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Sourdoughs as a function of their species diversity and process conditions, a meta-analysis



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ABSTRACT

Background: Sourdough is a cereal flour-water mixture that is fermented by communities of yeasts and lactic acid bacteria (LAB) and that is used for the production of baked goods. Its use has been subject to a renewed interest in the past years. The classical classification concept of sourdoughs distinguishes two major types (I and II), based on the process conditions applied for their production.

Scope and approach: In this study, both species diversity (LAB and yeasts) and processing conditions of sourdoughs were taken into account for the classification of sourdoughs. Therefore, a meta-analysis of such literature data on hundreds of backslotted sourdoughs is described.

Key findings and conclusions: The meta-analysis agreed with the subdivision into Type I and Type II sourdoughs. In general, the number of prevalent yeast species in a given sourdough was lower than the number of prevalent LAB species. Also, a lower number of prevalent LAB and yeast species characterized the microbial species diversity of Type I sourdoughs compared to Type II ones. This could be attributed to the prevalence of *Lactobacillus sanfranciscensis* in sourdoughs of the former type. The process conditions impacted the yeast species diversity, as differences were found for the fermentation temperature, dough yield, and fermentation time between sourdoughs. No influence could be found concerning the region of origin, albeit that literature data reflected regionally important sourdoughs.

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1. Introduction

Sourdough is a cereal flour-water mixture that is fermented to a low pH by the growth and metabolic action of mainly lactic acid bacteria (LAB) and yeasts (De Vuyst, Harth, Van Kerrebroeck, & Leroy, 2016; De Vuyst et al., 2014; Gobbetti, Minervini, Pontonio, Di Cagno, & De Angelis, 2016; Minervini, De Angelis, Di Cagno, & Gobbetti, 2014; Minervini, Di Cagno et al., 2012). Acetic acid bacteria occur sporadically (Li, Li, & Bian, 2016; Minervini, Di Cagno et al., 2012; Ripari, Gänzle, & Berardi, 2016; Zhang & He, 2013). The sourdough ecosystem is a very specific, stressful, microbial ecosystem, characterized by specific adaptations of the microbiota to the variable carbohydrate and nutrient contents, low pH, and variable oxygen tension and redox potential. The sourdough microbiota can develop spontaneously or can be added as a starter culture (De Vuyst et al., 2014; De Vuyst et al., 2016).

The microbial ecology of sourdoughs has been reviewed in

general (De Vuyst, Vrancken, Ravyts, Rimaux, & Weckx, 2009; De Vuyst et al., 2014; Gobbetti et al., 2016; Minervini et al., 2014) and with a focus on LAB (Gobbetti et al., 2016; Gänzle & Gobbetti, 2013; Gänzle & Ripari, 2016; Minervini, Celano, Lattanzi, De Angelis, & Gobbetti, 2016) and yeasts (De Vuyst et al., 2016; Guerzoni, Serrazanetti, Vernocchi, & Gianotti, 2013). These reviews deal with a description of the microbial species diversity, its origin, drivers of its establishment, and the influence of raw materials and process conditions. In general, the most prevalent LAB species are *Lactobacillus sanfranciscensis* (belonging to the *Lactobacillus fructivorans* group), *Lactobacillus plantarum* (*Lb. plantarum* group), *Lactobacillus brevis* (*Lb. brevis* group), *Pediococcus pentosaceus* (pediococci), *Lactobacillus paralimentarius* (*Lactobacillus alimentarius* group), and *Lactobacillus fermentum* (*Lactobacillus reuteri* group). Some sourdoughs also harbor *Leuconostoc* and *Weissella* species. The most prevalent yeast species are *Candida humilis* (recently reclassified as *Kazachstania humilis*) and other *Kazachstania* species (belonging to the *Kazachstania* clade), and *Saccharomyces cerevisiae* (*Saccharomyces* clade).

It is postulated that the prevalence of *Lb. sanfranciscensis* in many sourdoughs indicates a dispersal-limited development of the

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sourdough LAB communities (Gänzle & Ripari, 2016). Yet, the impact of process factors may not be neglected. Temperature, dough yield [DY or (dough mass/flour mass) × 100], and back-slopping, fermentation and resting times can result in different microbial associations prevailing in sourdoughs produced under different circumstances. Furthermore, a complex interplay between the flour used and the process conditions applied influence the microorganisms prevailing in a sourdough ecosystem and select for the species that are most adapted. In general, upon back-slopping of the flour-water mixture, the microbiota develops into a consortium that often encompasses one to several LAB species and one or two yeast species in the mature sourdoughs (De Vuyst et al., 2014; Huys, Daniel, & De Vuyst, 2013; Minervini et al., 2014).

Sourdoughs are traditionally subdivided into Type I and Type II sourdoughs, based on the process technology applied for their production (Böcker, Stolz, & Hammes, 1995; Hammes et al., 2005; Huys et al., 2013). Type I sourdoughs are firm sourdoughs, produced with a low DY (<200), fermented at ambient temperature (<30 °C) for 24 h or less, and back-slopped regularly. Type II sourdoughs are liquid sourdoughs, produced with a high DY (>200), fermented at elevated temperatures (>30 °C) and in one stage for a long time (24–72 h). In general, they represent bakery and industrial practices, respectively. This division is reflected in the LAB species diversity, whereby *Lb. sanfranciscensis* and *C. humilis* are considered typical Type I sourdough LAB and yeast species, respectively, whereas acid-tolerant LAB species (e.g., *Lb. fermentum*) prevail in Type II sourdoughs (Müller, Wolfrum, Stolz, Ehrmann, & Vogel, 2001; Sekwati-Monang & Gänzle, 2011; Vogelmann & Hertel, 2011). During Type II sourdough production, baker's yeast is frequently added to the sourdough at the end of the fermentation process, as yeast growth in the flour-water mixture is often limited due to the fast and high acidification during fermentation (De Vuyst et al., 2016). Sometimes, a resting time at low temperature is applied, in particular by bakeries (Type I), to allow for less frequent back-slopping (De Vuyst, Van Kerrebroeck, & Leroy, 2017). While not having been examined extensively, this resting time could impact the microbial composition, by favoring cold-tolerant LAB species, notably *Leuconostocs* and *Lb. sanfranciscensis* (Di Cagno et al., 2014; Venturi, Guerrini, & Vincenzini, 2012). Additionally, Type III sourdoughs are distinguished, which are dried preparations of Type II sourdoughs (De Vuyst et al., 2014).

A first analysis of literature data on the LAB species diversity of sourdoughs, making use of the ecological community assembly theory, has focused on dispersal, diversification, drift, and selection as driving forces behind this community assembly (Gänzle & Ripari, 2016). These authors reported on the prevalence of *Lb. sanfranciscensis* in Type I sourdoughs and a high β -diversity of LAB species in Type II sourdoughs. However, the sourdough ecosystem as a whole was not taken into account. Therefore, this commentary attempts to do so, taking both the LAB and yeast species diversity as well as the process conditions of sourdough productions into account. It was based on a first meta-analysis of literature data on both species diversity and process conditions of sourdoughs reported in the period 1999–February 2017, despite the multilevel and fragmented nature of the data available. To this end, these literature data were converted into a database format of quantitative data, presence/absence data, or combined data. Combined data were constructed in such a way that every combination had a sufficient number of positive entries. All these data were used to perform statistical analyses as indicated in the figure legends. Several insights into the sourdough ecosystem composition were thus obtained, either confirming existing definitions and hypotheses or revealing new data. For instance, it allowed to decide if the traditional classification concept of sourdoughs, based on process factors, is indeed reflected in their microbial ecology.

2. Meta-analysis of back-slopped sourdoughs

During the present study, a meta-analysis was performed on 583 back-slopped sourdoughs reported in the literature encompassing back-slopped sourdoughs that were starter culture-initiated [extended version of that reported in De Vuyst et al. (2017)]. Therefore, back-slopped sourdoughs with a DY of maximally 200, a fermentation temperature of maximally 30 °C, and a fermentation time of 24 h or less were defined as Type I sourdoughs, whereas sourdoughs with a DY above 200, a fermentation temperature higher than 30 °C and a fermentation time of 24 h or more, were defined as Type II. Type III sourdoughs were not classified separately, but considered as Type II, according to the process conditions used for fermentation. Most sourdoughs reported in the literature were, according to these criteria, classified as Type I sourdoughs (77%), whereas 10% was classified as Type II sourdoughs. The remainder could not be classified because of lack of data. All these sourdoughs were considered mature. On average, Type I sourdoughs had a pH of 4.0 ± 0.4 , whereas Type II sourdoughs had a pH of 3.7 ± 0.3 , confirming a pH value of 4.0 as a pivotal pH for sourdough fermentation (Van Kerrebroeck, Bastos, Harth, & De Vuyst, 2016).

3. Microbial species diversity of back-slopped sourdoughs

3.1. The number of microbial species in a given sourdough is limited

Based on the meta-analysis of the 583 back-slopped sourdoughs, the number of prevalent LAB species in a given sourdough was higher than that of prevalent yeast species, averaging a number of 2.0 effective LAB species and 1.3 effective yeast species per sourdough (Fig. 1). This could indicate a high competition and a lack of non-competitive associations among yeast species (Ciani et al., 2016; Wang, Mas, & Esteve-Zarzoso, 2016). The skewed distributions of three indices [species richness, effective number of species associated with the Shannon diversity index $\exp(H')$, and Simpson dominance (1/D) of prevalent LAB and yeast species] indicated a difference in LAB and yeast species diversity between the sourdough types (Fig. 1). The prevalent LAB species actually reflected the classification of sourdoughs into Type I and Type II sourdoughs, a classification based on the process technology applied (Gänzle & Ripari, 2016; Hammes et al., 2005; Huys et al., 2013). Hence, a higher maximal number of both LAB and yeast species occurred in certain Type I sourdoughs. This reflected the generally lower LAB species diversity of liquid sourdoughs compared to firm sourdoughs (Di Cagno et al., 2014), possibly as a consequence of spatial gradients in the latter ones (Ampe, ben Omar, Moizan, Wacher, & Guyot, 1999).

The convergence toward a limited number of prevalent LAB species was typical for Type I sourdoughs, whereas variability in the number of prevalent LAB species was seen for Type II sourdoughs. This difference could be attributed to the convergence toward a prevalence of *Lb. sanfranciscensis* in Type I sourdoughs, which impacted the data of the species distribution of the other LAB species. Indeed, Type I sourdoughs harboring *Lb. sanfranciscensis* were characterized by a lower prevalent LAB species diversity than sourdoughs lacking *Lb. sanfranciscensis*, as indicated by the lower median and average number of prevalent LAB species for the former sourdoughs (Fig. 1). When only Type I sourdoughs in which this LAB species did not occur were taken into account, the median and average effective number of LAB species were comparable for both Type I and Type II sourdoughs. This indicates the competitiveness and prevalence of *Lb. sanfranciscensis* as a characteristic LAB species in sourdoughs, provided the process conditions are suited for its growth and metabolic activity (De Vuyst et al., 2014;

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