarray technology (Weckx et al., 2009). So far, no sourdough-related metatranscriptomic studies applying high-throughput sequencing, either using messenger RNA (mRNA) enriched from the total RNA extracted or total RNA, have been reported. In addition to metatranscriptomics, studies of the transcriptome of sourdough-isolated LAB strains, in particular *Lb. reuteri* ATCC 55730 and *Lc. lactis* subsp. *lactis* A12, have shown the adaptation of these strains to the sourdough matrix (Hüfner et al., 2008; Passerini et al., 2013). Additionally, comparative transcriptomic analysis of *Lb. sanfranciscensis* TMW 1.1304 in monocultures or in coculture with *K. humilis* TMW 3.191 has revealed that the yeast strain causes oxidative stress to the LAB strain (Vogel, 2015).

6. Metaproteomics

Metaproteomics of sourdough fermentation processes involves the elucidation of the proteins present in the ecosystem through their separation, for instance by applying two-dimensional acrylamide gel electrophoresis, followed by their identification with advanced mass spectrometry [*e.g.*, matrix-assisted laser desorption/ionisation-time-of-flight mass spectrometry (MALDI-TOF-MS), liquid chromatography coupled to tandem mass spectrometry (LC-MS/MS), or quadrupole time-of-flight mass spectrometry (Q-TOF-MS)]. Alternatively, a direct, gel-free, approach can be followed, in which the proteins are immediately separated and identified with advanced mass spectrometric techniques, such as MALDI-TOF-MS, LC-MS/MS, or Q-TOF-MS. As such, (meta)proteomics can be regarded as a technique of choice to reveal the actual functional traits of microbial strains (proteomics) or a whole microbial ecosystem (metaproteomics). So far, no studies are available focussing on metaproteome analysis of sourdoughs. Actually, only a few studies have reported on the investigation of (fermented) food metaproteomes in general (Ji et al., 2017; Soggiu et al., 2016; Zhao et al., 2015; Zheng et al., 2015b). Also, peptide sequencing has been used to identify the composition of a 2500-year old sourdough bread found in a cemetery along the Silk route in Western China (Shevchenko et al., 2014). Evidence has been found that this sourdough was fermented by *Saccharomycetaceae*, *Leuconostocaceae*, and lactobacilli and was composed of barley (*Hordeum vulgare*) and millet. The latter has been identified as broomcorn (*Panicum miliaceum*), based on a comparison of the peptide sequences of characteristic proteins of modern millet varieties with peptide sequences determined by LC-MS in the ancient food sample.

Despite this lack of reports on metaproteomes, several *Lactobacillus* species have been subjected to multiple studies dealing with functional proteomics, mostly when grown in culture media (De Angelis et al.,

Table 1
Overview of the lactic acid bacterial strains used for genome exploration. The superscripts a and b reflect the two sequencing and annotation projects for *Lactobacillus panis* and *Lactobacillus rossiae*.

Species	Strain	Source	Accession number	Assembly identifier	Reference
Lactobacillus acidifarinae	DSM 19394	Wheat sourdough, Belgium	NZ_AZDV01000006.1	GCF_001434835.1	Sun et al., 2015
Lactobacillus brevis	CRL 2013	Amaranth sourdough, Argentina	NZ_MZMW01000001.1	GCA_002093065.1	Cataldo, P.G., CERELA-CONICET, direct submission to NCBI, 2017
Lactobacillus crustorum	JCM 15951	Wheat sourdough	NZ_AZDB01000001.1	GCF_001434585.1	Sun et al., 2015
Lactobacillus fermentum	IMDO 130101	Backslopped laboratory rye sourdough, Belgium	PRJEB24519		Verce et al., 2018
Lactobacillus frumenti	DSM 13145	Rye-bran sourdough, Germany	NZ_AZER01000005.1	GCF_001436045.1	Sun et al., 2015
Lactobacillus hammesii	DSM 16381	Wheat sourdough, France	NZ_AZFS01000006.1	GCF_001434395.1	Sun et al., 2015
Lactobacillus mindensis	DSM 14500	Sourdough, Germany	NZ_AZEZ01000008.1	GCF_001434275.1	Sun et al., 2015
Lactobacillus namurensis	DSM 19117	Wheat, rye, spelt sourdough, Belgium	NZ_AZDT01000001.1	GCF_001434785.1	Sun et al., 2015
Lactobacillus nantensis	DSM 16982	Wheat sourdough, France	NZ_AZFV01000001.1	GCF_001435815.1	Sun et al., 2015
Lactobacillus panis	DSM 6035[a]	Sourdough, Germany	NZ_AZGM01000056.1	GCF_001435935.1	Sun et al., 2015
Lactobacillus panis	DSM 6035[b]	Sourdough, Germany	NZ_LDPB01000001.1	GCF_001027985.1	Zhu et al., 2015
Lactobacillus paralimentarius	DSM 13238	Sourdough, Japan	NZ_AZES01000005.1	GCA_001434985.1	Sun et al., 2015
Lactobacillus paralimentarius	JCM 10415	Sourdough, Japan	NZ_BAMH01000210.1	GCA_000615725.1	Hattori et al., University of Tokyo, direct submission to NCBI, 2012
Lactobacillus paraplantarum	CRL 1905	Quinoa sourdough, Argentina	NZ_LUHM01000001.1	GCF_001660655.1	Saveedra et al., CERELA-CONICET, direct submission to NCBI, 2016
Lactobacillus plantarum	IPLA 88	Type I sourdough, Italy	NZ_ASJE01000001.1	GCA_000410795.1	Ladero et al., 2013
Lactobacillus plantarum	NIZO 2753	Sourdough, Italy	NZ_ASJE01000001.1	GCA_001633435.1	Martino et al., 2016
Lactobacillus plantarum	NIZO 2757	Sourdough, Italy	NZ_LUWV01000047.1	GCA_001633485.1	Martino et al., 2016
Lactobacillus plantarum	NIZO 2766	Sourdough, Italy	NZ_LUWW01000077.1	GCA_001633495.1	Martino et al., 2016
Lactobacillus plantarum	NIZO 1840	Fermented cereal, Nigeria	NZ_LUWC01000032.1	GCA_001639455.1	Martino et al., 2016
Lactobacillus plantarum	RI-123	Sourdough, Switzerland	NZ_MKDQ01000001.1	GCA_001982005.1	Inglin et al., ETH Zürich, direct submission to NCBI, 2017
Lactobacillus pontis	DSM 8475	Rye sourdough, Germany	NZ_AZGO01000001.1	GCF_001435345.1	Sun et al., 2015
Lactobacillus reuteri	CRL 1098	Sourdough, Germany	NZ_LYWI01000001.1	GCF_001657495.1	Torres et al., 2016
Lactobacillus reuteri	LTH 5448	Type II sourdough, Germany	NZ_JOOG01000001.1	GCF_000758185.1	Lin et al., 2015
Lactobacillus reuteri	TMW 1.656	Type II sourdough, Germany	JOSW02000001.1	JOSW02.1	Lin et al., 2015
Lactobacillus reuteri	TMW 1.112	Type II sourdough, Germany	NZ_JOKX02000001.1	GCF_000722535.2	Lin et al., 2015
Lactobacillus reuteri	LTH 2584	Type II sourdough, Germany	NZ_JOSX01000001.1	GCF_000712555.1	Lin et al., 2015
Lactobacillus rossiae	DSM 15814[a]	Wheat sourdough, Italy	NZ_AZFF01000001.1	GCF_001435135.1	Sun et al., 2015
Lactobacillus rossiae	DSM 15814[b]	Wheat sourdough, Italy	NZ_AUAW01000001.1	GCF_000428925.1	Kyrpides et al., DoE Joint Genome Institute, direct submission to NCBI, 2013
Lactobacillus sanfranciscensis	TMW 1.1304	Rye sourdough starter, Germany	NC_015978.1	GCA_000225325.1	Vogel et al., 2011
Lactobacillus sanfranciscensis	DSM 20451	San Francisco sourdough	NZ_AYYM01000001.1	GCA_001436035.1	Sun et al., 2015
Lactobacillus secaliphilus	DSM 17896	Type II sourdough	NZ_JQBW01000001.1	GCF_001437055.1	Sun et al., 2015
Lactobacillus siliginis	DSM 22696	Wheat sourdough, South Korea	NZ_JQCB01000001.1	GCF_001437435.1	Sun et al., 2015
Lactobacillus spicheri	DSM 15429	Rice sourdough, Germany	NZ_AZFC01000007.1	GCF_001435095.1	Sun et al., 2015
Lactobacillus zymae	ACA-DC 3411	Wheat sourdough, Greece	NZ_LT854705.1	GCF_900183405.1	Kazou et al., 2017
Lactobacillus zymae	DSM 19395	Wheat sourdough, Belgium	NZ_AZDW01000001.1	GCF_001434115.1	Sun et al., 2015
Lactococcus lactis subsp. *lactis*	A12	Wheat sourdough	NZ_CBLU010000006.1	GCF_000442845.1	Guellerin et al., 2016
Leuconostoc citreum	LBAE C10	Wheat sourdough	NZ_CAGE00000000.1	GCF_000239895.1	Laguerre et al., 2012
Leuconostoc citreum	LBAE C11	Wheat sourdough	NZ_CAGF00000000.1	GCF_000239915.1	Laguerre et al., 2012
Leuconostoc citreum	LBAE E16	Wheat sourdough	NZ_CAGG00000000.1	GCF_000239935.1	Laguerre et al., 2012
Weissella cibaria	MG1	Sourdough, Ireland	NZ_JWHU01000001.1	GCF_000878205.1	Lynch et al., 2015
Weissella cibaria	ff3PR	Sourdough from porcine feces, Ireland	NZ_JWHV01000001.1	GCF_000878215.1	Lynch et al., 2015
Weissella cibaria	AB3b	Sourdough, Ireland	NZ_JWHT01000001.1	GCF_000878185.1	Lynch et al., 2015
Weissella confusa	LBAE C39-2	Wheat sourdough	NZ_CAGH01000000.1	GCF_000239955.1	Amari et al., 2012

2016). Proteomic studies on cultures of sourdough LAB have revealed the production of stress proteins responding to environmental stresses and cell communication in *Lb. plantarum* (Calasso et al., 2013; Di Cagno et al., 2009, 2010).

7. Meta-metabolomics

Meta-metabolomics of a microbial ecosystem involves the determination of as much chemical compounds present in the matrix samples as possible, thereby applying a metabolite analysis platform on the same sample, *i.e.*, a multitude of chromatographic separation and analyte detection techniques. As such, it has not been applied on the sourdough ecosystem up to now. Instead, metabolite target analysis is often applied as part of a meta-metabolomics approach to determine the concentrations of carbohydrates, organic acids, sugar alcohols, amino acids, *etc.* and hence understand substrate consumption and metabolite production upon sourdough fermentation (Harth et al., 2016; Minervini et al., 2012; Montanari et al., 2014; Ripari et al., 2016; Rizzello et al., 2016; Van der Meulen et al., 2007; Van Kerrebroeck et al., 2016; Weckx et al., 2010a; Zhao et al., 2016). However, (headspace) solid-phase microextraction in combination with gas chromatography coupled to MS analysis [(HS-)SPME-GC–MS] is sometimes considered as a

metabolomic approach to study sourdough matrices. Albeit that this can be the case for certain matrices (Balestra et al., 2015; Bojko et al., 2014), it should not be considered as such for sourdough, at least not when applied solely (Balestra et al., 2015; Ripari et al., 2016). In contrast, (HS-)SPME-GC–MS analysis should be considered as a metabolite profiling technique to determine part of the volatilome solely, as only a limited number of compounds (for example those with sufficient volatility) can be detected. Moreover, just a list of such compounds does not give much added value, as some of these compounds cannot always be linked with the sourdough matrix, but instead have to be linked to the equipment and extraction procedure used. Additionally, the quantitative potential of this method can be contested, as there is for example not necessarily a relationship between the surface area of the peaks of the chromatograms and the actual sample concentrations. Likewise, competition and replacement on the sorption material used can also lead to false negatives when only presence/absence of compounds are considered. For the determination of the concentrations of residual substrates and metabolites produced present in sourdough fermentation samples, other techniques should be applied, in particular based on LC with various detection methods (Van der Meulen et al., 2007; Van Kerrebroeck et al., 2016; Zhao et al., 2016). For volatile determination in sourdoughs, alternative techniques have been examined, for example selected ion flow tube–mass spectrometry (SIFT-MS; Van Kerrebroeck et al., 2015, 2018). However, the full volatilome of fermented foods and their microbial starters has been studied less, albeit that it could give more insight into the microbial metabolism and interaction with the sourdough matrix, as has been investigated for *S. cerevisiae* in standard media and bread dough (Makhoul et al., 2014; Khomenko et al., 2017).

8. Genomics

Genomics of sourdough-specific microorganisms involves the elucidation of the DNA sequence of their entire genome as well as functional annotation of the genes predicted, and eventual *in silico* pathway reconstruction based on the gene repertoire. Based on searches in the Genomes, BioProject, and BioSamples databases of NCBI for sourdough-specific strains (accessed in December 2017), only one high-quality draft genome sequence of a yeast strain was available, namely that of *Kazachstania saulgeensis* CLIB 1764^T, a strain isolated from an organic sourdough in Saulgé, France (Jacques et al., 2016; Sarilar et al., 2017). Further, also the genome sequence of *Bacillus subtilis* GS 188 was available (NCBI RefSeq accession number NZ_CP022391), a gluten-hydrolysing indigenous strain isolated from a wheat sourdough in Khaagipur, India. Concerning LAB species, genome sequences of 36 strains originally isolated from spontaneous sourdoughs, were found (Table 1). For two strains, namely *Lactobacillus panis* DSM 6035 and *Lb. rossiae* DSM 15814, two entries were present, meaning that there have been two sequencing and annotation projects. Also, an annotated genome sequence was available for *Lb. paralimentarius* DSM 13238 and *Lb. paralimentarius* JCM 10415. Both strains represent in fact the same strain but are coming from different culture collections and have both been sequenced and annotated within different projects. However, using the searches in the Genomes, BioProject, and BioSamples databases, the genomes of the *Leuconostoc citreum* strains LBAE C10, LBAE C11, and LBAE E16, of *Weissella confusa* LBAE C39-2, and of *Lc. lactis* subsp. *lactis* A12 were not retrieved, suggesting that these five genome sequences and the related BioProject were not properly annotated for the origin of the strains sequenced.

In what follows, an overview of the 41 sourdough LAB genomes available, belonging to 25 different species, is given, regarding genes annotated as encoding enzymes that are important for the cellular processes contributing to a strain's competitiveness in the sourdough environment (Table 2). In the case that a gene was not found, although phenotypic indications for its expression are present, it was tried to retrieve evidence for its presence by aligning the protein sequence of the corresponding enzyme from a known strain to a database consisting of all protein sequences encoded by the 41 LAB genomes examined, using the blastp algorithm (Altschul et al., 1990).

8.1. Maltose phosphorylase activity

A gene encoding maltose phosphorylase was present in 36 out of the 41 sourdough-specific LAB strains examined *in silico*. Of those strains, 13 strains contained two genes and three strains (*i.e.*, *Lb. paraplantarum* CRL 1905, *Lb. plantarum* IPLA 88, and *Leuc. citreum* LBAE E16) contained even three genes encoding this enzyme. Maltose is the most abundant saccharide present during sourdough fermentation, being continuously elaborated upon time through flour amylase activity (being most active in the pH range 4.5–5.0 and thus after each backslopping step, in particular the first ones during a sourdough production process, until a low pH is reached) (Gänzle, 2014; Van Kerrebroeck et al., 2016). Maltose hence accumulates up to four days of backslopping, probably due to a higher release than consumption. This is followed by a continuous decrease upon further backslopping, likely due to a higher consumption than release. It is interesting to see that *Lb. paralimentarius* DSM 13238 contained one copy of the maltose phosphorylase gene, whereas *Lb. paralimentarius* JCM 10415 did not contain a gene annotated as coding for maltose phosphorylase. Based on the genomic context of the gene annotated as encoding maltose phosphorylase in *Lb. paralimentarius* DSM 13238, the corresponding gene in *Lb. paralimentarius* JCM 10415 has been annotated as a pseudogene, encoding a family 65 glycosyl hydrolase (locus tag JCM10415_RS14035). However, this annotation was inferred based on the Protein database accession WP_010019562.1, which actually corresponds with a maltose phosphorylase of *Lactobacillus farciminis*.

Searching the genomes of all 41 LAB strains, a gene encoding a family 65 glycosyl hydrolase was present in 12 strains. These family 65 glycosyl hydrolases act on substrates containing α-glucosidic linkages, including maltose. For *Lactobacillus zymae* ACA-DC 3411, *Lactobacillus mindensis* DSM 14500, and *Lb. plantarum* RI-123, at least one gene annotated as encoding a family 65 glycosyl hydrolase was inferred, based on a maltose phosphorylase protein sequence. It is unclear why the enzyme family name was sometimes used as annotation and not the maltose phosphorylase enzyme itself.

No gene encoding a maltose/proton symporter was found in the genome annotation of any of the strains considered, although its presence has been suggested in several studies as responsible for maltose uptake in sourdough-characteristic LAB species (Gänzle and Follador, 2012; Stolz et al., 1996). However, the more general annotation carbohydrate:proton symporter was found for a gene of *Lb. plantarum* NIZO 2753, and that of sugar:proton symporter was found for genes of *Lb. plantarum* NIZO 1840, *Lb. reuteri* TMW1.656, and *W. cibaria* strains ff3PR and MG1. Using the protein sequence of a previously annotated carbohydrate (maltose)/proton symport transporter for *Leuc. citreum* LBAE E16, which was not listed in the genome annotation file considered in this comparison but was retrieved from the CAMPS database (Neumann et al., 2012), a sequence alignment was performed, using blastp, to search for homologous protein sequences within the 41 LAB strains considered. All but four strains, namely *Lb. crustorum* JCM 15951, *Lb. mindensis* DSM 14500, *Lb. nantensis* DSM 16982, and *Lc. lactis* subsp. *lactis* A12, contained one or more genes encoding a homologous protein that was annotated with the general terminology major facilitator superfamily (MFS) transporter, which represents a large and diverse group of transporters.

Lactobacillus paraplantarum CRL 1905 and *Lb. plantarum* RI-123 harboured a gene encoding a maltose ABC superfamily ATP-binding cassette transporter permease, which is known to have a higher affinity for maltodextrin transport than for maltose (Gänzle and Follador, 2012), whereas *Lb. rossiae* DSM 15814 contained a gene encoding a phosphotransferase system (PTS) maltose transporter subunit IIABC.

Table 2
Overview of the presence or absence of key genes important for the competitiveness in a sourdough matrix for the lactic acid bacterial strains considered. The superscripts a and b reflect the two sequencing and annotation projects for *Lactobacillus panis* and *Lactobacillus rossiae*. FS, gene is present but has a frameshift mutation; IN, gene is present but is incomplete.

Species	Strain	Maltose/proton symporter	MFS transporter	Maltose phosphorylase	Family 65 glycosyl hydrolase	Fructose-1,6-bisphosphate aldolase	Phosphoketolase	Mannitol dehydrogenase	Mannitol 2-dehydrogenase	Homologue of mannitol 2-dehydrogenase
Lactobacillus acidifarinae	DSM 19394	0	1	1	0	0	2	1	0	2
Lactobacillus brevis	CRL 2013	0	3	1	0	0	1	1	0	1
Lactobacillus crustorum	JCM 15951	0	0	1	1	1	1	0	0	0
Lactobacillus fermentum	IMDO 130101	0	2	1	0	0	1	0	1	1
Lactobacillus frumenti	DSM 13145	0	1	1	0	0	1	0	0	2
Lactobacillus hammessii	DSM 16381	0	2	1	0	0	2	1	0	2
Lactobacillus mindensis	DSM 14500	0	0	0	3	1	1	0	0	0
Lactobacillus namurensis	DSM 19117	0	3	2	0	1	3	0	0	1
Lactobacillus nantensis	DSM 16982	0	0	1	1	0	1	0	0	0
Lactobacillus panis	DSM 6035[a]	0	4	1	0	1	1	0	0	2
Lactobacillus panis	DSM 6035[b]	0	4	1	0	1	2IN	0	0	2
Lactobacillus paralimentarius	DSM 13238	0	1	1	1	1	1	0	0	0
Lactobacillus paralimentarius	JCM 10415	0	1	0	2	1	FS	0	0	0
Lactobacillus paraplantarum	CRL 1905	0	2	3	0	1	1	0	0	0
Lactobacillus plantarum	IPLA 88	0	2	3	0	0	2	0	0	0
Lactobacillus plantarum	NIZO 2753	0	2	2	0	2	2	0	0	0
Lactobacillus plantarum	NIZO 2757	0	1	2	0	1	2	0	0	0
Lactobacillus plantarum	NIZO 2766	0	1	2	0	1	2	0	0	0
Lactobacillus plantarum	NIZO 1840	0	1	2	0	1	2	0	0	0
Lactobacillus plantarum	RI-123	0	2	2	2	2	2	0	0	0
Lactobacillus pontis	DSM 8475	0	1	1	0	0	1	0	0	1
Lactobacillus reuteri	CRL 1098	0	4	1	0	1	1	0	0	1
Lactobacillus reuteri	LTH 5448	0	3	1	0	1	1	0	0	1
Lactobacillus reuteri	TMW 1.656	0	2	1	0	1	1	0	0	1
Lactobacillus reuteri	TMW 1.112	0	3	0	1	1	1	0	0	1
Lactobacillus reuteri	LTH 2584	0	3	0	1	1	1	0	0	1
Lactobacillus rossiae	DSM 15814[a]	0	3	2	2	0	1	0	0	1
Lactobacillus rossiae	DSM 15814[b]	0	3	2	2	0	1	0	0	1
Lactobacillus sanfranciscensis	TMW 1.1304	0	2	1	0	0	1	0	0	1
Lactobacillus sanfranciscensis	DSM 20451	0	2	2	0	0	1	0	0	1
Lactobacillus secaliphilus	DSM 17896	0	3	1	0	0	1	1	0	1
Lactobacillus siliginis	DSM 22696	0	2	1	0	0	1	0	0	0
Lactobacillus spicheri	DSM 15429	0	3	1	0	0	2	0	0	1
Lactobacillus zymae	ACA-DC 3411	0	1	0	2	0	3	0	0	2
Lactobacillus zymae	DSM 19395	0	1	1	0	0	3	1	0	0
Lactococcus lactis subsp. *lactis*	A12	0	0	1	2	0	1	0	0	0
Leuconostoc citreum	LBAE C10	0	3	2	0	0	1	0	0	1
Leuconostoc citreum	LBAE C11	0	3	2	0	0	1	0	0	1
Leuconostoc citreum	LBAE E16	0	4	3	0	0	1	0	0	1
Weissella cibaria	MG1	0	1	1	0	0	1	0	0	0
Weissella cibaria	ff3PR	0	1	1	0	0	1	0	0	0
Weissella cibaria	AB3b	0	2	2	0	0	1	0	0	1
Weissella confusa	LBAE C39-2	0	1	1	0	0	1	0	0	0

Species	Mannitol-1-phosphate 5-dehydrogenase	Pyruvate oxidase	NADH-dependent alcohol dehydrogenase	Oleate hydratase	Sucrose phosphorylase	Glucansucrase	Homologue of glucosyltransferase	Fructansucrase	Levansucrase	Arginine deiminase	Ornithine carbamoyltransferase	Carbamate kinase
Lactobacillus acidifarinae	0	2	0	1	0	0	0	0	0	0	0	1
Lactobacillus brevis	0	1	0	1	0	0	0	0	0	2	1	2
Lactobacillus crustorum	0	1, IN	0	2	0	0	0	0	0	1	1	1
Lactobacillus fermentum	0	1	0	1	0	0	0	0	0	1	1	2
Lactobacillus frumenti	0	0	0	0	1	0	0	0	0	1	1	1

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Table 2 (*continued*)

Species	Mannitol-1-phosphate 5-dehydrogenase	Pyruvate oxidase	NADH-dependent alcohol dehydrogenase	Oleate hydratase	Sucrose phosphorylase	Glucansucrase	Homologue of glucosyltransferase	Fructansucrase	Levansucrase	Arginine deiminase	Ornithine carbamoyltransferase	Carbamate kinase
Lactobacillus hammessii	0	2	0	2	0	0	0	0	0	0	1	2
Lactobacillus mindensis	0	1	0	3	0	0	0	0	0	1	1	1
Lactobacillus namurensis	0	1	0	1	0	0	0	0	0	2	2	2
Lactobacillus nantensis	0	2	0	3	0	0	0	0	0	1	0	1
Lactobacillus panis	0	0	0	0	1	0	1	0	0	0	0	0
Lactobacillus panis	0	0	0	0	1	0	1	0	0	0	0	0
Lactobacillus paralimentarius	0	2	0	3	0	0	0	0	0	0	0	0
Lactobacillus paralimentarius	0	1, FS	0	2, FS	0	0	0	0	0	0	0	0
Lactobacillus paraplantarum	1	3	0	1	0	0	0	0	0	0	1	0
Lactobacillus plantarum	1	5	0	1	0	0	0	0	0	0	1	0
Lactobacillus plantarum	1	3, IN	0	1	0	0	1	0	0	0	1	0
Lactobacillus plantarum	1	3, IN, FS	0	1	0	0	0	0	0	0	1	0
Lactobacillus plantarum	1	3, IN, FS	0	1	0	0	0	0	0	0	1	0
Lactobacillus plantarum	1	5	0	2	0	0	1	0	0	0	1	0
Lactobacillus plantarum	1	5	0	1	0	0	0	0	0	0	1	0
Lactobacillus pontis	0	0	0	FS	1	0	0	0	1	1	1	1
Lactobacillus reuteri	0	0	0	1	1	0	1	0	0	1	1	1
Lactobacillus reuteri	0	0	0	1	1	0	0	0	1	1	1	1
Lactobacillus reuteri	0	0	0	0	0	0	1	0	1	1	1	0
Lactobacillus reuteri	0	0	0	1	1	0	0	0	1	1	1	1
Lactobacillus reuteri	0	0	0	1	1	0	0	0	FS	1	1	1
Lactobacillus rossiae	0	2	1	1	0	0	0	0	0	1	1	2
Lactobacillus rossiae	0	2	1	1	0	0	0	0	0	1	1	2
Lactobacillus sanfranciscensis	0	IN	0	0	0	0	0	0	1	0	0	0
Lactobacillus sanfranciscensis	0	1	0	0	0	0	1	0	0	0	0	0
Lactobacillus secaliphilus	0	0	0	0	1	0	0	0	0	0	0	0
Lactobacillus siliginis	0	1	0	1	0	0	0	0	0	0	0	0
Lactobacillus spicheri	0	1	0	1	0	0	0	0	0	2	2	2
Lactobacillus zymae	0	2	0	1	0	0	0	0	0	0	0	1
Lactobacillus zymae	0	2	0	1	0	0	0	0	0	0	0	0
Lactococcus lactis subsp. *lactis*	1	FS	0	1	1	0	0	0	0	1	2	3
Leuconostoc citreum	0	0	0	1	2	0	0	0	0	0	IN	0
Leuconostoc citreum	0	0	0	1	2	0	0	0	0	1	2	1
Leuconostoc citreum	0	0	0	1	2	0	0	0	IN	0	1	0
Weissella cibaria	0	2, FS	2	1	0	0	0	0	0	1	2	1
Weissella cibaria	0	2, FS	2	1	0	0	0	0	0	1	2	1
Weissella cibaria	0	3	2	1	0	0	0	0	0	1	2	1
Weissella confusa	0	2	2	1	0	0	0	0	0	1	1	1

Species	Arginine/ornithine (A/O) antiporter	Glutaminase	Glutamate dehydrogenase	Glutamate decarboxylase	Glutathione reductase	Cystathionine lyase	Glycerol dehydrogenase	Tannase/tannin acyl hydrolase	Glycosyl dehydrogenase	Phenolic acid decarboxylase
Lactobacillus acidifarinae	0	0	0	0	2	1	1	0	1	1
Lactobacillus brevis	3	0	0	2	1	0	1	0	1	2
Lactobacillus crustorum	2	0	0	0	2	1	0	0	0	IN
Lactobacillus fermentum	2	0	0	0	1	3	0	0	0	1
Lactobacillus frumenti	4	0	0	0	2	0	0	0	0	0
Lactobacillus hammessii	0	0	0	0	1	0	0	0	0	1
Lactobacillus mindensis	FS	0	1	0	2	1	0	0	0	0
Lactobacillus namurensis	2	0	0	0	3	0	0	0	0	1
Lactobacillus nantensis	2	0	1	0	2	1	0	0	0	1
Lactobacillus panis	0	0	0	0	0	1	1	0	1	0
Lactobacillus panis	0	0	0	0	0	1	1	0	1	0

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Table 2 (*continued*)

Species	Arginine/ ornithine (A/ O) antiporter	Glutaminase	Glutamate dehydro-genase	Glutamate decarboxylase	Glutathione reductase	Cystathionine lyase	Glycerol dehydro-genase	Tannase/ tannin acyl hydrolase	Glycosyl dehydro-genase	Phenolic acid decarboxy-lase
Lactobacillus paralimentarius	1	0	0	0	2	1	0	0	0	1
Lactobacillus paralimentarius	1	0	0	0	1, FS	1	0	0	0	1
Lactobacillus paraplantarum	0	0	1	0	3	0	0	0	0	1
Lactobacillus plantarum	0	0	1	1	4	1	0	1	0	1
Lactobacillus plantarum	0	0	1	1	4	1	0	1	0	1
Lactobacillus plantarum	0	0	1	1	3	0	0	1	0	1
Lactobacillus plantarum	0	0	1	1	3	0	0	1	0	1
Lactobacillus plantarum	0	0	1	1	3	0	0	0	0	1
Lactobacillus plantarum	0	0	1	1	3	1	0	1	0	1
Lactobacillus pontis	2	0	0	0	0	0	1	0	1	1
Lactobacillus reuteri	1	2	0	0	0	0	1	0	1	0
Lactobacillus reuteri	1	3	0	1	0	0	1	0	1	0
Lactobacillus reuteri	1	3	0	1	0	0	0	0	0	0
Lactobacillus reuteri	1	3	0	1	0	0	1	0	1	FS
Lactobacillus reuteri	1, FS	2	0	0	0	0	1	0	1	FS
Lactobacillus rossiae	1	0	0	1	1	0	1	0	1	1
Lactobacillus rossiae	1	0	0	1	0	0	1	0	1	1
Lactobacillus sanfranciscensis	0	0	0	0	1	0	0	0	0	0
Lactobacillus sanfranciscensis	1	0	0	0	1	0	0	0	0	0
Lactobacillus secaliphilus	0	0	0	0	0	0	0	0	0	0
Lactobacillus siliginis	1	0	0	0	1	0	0	0	0	0
Lactobacillus spicheri	3	0	0	0	2	0	1	0	1	0
Lactobacillus zymae	0	0	0	0	2	0	1	0	1	1
Lactobacillus zymae	0	0	0	0	3	1	1	1	1	1
Lactococcus lactis subsp. *lactis*	FS	0	0	1	0	1	0	0	0	1
Leuconostoc citreum	0	0	0	0	2, 2IN	0	1	0	0	0
Leuconostoc citreum	0	0	0	0	4	0	1	0	0	0
Leuconostoc citreum	0	0	0	0	4	0	1	0	0	0
Weissella cibaria	1	0	0	0	3	0	0	0	0	0
Weissella cibaria	1	0	0	0	3	0	0	0	0	0
Weissella cibaria	0	0	0	0	3	0	0	0	0	0
Weissella confusa	0	0	0	0	4	0	0	0	0	0

8.2. Fermentation of both hexoses and pentoses

Besides maltose, the sourdough matrix contains sucrose, glucose (as a result of endogenous flour amylase activity and glucofructan degradation by yeasts) and fructose (elaborated from glucofructans through yeast activity) (De Vuyst et al., 2017). It is known that many LAB sourdough isolates are (facultatively) heterofermentative (De Vuyst et al., 2014, 2017; Van Kerrebroeck et al., 2017). As marker enzymes, fructose-1,6-bisphosphate aldolase representing the Embden-Meyerhoff-Parnas pathway (homofermentative pathway for the degradation of hexoses) and phosphoketolase representing the phosphogluconate pathway (heterofermentative pathway allowing the degradation of hexoses and pentoses), were searched for in the genome annotation of the 41 LAB strains considered. All genomes contained a gene encoding phosphoketolase, although differences were noticed for the two genome annotations of *Lb. panis* DSM 6035, *i.e.,* one genome annotation contained two short, incomplete genes, pointing to a gap in the genome sequence, and for *Lb. paralimentarius,* for which species strain JCM 10415 contained a frameshifted gene. Fructose-1,6-bisphosphate aldolase was present in 17 LAB strains. Although facultatively heterofermentative LAB strains possess both aldolase and phosphoketolase activities, these findings are in contrast with the previously reported metabolism for several of the strains, such as for *Lb. crustorum* JCM 15951 as a homofermentative LAB strain or for *Lb. sanfranciscensis* TMW 1.1304 and strains of *Lb. reuteri* as heterofermentative LAB strains. Yet, the presence of one gene does not equal the presence of an entire functional pathway. Alternatively, it could be significative of an overflow metabolism (Arskold et al., 2008).

8.3. Redox balancing

Whereas heterofermentation of glucose and fructose through the phosphogluconate pathway is widespread among strains of sourdough-characteristic LAB species, fructose is often used as alternative external electron acceptor through NADH-dependent mannitol dehydrogenase activity (De Vuyst et al., 2017; Gänzle et al., 2007). This way of cofactor regeneration is energetically advantageous, because there is no need to reduce acetyl-CoA into ethanol for NAD^+ recuperation and hence an additional ATP can be formed through acetate kinase activity as well as one additional mole of acetate that contributes to the acidity and flavour of sourdoughs. Only one strain, *Lb. fermentum* IMDO 130101, was annotated as containing a gene encoding a mannitol 2-dehydrogenase (EC 1.1.1.67) that reduces D-fructose into D-mannitol, in line with its mannitol production in a sourdough simulation medium (Vrancken et al., 2008). However, five LAB genomes contained a gene encoding a mannitol dehydrogenase, namely *Lb. acidifarinae* DSM 19394, *Lb. brevis* CRL 2013, *Lb. hammesii* DSM 16381, *Lb. secaliphilus* DSM 17896, and *Lb. zymae* DSM 19395. According to the BRENDA database (Placzek et al., 2017), mannitol dehydrogenase (EC 1.1.1.255) reduces D-mannose into D-mannitol. In addition, *Lb. paraplantarum* CRL 1905 and the *Lb. plantarum* strains NIZO 1840, NIZO 2753, NIZO 2757, NIZO 2766, RI-123, and IPLA88, and *Lc. lactis* subsp. *lactis* A12 contained a gene encoding a mannitol-1-phosphate 5-dehydrogenase, an enzyme that catalyses the reduction of D-fructose 6-phosphate into D-mannitol 1-phosphate. The latter strain also contained a gene encoding a mannitol dehydrogenase family protein. However, mannitol dehydrogenase activity was not found in this strain phenotypically (Passerini et al., 2013).

Given the fact that mannitol 2-dehydrogenase is an important enzyme for sourdough LAB strains, contributing to their competitive advantage in the sourdough matrix (De Vuyst et al., 2017; Gänzle et al., 2007; Vrancken et al., 2008), the protein sequence of mannitol 2-dehydrogenase from *Lb. fermentum* IMDO 130101 was used to search for homologous protein sequences within the protein sequences of the 41 LAB strains considered, using blastp. High scoring hits were found with proteins annotated with the more general description alcohol dehydrogenase or L-threonine dehydrogenase in 23 LAB strains, including *Lb. sanfranciscensis* TMW 1.1304, which was originally annotated as containing a gene encoding a mannitol 2-dehydrogenase (original locus tag LSA_02820; Vogel et al., 2011). The strains lacking the gene encoding a mannitol 2-dehydrogenase/alcohol dehydrogenase included *Lb. crustorum* JCM 15951, *Lb. mindensis* DSM 14500, and *Lb. nantensis* DSM 16982.

Other alternative external electron acceptors that can be used for cofactor regeneration, thereby activating the acetate kinase branch of the phosphogluconate pathway, are oxygen (available through sourdough mixing) and aldehydes such as hexanal, 2-nonenal, and 2,4-decadienal (obtained through lipid oxidation by endogenous flour lipoxygenase) by pyruvate oxidase and NADH-dependent alcohol dehydrogenase activity, respectively (De Vuyst et al., 2017; Gänzle, 2014). All but 13 LAB strains contained a gene encoding a pyruvate oxidase. The LAB strains lacking this gene included those of *Lb. reuteri* and *Leuc. citreum*, as well as *Lb. sanfranciscensis* TMW 1.1304 that had a frameshift mutation in this gene. Only *Lb. rossiae* DSM 15814, the three *W. cibaria* strains, and *W. confusa* LBAE C39-2 contained a gene encoding a NADH-dependent alcohol dehydrogenase.

According to Gänzle (2014), enzymes involved in lipid oxidation are hydratases and alcohol dehydrogenases. Regarding the former enzymes, lactobacilli hydrate oleic acid, linoleic acid, and linolenic acid to hydroxyl fatty acids. Genes encoding an oleate hydratase were found in all strains, except for *Lb. frumenti* DSM 13145, *Lb. panis* DSM 6035, *Lb. reuteri* TMW 1.656, *Lb. sanfranciscensis* strains TMW 1.1304 and DSM 20451, and *Lb. secaliphilus* DSM 17896. *Lactobacillus pontis* DSM 8475 had a frameshift mutation in its gene encoding oleate hydratase. All 41 LAB strains together contained in total 336 genes encoding several types of alcohol dehydrogenases, including alcohol dehydrogenase (141 genes), zinc-dependent alcohol dehydrogenase (77 genes), bifunctional acetaldehyde-CoA/alcohol dehydrogenase (51 genes), and aryl-alcohol dehydrogenase (31 genes). Given this rather generally annotated genes, it was difficult to search for genes that are involved in specific functions in lipid oxidation.

8.4. Sucrose fermentation ability

The consumption of sucrose by means of a sucrose phosphorylase is energetically advantageous (De Vuyst et al., 2017). A gene encoding this enzyme occurred in 12 of the LAB strains considered, namely in *Lb. frumenti* DSM 13145, *Lb. panis* DSM 6035, *Lb. pontis* DSM 8475, *Lb. reuteri* CRL 1098, LTH 2584, LTH 5448, and TMW 1.112, and *Lb. secaliphilus* DSM 17896. Also, glucan- and fructansucrase or levansucrase use sucrose, thereby producing oligo- or polysaccharides and impacting sourdough functionality (Chen et al., 2016; Gobbetti et al., 2014). However, no genes encoding glucansucrase or fructansucrase were found. Therefore, regarding glucansucrase, the protein sequence of glucosyltransferase of *Lb. fermentum* IMDO 130101 was used to search for homologous protein sequences within the protein sequences of the 41 LAB strains considered, using blastp. In six strains, high scoring hits (E value of 0.0, high bit score) were obtained for protein sequences related to *Lb. reuteri* CRL 1098 (dextransucrase), *Lb. sanfranciscensis* DSM 20451 (glycosyl hydrolase family 70), *Lb. plantarum* NIZO 2753 and NIZO 1840 (both glycosyl hydrolase family 70), *Lb. reuteri* TMW 1.656 (hypothetical protein), and *Lb. panis* DSM 6035 (hypothetical protein). A gene encoding a levansucrase was present in five LAB strains, namely *Lb. pontis* DSM 8475, *Lb. reuteri* LTH 5448, TMW 1.112, and TMW 1.656, and *Lb. sanfranciscensis* TMW 1.1304. In addition, *Lb. reuteri* LTH2584 contained a pseudogene annotated as encoding a levansucrase/inulosucrase and *Leuc. citreum* LBAE E16 contained a too short gene to be conclusive, possibly due to a gap in the genome sequence.

8.5. Arginine deiminase (ADI) pathway

Arginine deiminase activity in LAB species converts arginine, an

amino acid that is present in the flour matrix (released through endogenous flour protease activity), into citrulline and ammonia, which takes place optimally under acidic conditions (De Vuyst et al., 2017; Gänzle et al., 2007). Citrulline can be secreted by the cells into the environment (depending on the pH) or further converted by ornithine carbamoyltransferase activity into carbamoyl phosphate and ornithine (released into the environment by means of an arginine/ornithine antiporter and serving as a flavour precursor molecule), and further into carbon dioxide, ammonia, and ATP by carbamate kinase activity. Hence, ADI pathway activity contributes to acidic stress response (by the release of ammonia) and competitiveness (by the production of additional ATP). Fourteen LAB strains harboured at least one copy of each of the four genes of the ADI pathway, namely *Lb. brevis* CRL 2013, *Lb. crustorum* JCM 15951, *Lb. fermentum* IMDO 130101, *Lb. frumenti* DSM 13145, *Lb. namurensis* DSM 19117, *Lb. pontis* DSM 8475, *Lb. reuteri* CRL 1098, LTH 5448, TMW 1.112, and LTH 2584, *Lb. rossiae* DSM 15814, *Lb. spicheri* DSM 15429, and *W. cibaria* MG1 and ff3PR. Whereas most of these strains had multiple copies of some of the four genes, *Lb. namurensis* DSM 19117 and *Lb. frumenti* DSM 13145 had at least two copies of each gene. The strains *Lb. panis* DSM 6035, *Lb. sanfranciscensis* TMW 1.1304, *Lb. secaliphilus* DSM 17896, and *Lb. zymae* DSM 19395 did not contain any of the four genes related to the ADI pathway, confirming for instance the absence of ADI activity in *Lb. sanfranciscensis*; in contrast with a former report, indicating misidentification of the strain used (De Angelis et al., 2002). The wide spread of this pathway is in line with the (acidic) stressful conditions prevailing in sourdough (De Vuyst et al., 2017). Indeed, the ADI pathway activity in *Lb. fermentum* IMDO 130101 seems to play an important role for the growth of this strain under suboptimal conditions (Vrancken et al., 2009a, 2009b).

8.6. Acidic stress response

Acidic stress in sourdoughs is caused by the production of lactic acid and elevated concentrations of acetic acid produced by heterofermentative LAB species. Except for ADI activity, LAB species respond to acidic stress through the removal of protons, thereby producing ammonia, from diverse substrates. Glutaminase and glutamate dehydrogenase convert glutamine into glutamate and glutamate into α-ketoglutarate (that participates in amino acid conversions contributing to flavour formation), respectively (Zhang and Gänzle, 2010). Only the five strains of *Lb. reuteri* considered contained a gene encoding glutaminase, whereas only all six strains of *Lb. plantarum*, *Lb. paraplantarum* CRL 1905, *Lb. mindensis* DSM 14500, and *Lb. nantensis* DSM 16982 contained a gene encoding glutamate dehydrogenase. Also, the gene encoding glutamate decarboxylase, catalysing the production of γ-aminobutyrate (GABA) from glutamate, was not widespread. Besides all *Lb. plantarum* strains and three out of the five *Lb. reuteri* strains (LTH 5448, TMW 1.656, and TMW 1.112) considered, only *Lb. rossiae* DSM 15814, *Lb. brevis* CRL 2013, and *Lc. lactis* subsp. *lactis* A12 contained such gene, with the *Lb. brevis* strain containing two genes. The presence of glutamate decarboxylase in certain *Lb. reuteri* strains contributes to their competitiveness in sourdoughs with long fermentation times (Lin and Gänzle, 2014a; Zheng et al., 2015a). Given the low concentration of glutamate/glutamine in the cereal matrix, the presence of these genes has been linked to an intestinal origin of *Lb. reuteri* (Su et al., 2011; Zheng et al., 2015a).

8.7. Oxidative stress response

Oxidative stress in sourdoughs is caused by, among others, reactive oxygen species and oxidation of the thiol groups of the gluten network by the sourdough yeasts (Vogel, 2015). Redox homeostasis enables the sourdough LAB species to respond to this oxidative stress. Most of the LAB strains considered contained at least one gene encoding a glutathione reductase; only *Lb. panis* DSM 6035, *Lb. pontis* DSM 8475, *Lb. secaliphilus* DSM 17896, *Lc. lactis* subsp. *lactis* A12, and all five strains of *Lb. reuteri* did not contain such gene. Furthermore, *Lb. namurensis* DSM 19117, all six *Lb. plantarum* strains, *Lb. paraplantarum* CRL 1905, *Lb. zymae* DSM 19395, *W. cibaria* strains MG1, ff3PR, and AB3b, *W. confusa* LBAE C39-2, and *Leuc. citreum* strains LBAE C11 and LBAE E16 contained at least three copies of this gene. The absence of a glutathione reductase strongly impairs aerobic growth, as shown for a mutant of *Lb. sanfranciscensis*, unless cysteine is added to the growth medium (Jänsch et al., 2007). Besides cystathionine metabolism, with cystathionine lyase as a key enzyme, contributing to flavour development in cheese ripening, especially cysteine uptake is essential for oxygen tolerance (Turner et al., 1999), as evidenced by the presence of a cysteine ABC transporter permease that is present in 24 of the LAB strains examined. A gene coding for a cystathionine lyase was present in 13 strains (three genes in *Lb. fermentum* IMDO 130101), among which only seven contained both genes, namely *Lb. acidifarinae* DSM 19394, *Lb. crustorum* JCM 15951, *Lb. mindensis* DSM 14500, *Lb. nantensis* DSM 16982, *Lb. paralimentarius* DSM 13238 and JCM 10415, and *Lb. zymae* DSM 19395. Fifteen LAB strains, more precisely *Lb. acidifarinae* DSM 19394, *Lb. brevis* CRL 2013, *Lb. panis* DSM 6035, *Lb. pontis* DSM 8475, *Lb. reuteri* CRL 1098, LTH 2584, LTH 5448, and TMW1.112, *Lb. rossiae* DSM 15814, *Lb. zymae* ACA-DC 3411 and DSM 19395, and *Leuc. citreum* LBAE C10, LBAE C11, and LBAE E16 contained a gene encoding glycerol dehydrogenase, allowing these strains to regenerate reduced cofactors much faster, resulting in a higher growth rate, which is a competitive advantage in backslopped sourdoughs (Lin and Gänzle, 2014a).

8.8. Phenolic compound conversions

Although phenolic compounds are minor constituents of cereal flours, being more elevated in (whole) sorghum and millet flours compared with (refined) wheat flours, they are an important source of antioxidant activity and flavour potential (Dykes and Rooney, 2006). They could exert a selective pressure toward resistant LAB strains (Lin and Gänzle, 2014b; Sekwati-Monang et al., 2012). Although it has been shown that intestinal lactobacilli possess feruloyl esterase activity (Gänzle, 2014), no genes annotated as encoding this enzyme were found in the LAB strains considered, albeit that ferulic acid is a major cereal phenolic compound (Dykes and Rooney, 2006). A gene encoding tannase was found in five *Lb. plantarum* strains (NIZO 2753, NIZO 2757, NIZO 2766, RI-123, and IPLA 88) and in *Lb. zymae* ACA-DC 3411. Since the metabolism of phenolic compounds relies on glycosyl hydrolases, reductases, and decarboxylases, retrieving specific information from the genome annotations was not trivial. Nevertheless, genes encoding phenolic acid decarboxylases, converting phenolic acids into flavour precursors, were found in 19 of the 41 LAB genomes examined. No genes encoding cinnamic acid reductases were found, although its activity was associated with LAB, albeit with strains isolated during malt whisky fermentation (van Beek and Priest, 2000).

8.9. Phytate hydrolase activity

A gene encoding phytase was not found in any of the LAB genomes examined, although phytase activity has been linked with LAB (De Vuyst et al., 2017; Gänzle, 2014). During sourdough production, phytate is primarily degraded through endogenous enzymes, aided by acidification of the matrix through the LAB metabolism (Reale et al., 2007). Nevertheless, phytase activity is assigned to a minority of LAB isolates from fermented gruels and sourdoughs, albeit that the peptide sequence of the corresponding enzymes isolated has not been determined (Nuobariene et al., 2015; Songré-Ouattara et al., 2008). Similarly, phytase activity has been associated with sourdough yeasts (De Vuyst et al., 2016).

9. Conclusions

The availability of a wide range of omics methodologies has the potential to enable understanding sourdough fermentation processes more profoundly. Although several omics methodologies have been applied so far, there are still many open opportunities, as for example no shotgun metagenomics or meta-metabolomics studies *sensu stricto* have been performed yet. Anyway, it is crucial to not only use the proper terminologies, but also to take care of data and metadata correctness. Indeed, given the steady increase of the number of bacterial genome sequences, including those from sourdough isolates, it is assumed that the scientific community has a gold mine of data at its disposal to explore and improve research. However, key in this process is proper and trustworthy genome annotation, and this at the gene level as well as at the level of genome metadata. Concerning the latter, of all 41 LAB strains considered for genome exploration during the present study, five could not be retrieved purely based on searches in the BioProject and BioSamples databases of NCBI, since the genome metadata did not contain the proper isolate source information. Regarding the annotation at the gene level, some important lessons could be learned too. Text-based searches for the presence of key enzymes important for competitiveness in sourdoughs in the genome annotation of the 41 LAB strains considered showed that it was not as trivial as one might think. Without knowledge of previously described phenotypic traits, and without some bioinformatics skills allowing to search sequence alignment-based instead of text-based, one would for example conclude that only one of the LAB strains examined possessed a gene encoding a mannitol 2-dehydrogenase, although this enzyme has been described in many sourdough-characteristic LAB strains, including *Lb. sanfranciscensis* TMW 1.1304. Precisely this example is worth mentioning, and from a point of view of the authors illustrative for what is happening in genomics nowadays. Whereas Vogel et al. (2011) annotated the gene with original locus tag LSA_02820 as encoding a mannitol 2-dehydrogenase, the current annotation in public databases mentions an alcohol dehydrogenase. This is most likely the result of automated annotation pipelines of institutes as NCBI that reannotate genome sequences, apparently with the loss of well-curated, detailed information as a result. This urgently triggers the question whether there is a need for dedicated, niche-specific databases containing highly-curated information, obtained during wet lab studies, that can be used to combat the apparently too general automated genome annotation pipelines.

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