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Enzymatic and bacterial conversions during sourdough fermentation

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ABSTRACT

Enzymatic and microbial conversion of flour components during bread making determines bread quality. Metabolism of sourdough microbiota and the activity of cereal enzymes are interdependent. Acidification, oxygen consumption, and thiols accumulation by microbial metabolism modulate the activity of cereal enzymes. In turn, cereal enzymes provide substrates for bacterial growth. This review highlights the role of cereal enzymes and the metabolism of lactic acid bacteria in conversion of carbohydrates, proteins, phenolic compounds and lipids.

Heterofermentative lactic acid bacteria prevailing in wheat and rye sourdoughs preferentially metabolise sucrose and maltose; the latter is released by cereal enzymes during fermentation. Sucrose supports formation of acetate by heterofermentative lactobacilli, and the formation of exopolysaccharides. The release of maltose and glucose by cereal enzymes during fermentation determines the exopolysaccharide yield in sourdough fermentations.

Proteolysis is dependent on cereal proteases. Peptidase activities of sourdough lactic acid bacteria determine the accumulation of (bioactive) peptides, amino acids, and amino acid metabolites in dough and bread.

Enzymatic conversion and microbial metabolism of phenolic compounds is relevant in sorghum and millet containing high levels of phenolic compounds. The presence of phenolic compounds with antimicrobial activity in sorghum selects for fermentation microbiota that are resistant to the phenolic compounds.

1. Introduction

Sourdough has traditionally been used as leavening agent in bread making. The use as leavening agent continues in artisanal baking and for production of specialty products; the resulting bread has an otherwise irreproducible quality. Few bakeries employ sourdough as leaving agent at an industrial scale. The industrial use of sourdough predominantly primarily aims to improve bread quality, and to replace additives. This shift of the technological aims resulted in the development of novel fermentation technologies and starter cultures with defined metabolic properties (Gobbetti and Gänzle, 2007; Brandt, 2007). The use of sourdough in bread making influences all aspects of bread quality. The technological effects of sourdough on the flavour, texture, shelf-life, and nutritional quality of bread are dependent on bioconversion of flour components at the dough stage (Table 1). Two main factors differentiate sourdough processes from straight dough processes. First, the presence of lactic acid bacteria adds the metabolic potential of this heterogeneous group of organisms to the metabolic potential of yeasts (Decock and Capelle, 2005; De Vuyst and Neysens, 2005). Second, the fermentation time of sourdough processes ranges from 8 h (sponge doughs) to over 144 h (Brandt, 2007). This long fermentation time compared to straight dough processes allows for a substantial contribution of endogenous enzymes to biochemical conversions at the dough stage.

The metabolism of sourdough microbiota and the activity of cereal enzymes are interdependent. Acidification modulates the activity of cereal enzymes and the solubility of substrates, particularly gluten proteins and phytate. Sourdough fermentations are generally dominated by obligately heterofermentative lactic acid bacteria (De Vuyst and Neysens, 2005). Carbohydrate metabolism in the phosphate pentose pathway generates an abundant supply of reduced co-factors. Heterofermentative lactobacilli use a wide array of dough constituents as electron acceptors to regenerate these reduced co-factors (Gänzle et al., 2007). Heterolactic metabolism thus influences enzyme activities by decreasing the oxidation–reduction potential of sourdoughs, and by accumulation of low-molecular weight thiol compounds (Jänsch et al., 2007; Capuani et al., 2012). Cereal enzymes, in turn, provide substrates for bacterial growth (Hammes and Gänzle, 1998). *Lactobacillus*

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Table 1
Overview on the role of microbial and enzymatic conversions during sourdough fermentation in microbial physiology, and their contribution to bread quality.

Role in microbial physiology	Contribution to bread quality
Carbohydrate conversion and metabolism	
Metabolic energy (maltose, sucrose)	Texture (starch)
Cofactor regeneration (fructose)	Water binding, staling (starch, pentosans, EPS)
Protection against environmental insults (oligosaccharides, exopolysaccharides)	Taste and shelf life (organic acids)
Biofilm formation (exopolysaccharides)	Generation of reducing sugars for flavour generation during baking
	Dietary fibre and prebiotic oligosaccharides
Protein conversion and metabolism	
Nitrogen source	Volume (gluten)
Metabolic energy (alanine)	Taste and flavour (glutamate, ornithine, other amino acids)
Acid resistance (Gln, Glu, Arg)	Bioactive compounds (γ-aminobutyrate)
Cofactor regeneration (Glu, glutathione); and protection against oxidative stress (Cys)	Bioactive peptides (taste-active, ACE-inhibitory)
Conversion of phenolic compounds	
Metabolic energy (hydrolysis of flavonoid hexosides)	Elimination of anti-nutritive factors (enzyme inhibitors)
Removal of noxious compounds	Elimination of bitter taste (tannins)
	Increased bioavailability of phenolics as antioxidants
	Flavour volatiles
Lipid metabolism	
Metabolic energy (cofactor regeneration)	Control of lipid oxidation (taste, flavour)
Membrane homeostasis (synthesis of unsaturated and hydroxy fatty acids)	Formation of antifungal compounds

sanfranciscensis, a key species in sourdoughs, has the smallest genome described in lactobacilli. The species has particularly abandoned the synthesis of extracellular hydrolytic enzymes and relies on substrate-derived enzymes (Vogel et al., 2011).

The use of sourdough has focused on wheat and rye baking (De Vuyst and Neysens, 2005). Wheat and rye sourdoughs do not exhibit characteristic differences in fermentation microbiota or their metabolic activity (De Vuyst and Neysens, 2005; Gänzle et al., 2007). Non-conventional substrates have recently been used for sourdough fermentations in gluten-free baking (Moroni et al., 2009). These substrates overlap with traditional fermentations in tropical climates (Nout, 2009). Studies on the microbial ecology of conventional and gluten-free sourdoughs demonstrated that the cereal substrate and substrate-derived enzymatic activities are key determinants of the microbial ecology of sourdough (Hammes and Gänzle, 1998; Vogelmann et al., 2009; Sekwati-Monang et al., 2012).

This review aims to provide an overview on microbial and enzymatic conversions in sourdough. Emphasis is placed on wheat and rye; information related to non-conventional substrates is provided where available. The carbohydrate metabolism of heterofermentative lactic acid bacteria, proteolysis in sourdough, and exopolysaccharide synthesis were subject of recent reviews (Gänzle et al., 2007; Gänzle et al., 2008; Galle and Arendt, 2013) and are discussed only briefly. Moreover, the review emphasises metabolism of lactic acid bacteria as the microbial group that differentiates sourdough from straight dough processes. For information on yeast metabolism, the reader is referred to a recent review provided by Guerzoni et al. (2013).

2. Starch and carbohydrate metabolism

2.1. Starch degradation and metabolism

Wheat and rye contain about 60–70% starch. Starch is the major determinant of the crumb structure of bread and amylopectin retrogradation is the major cause for the staling of bread (Table 1). Starch degradation at the dough stage is the predominant source of fermentable carbohydrates and reducing sugars (Table 1). The concentration of fermentable carbohydrates in wheat and rye flours is relatively low. Sucrose and raffinose are present in concentrations of 0.6–1.8% and 0.1–0.4%, respectively. Other mono- and disaccharides are essentially absent unless the grains germinated (Brandt, 2006; Belitz et al., 2004). Resting grains of wheat and rye contain α-amylase, β-amylase, and glucoamylase activities (Fig. 1A, Belitz et al., 2004; Brandt, 2006). The amylase activity of rye flour was sufficient to attain substantial starch degradation during baking (Neumann et al., 2006). Starch degradation in rye baking is further favoured by the proximity of the temperature optimum of rye amylase (50–52 °C) and the gelatinization temperature of rye starch (55–68 °C). Heating of the crumb to 100 °C during baking traverses the temperature range of 55–68 °C where active amylase and gelatinized starch co-exist, leading to rapid starch degradation. In flour with high amylase activity, this starch hydrolysis during baking crumb results in substantial damage and rye baking thus necessitated acidification to inhibit of endogenous amylases. However, the amylase activity of rye flours decreased over the last three decades, corresponding to higher falling numbers. Accordingly, the use of sourdough fermentation in rye baking to inhibit amylases is no longer a necessity (Neumann et al., 2006).

Amylase activities in wheat and rye sourdough liberate maltodextrins, maltose, and glucose during fermentation (Röcken and Voysey, 1995; Brandt, 2006). In simulated sourdough fermentations without microbial activity, maltose accumulates at the initial stage of fermentation. After reduction of the pH of 4.5, maltogenic amylases are inhibited but glucoamylase continues to release glucose from starch and maltodextrins (Röcken and Voysey, 1995; Brandt, 2006). In keeping with the availability of maltose as main carbon source in wheat and rye sourdoughs, key sourdough lactobacilli, including *L. sanfranciscensis*, *Lactobacillus fermentum*, and *Lactobacillis reuteri*, are highly adapted to maltose (Fig. 1A, for review, see Gobbetti et al., 2005; Gänzle et al., 2007). In *L. sanfranciscensis*, maltose phosphorylase is constitutively expressed. Maltose metabolism is preferred over metabolism of other carbon sources, or occurs simultaneously (Stolz et al., 1993; Ehrmann and Vogel, 1998; Gobbetti et al., 2005). Maltose phosphorylase is highly specific for maltose; most sourdough lactobacilli including *L. sanfranciscensis* and *L. reuteri* additionally harbour DexB, a glucosidase hydrolysing α(1→6)-linked gluco-oligosaccharides (Vogel et al., 2011; Møller et al., 2012). The contribution of DexB to carbohydrate conversion during sourdough fermentation is unknown. The widespread distribution of DexB in genomes of lactobacilli, however, implies an essential role in carbohydrate metabolism of cereal-associated lactobacilli (Gänzle and Follador, 2012).