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Review

Sourdough improves the quality of whole-wheat flour products: Mechanisms and challenges—A review

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ABSTRACT

Increasing the intake of whole-wheat flour (WWF) products is one of the methods to promote health. Sourdough fermentation is increasingly being used in improving the quality of WWF products. This review aims to analyze the effect of sourdough fermentation on WWF products. The effects of sourdough on bran particles, starch, and gluten, as well as the rheology, antinutritional factors, and flavor components in WWF dough/products are comprehensively reviewed. Meanwhile, sourdough fermentation technology has a promising future in reducing anti-nutritional factors and toxic and harmful substances in WFF products. Finally, researchers are encouraged to focus on the efficient strain screening and metabolic pathway control of sourdough for WWF products, as well as the use of bran pre-fermentation and integrated biotechnology to improve the quality of whole-wheat products. This review provides a comprehensive understanding of the effect of sourdough fermentation technology on wholemeal products to promote WWF production.

1. Introduction

Recent evidence suggests that increased intake of whole grains, such as wheat flour products containing bran, helps reduce the incidence of type 2 diabetes, chronic diseases, cardiovascular diseases, and intestinal diseases (Adams et al., 2020; Hu et al., 2020; Reynolds et al., 2020). Compared with refined wheat flour, whole-wheat flour (WWF) contains higher levels of vitamins, minerals, dietary fiber (non-starch polysaccharides), antioxidants, and other phytochemicals such as carotenoids, flavonoids, and phenolic acids (Gómez et al., 2020; Tebben et al., 2018). WWF provides non-starch polysaccharides and can deliver various micronutrients and phytochemicals associated with bran into the diet (Chris & Frank, 2018).

However, informing consumers of the health benefits of whole-grain products and then recommending an increase in their dietary intake is a compromise. For most of human history, flour has been produced in stone mills, which grind and crush small grains of wheat in a single mill to produce 100% WWF (Cappelli et al., 2020). In the second half of the 19th century, the introduction of roller mills revolutionized the milling process, which set the trend of separating starchy endosperm, bran, and germ of wheat (Jones et al., 2015). Compared with refined flour products, whole-wheat products have specific sensory qualities, including their dark color, speckled appearance, coarse and hard texture, bitter/sour taste, malted note, and mustiness (Heiniö et al., 2016). The desire of consumers for sensory quality has led to the broader use of refined flour than of WWF (Chris & Frank, 2018). Therefore, how to make consumers accept the health benefits of WWF, together with an improved sensory evaluation of WWF products, has become a concern to cereal scientists, food scientists, and engineers worldwide.

Fermentation is the oldest known biological technology for the manufacture of wheat flour products; compared with unfermented products, fermented bread products have a larger specific volume, a softer and more elastic structure, and a longer shelf life. The use of sourdough as a leavening agent for food fermentation is considered the gold standard (Gobbetti & Gänzle, 2012). The use of sourdough has a wide range of implications for improving the flavor, structure, and stability of baked goods. Compared with pure yeast, sourdough with lactic acid bacteria (LAB) as the dominant microbial flora has drawn research interest for improving the overall quality of WWF products (Gänzle & Zheng, 2019; Karaman et al., 2018). In whole-wheat sourdough bread, the synergistic effects of various organic acids, pH reduction, and enzymes during sourdough fermentation also cause hydrolysis and the

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solubilization of large molecules in WWF (e.g., gluten proteins, non-starch polysaccharides, and cell wall polysaccharides). The increase in free amino acids and the production of flavor substance precursors are among the reasons for the improvement in product flavor; the hydrolysis of polysaccharides can improve the rheological quality of whole-wheat dough and the texture of the product (Heiniö et al., 2016; Pei et al., 2020; Su et al., 2019). In addition, sourdough fermentation positively improves the nutritional quality of whole-wheat products by delaying starch digestibility, which leads to low glycemic response; increasing protein digestibility, which regulates the level and bioaccessibility of bioactive compounds; and improving the bioavailability of mineral substances (Gong et al., 2020; Montemurro et al., 2019; Siepmann et al., 2018). Sourdough fermentation increases the type and/or amount of beneficial microorganisms in whole wheat products; the intake of sourdough fermented foods allows these rich microorganisms, along with dietary fiber, to enter the intestine, replenishing the number and diversity of intestinal microbial flora (Ayua et al., 2020; Gong et al., 2018), which may benefit human health. Habitual consumption of whole-wheat sourdough bread helps reduce the risk of coronary heart disease, diabetes, and cancer (Capurso & Capurso, 2020).

This review aims to present new information on the improvement of texture and flavor of whole-wheat products via sourdough fermentation in recent years. The wide use of sourdough fermentation in addressing the challenges faced by whole-wheat products (mainly flour products

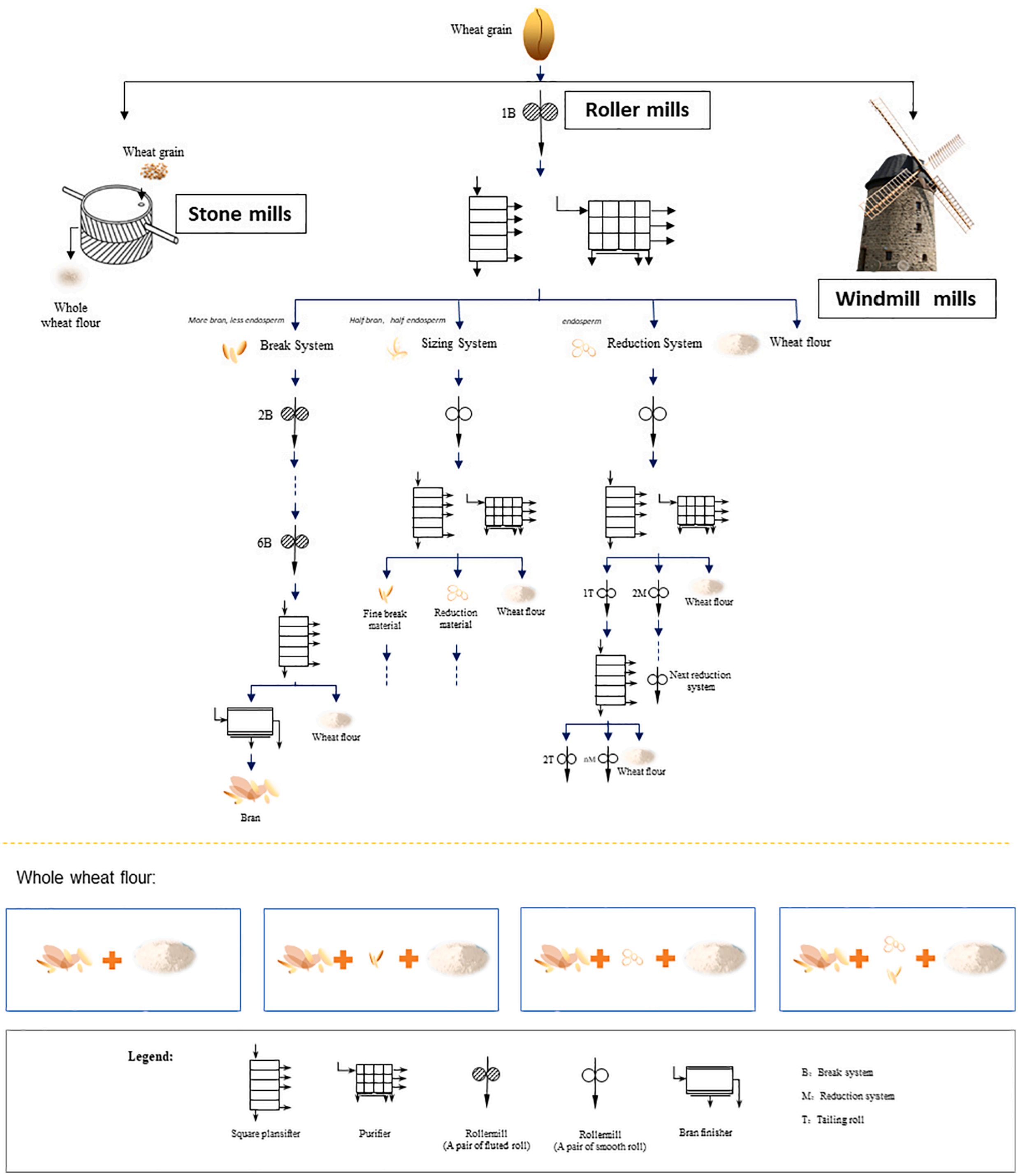

Fig. 1. Production methods of whole wheat flour.

that require fermentation) is described. The specific ways in which sourdough affects the rheological properties, nutritional properties, sensory properties, and shelf life extension of whole-wheat dough and WWF products are analyzed.

2. Whole grains, whole-wheat flour, and whole-wheat products

2.1. Whole grain definition: Evolution and development

The American Association of Cereal Chemists International (AACCI) originally proposed in 1999 that whole grain is composed of whole, ground, cracked, or peeled caryopsis, and its main anatomical components—the starch endosperm, germ, and bran—are similar in proportion to that of the whole caryopsis (AACC International, 1999). This definition was subsequently amended in 2008 to allow the inclusion of germinated and sprouted grains (AACC International, 2013). Based on the AACC definition of "whole grain," a modified definition of whole grains, which allows for small but unavoidable losses during processing, was proposed by the HEALTHGRAIN Forum in 2009 and 2014 (van der Kamp et al., 2014). The scope of the definition of "whole grains" and "whole grain foods" was also discussed in detail at the 2015 Whole Grains Summit. Moreover, the formation of a working group to discuss the definition of whole grains was recommended (Korczak et al., 2016). The 2017 HEALTHGRAIN Forum presented a complementary definition of "whole-grain foods" (Ross et al., 2017), proposing that foods be labeled as whole grains on the front of the food package if they contain more than 30% of the total weight of whole grains and if the whole grains exceed the refined grains.

2.2. Whole-wheat flour and whole-wheat products

Whole-wheat products are food products that are processed using WWF. WWF is usually distinguished from commercially available refined wheat flour. Unlike refined wheat flour, which provides almost exclusively carbohydrates and protein, WWF contains a broader range of beneficial nutritional components, including fiber, minerals, vitamins, and bioactive compounds, and even higher quality protein (from the aleurone layer). The criteria for defining WWF still meet all requirements of whole grains (Section 2.1). Meanwhile, the technical specifications for WWF have not been standardized because WWF production depends on the legal requirements of each country and region and the wheat processing methods used by each plant (Fig. 1). The *Whole Grain Initiative* (2020) has been recognized by the ICC, the HEALTHGRAIN Forum, and the Cereals & Grains Association. Notably, the support in this statement for the continued definition of germinated grains and fermented fractions by AACCI (e.g., wheat bran).

However, some cereal scientists have noted that wheat germ has a high fat content and enzymatic activity, leading to reduced shelf life of whole wheat flour; therefore, perhaps it is challenging to produce WWF of the expected quality using modern wheat milling process. Germ includes rich enzymatic and fatty components, and germ-containing WWF has a relatively high risk of rancidity and a considerably short shelf life. Therefore, the product obtained from this process is often flour with recycled bran, referred to as "unrefined wheat flour" (Parenti et al., 2020). Further discussions need to be conducted on whether a global definition of WWF is to be standardized to support the development of dietary recommendations and the implementation of labeling standards.

2.3. Challenges for whole-wheat products

In contrast to refined wheat flour, WWF contains complete wheat bran, particularly the nutrient-rich aleurone layer. Despite the nutritional benefits, the introduction of milling by-products in breadmaking has several disadvantages, and the solution remains a challenge for bread makers. First, poor-quality wheat kernels and kernels that have suffered from pests and diseases (e.g., head blight, etc.) are commonly produced with high levels of harmful bacterial and fungal toxins and contaminants, such as pesticide residues and heavy metals. Second, bran negatively affects the technical quality of sponge doughs, breads, and Chinese steamed breads because of the presence of numerous insoluble polysaccharides in bran and the physical structure of bran particles affecting the gluten network, the gluten–starch system, and the formation of air chambers (Hemdane et al., 2016; Ma et al., 2018). Many studies have discussed the influence of bran on the rheological properties of the dough, which further affect the texture of the product (Bondt et al., 2020; Li, Liu et al., 2017; Onipe et al., 2015). Bran limits the ability of gluten and starch to form a stable rheological system during processing via physical potential resistance and water absorption properties. This process involves the insoluble dietary fiber in the bran (Han et al., 2018). Moreover, bran always has a natural yellow or brown color, which influences the color of WWF and whole-wheat products. The appearance of these colors may be attributable to lignin and pigments. The color observed in bread and the distinct aroma of the crust are attributed to browning caused by the Maillard reaction. The color change brought about by bran is perceived differently by consumers. Owing to cultural differences, consumers in Asia often perceive white color as desirable and preferable. This view is also reflected in food, where the accumulation of pigment in bran results in a darkened color, as in the case of Chinese steamed bread (Ma et al., 2018). Such a change in color reduces the consumer acceptability of products. Finally, antinutritional factors (ANFs) such as phytic acid are significantly higher in WWF than in refined flour, which may cause impaired mineral absorption in people who regularly consume WWF products (Nsogning et al., 2018). In conclusion, the chemical composition of WWF products differs from that of refined flour products, and the complexity of the WWF composition is the most important factor that contributes to the inconsistent quality of WWF products. Therefore, some technologies have to be urgently adopted to overcome the disadvantages of WWF products. Sourdough fermentation may be the most promising treatment (Boukid et al., 2018).

3. Sourdough fermentation is used to enhance the quality of whole-wheat products

3.1. Sourdough and sourdough fermentation

Sourdough fermentation is the oldest biotechnology mastered for the manufacture of pasta products. Fermented wheat flour products are the primary means to meet future challenges in food production (Weegels, 2019; Zhu, 2016). Rapid fermentation using only commercial yeast is currently the most common technique in bread production. However, the use of dough fermented for more than 100 years is still the technique applied by some traditional bakeries (Gobbetti & Gänzle, 2012). Depending on the type of fermentation and the process used, sourdough can be divided into four categories: Type I in which sourdough fermentation occurs spontaneously using the yeast and LAB in the flour; Type II in which sourdough fermentation occurs after precise inoculation with an appropriate proportion of the leavening agent; Type III, which is the dehydrated form of Type II, and Type IV, which is a mixture of Type I and Type II and is currently produced only on a laboratory scale (Corsetti & Settanni, 2007; de Vuyst & Neysens, 2005). In China, traditional leavening agents include *Laomian*, *Jiaozi*, and *Jiuqu/Quzi* (Yan et al., 2019). Chinese steamed bread is also produced by the natural fermentation of wheat flour, which is similar to a type of sourdough. *Jiaozi* and *Jiuqu* may also be prepared by adding corn flour. All microbiological, biochemical, and/or technological features are found in typical/traditional fermented foods distributed in 47 countries and all continents (excluding Antarctica) (Fig. 2). Owing to their long experience and cultural heritage in using sourdough, Italy and France have an advantage in sourdough bakery products. Other sourdough products mainly include European traditional rye bread, Iranian Barbari, Chinese steamed bread, Indian Bhatura and Kulcha, African Egyptian Balady,

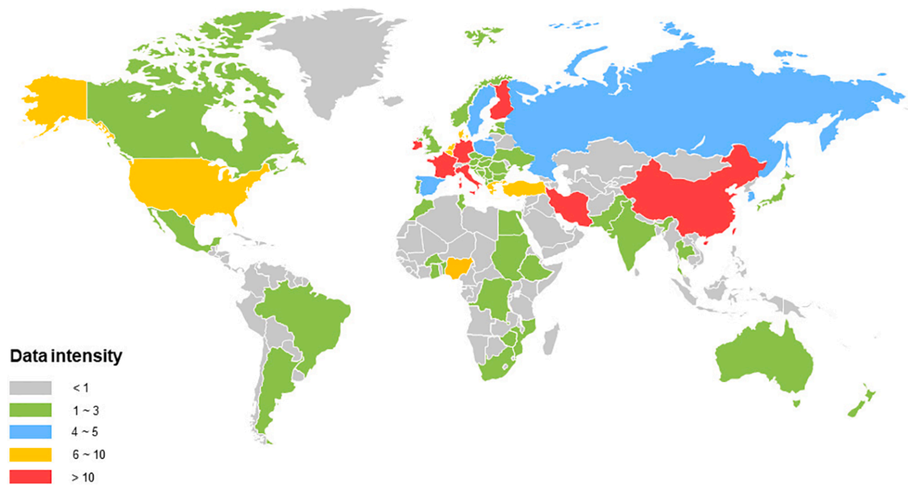

Fig. 2. The worldwide data intensity of sourdough reported over the past 30 years. Refer to Arora et al. (2021) and make some modifications.

Apprehenra and Ethiopian Injera, and tortillas, among others (Arora et al., 2021). Sourdough has a complex composition of fermentation organisms; however, if continuously colonized (greater than10 times) in the same area over a long period, sourdough generally exhibits a stable microbial community structure (Li, Li et al., 2017; Ripari, Gänzle, et al., 2016). The most common LAB species include *Lactobacillus sanfranciscensis* (heterofermentative), *Lactobacillus plantarum* (homofermentative), *Lactobacillus brevis* (heterofermentative), *Pediococcus pentosaceus* (homofermentation), *Lactobacillus paralimentarius*, and *Saccharomyces cerevisiae*. A wide variety of lactic acid bacteria has been isolated from sourdoughs, but only several *Lactobacillus* species are highly adapted to the sourdough environment—*L. sanfranciscensis*, *L. plantarum*, *L. pontis* (heterofermentative) and *L. rossiae* (heterofermentative) (Corsetti et al., 2005; Gänzle et al., 2008; Vogel et al., 1999). Secondary communities include other LAB species, such as *Lactobacillus reuteri*, species of *Leuconostoc* and *Weissella,* and other yeast species of the *Kazachstania* clade (Gänzle & Ripari, 2016; Siepmann et al., 2018; Weckx et al., 2019).

3.2. Effect of sourdough fermentation on main macromolecules in whole-wheat dough

First, sourdough fermentation is practically an effective method to consistently increase the bran content without negatively affecting product quality in whole-grain baked goods (Pontonio et al., 2020). Sourdough fermentation improves the characteristics of bran and the nutritional properties of bread containing bran; the technique also has the potential to inhibit the lipase activity of grain germ (Rizzello et al., 2010). Water-extractable arabinoxylan is a good hydrocolloid that can significantly improve dough properties. Owing to xylanase activation, sourdough fermentation maximizes the dissolution of water-unextractable arabinoxylan in the bran into water-extractable arabinoxylan (Ma et al., 2018; Nikinmaa et al., 2019). Second, sourdough fermentation leads to the swelling of starch granules and straight-chain starch melting (Nordlund et al., 2016). Some polyols contribute to the maintenance of healthy intestinal microbial flora (de Toro-Martín et al., 2017). The production of different sugars seems to be related to the type of fermentation of LAB. The monosaccharides (glucose and fructose), maltose/sucrose, isomaltose, and dextrin have been detected in homofermentative fermentation strains, whereas maltose/sucrose, isomaltose, and dextrin have been found in fermentations with heterofermentative fermentation strains (Lancetti et al., 2020).

Meanwhile, the hydrolytic effect of sourdough on gluten has continuously drawn attention. Sourdough exhibits proteolytic activity to sustain the growth of yeast flora. Thus, most yeast LAB carry intracellular peptidases but not extracellular proteases (Zheng et al., 2015). As previously mentioned, sourdough fermentation prompts a decrease in pH in the system, which may solubilize gluten proteins and enhance endogenous wheat protease activity via intramolecular electrostatic repulsion (Katina et al., 2006). The possible reason is that LAB synergistically interact with the lowered pH to first depolymerize the gluten macromolecular polymer into fibrous and laminar microstructures (Nutter et al., 2019). Endogenous protease then converts fibrous and lamellar proteins to free amino acids. Higher fermentation temperature, higher enzyme activity and longer fermentation time during sourdough fermentation may be the key factors to promote protein hydrolysis (Heiniö et al., 2016). The role of thiol accumulation should not be overlooked; heterofermentative LAB (e.g. *Lactobacillus sanfrancisco*) can reduce extracellular oxidized glutathione to glutathione by expressing glutathione reductase; glutathione undergoes thiol exchange reactions with gluten proteins and then reduces intermolecular disulfide bond cross-linking, thereby decreasing the GMP molecular weight (Gänzle et al., 2008; Vermeulen et al., 2006). Other studies also found that LAB induce changes in the secondary structure of gluten protein. Each LAB strain induces distinct changes in the protein structure, and the development of a protofibril network is associated with antiparallel β-sheets (Nutter et al., 2019; Siepmann et al., 2019). Specifically, gluten proteins undergo different degrees of depolymerization to form specific microstructures, such as fibrous networks and lamellar structures, and their appearance is associated with an increase in β-sheet structures. Nutter et al. (2019) suggested that these changes depend on the unique acidification kinetics of each strain: L. fermentum and L. plantarum improve the arrangement of the fermented gluten proteins in lamellar structures, and both are dominated by parallel β-sheet conformations. *L. delbrueckii* subsp. *bulgaricus* and *P. pentosaceus* were predominant in promoting the development of a three-dimensional fiber network accompanied by an increase in antiparallel β-sheets. Changes in the secondary structure of gluten proteins may influence the rheological properties of the dough and consequently, the quality of the dough product. Pure culture in a recent study also showed that LAB fermentation hydrolyzes gliadin in gluten and that after sourdough fermentation for 72 h, all wheat alcohol proteins are broken down (Fraberger et al., 2020) (Fig. 3).

3.3. Effects of sourdough fermentation on the rheology and texture properties of whole-wheat dough

The negative effects of bran and germ addition on the rheological properties of the dough and the resulting bread characteristics have been widely reported in the literature; (Cappelli et al., 2018; Ishwarya et al.,

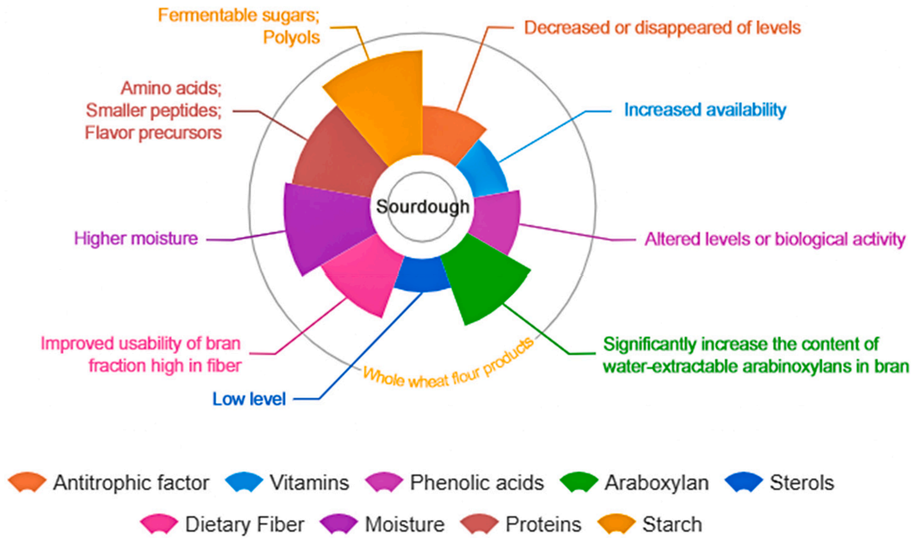

Fig. 3. Effect of sourdough dough fermentation on macromolecular nutrients in whole wheat dough.

2017; Packkia-Doss et al., 2019). The rheological properties of dough are influenced by the method used in the treatment of whole grains. High levels of insoluble dietary fiber, water-unextractable arabinoxylans, and bran granules in WWF have been proved to contribute to dough deterioration via different mechanisms: i) diluting gluten proteins and starch; ii) competing with proteins for water during gluten network formation, resulting in insufficient hydration of gluten proteins and starch; iii) formation of a physical barrier to gluten network formation (spatial barrier effect) by water-insoluble non-starch polysaccharides; iv) reduction in the mass of the gas chamber during fermentation and acceleration of CO_2 gas escape by a spatial barrier effect; and v) formation of dough with stiffer texture, lower recovery and viscoelasticity, and lower tensile strength (Han et al., 2019a, 2019b; Heiniö et al., 2016; Liu, Ma et al., 2020).

Improvement of whole-wheat dough rheology by sourdough targets various properties mainly related to texture (firmness, adhesion, resilience, cohesiveness, chewiness, elasticity, and gumminess, etc.). Specifically for end products, the targeted characteristics are shape, specific volume, the color of crust and crumb, moisture retention, and crumb structure. In general, hardness, gumminess, and chewiness are negatively correlated with bread quality but positively correlated with elasticity and cohesiveness (Sun et al., 2020). The outer layer of wheat is rich in dietary fiber, phytochemicals, minerals, and endogenous enzymes. Therefore, bran flakes offer various possibilities for modification by sourdough fermentation. Sourdough fermentation can partly offset the elevated energy storage modulus (G') and loss modulus (G'') that occur during whole-wheat dough production (Alioğlu et al., 2020); the hardness of the dough is reduced, and the tensile strength and ductility of the dough are increased (Sun et al., 2020). The production of organic acids during sourdough fermentation is potentially one of the most important effects, particularly the fermentation quotient (FQ, the ratio of acetic acid to lactic acid); acetic acid further hardens gluten, while lactic acid contributes to elasticity in gluten (Corsetti & Settanni, 2007; Oshiro et al., 2021). As mentioned earlier, the production of acetic and lactic acids in sourdough by LAB leads to the proteolytic degradation of gluten and moderate hydrolysis of starch, resulting in reduced pH. The presence of a more acidic medium leads to gluten proteolysis and increased solubility. The increase in intramolecular forces leads to protein unfolding, increasing the exposure of their hydrophobic portions. Consequently, large protein aggregates undergo proteolytic hydrolysis, producing more stable and less elastic emulsions with improved extensibility. The rheological properties of the final dough depend on the concentration of the yeast dough used as a leavening agent and the extension of gluten during fermentation (Siepmann et al., 2018). In addition, the selection of the bacterial strain in sourdough fermentation is also an important factor affecting the texture of the product. *L. plantarum* is selected because it can confer significant decreases and increases in the hardness, viscoelasticity, and cohesiveness of whole-wheat bread (Sun et al., 2020), helping produce a fresher, softer, more refreshing, and more consumer-friendly whole-wheat product. The beneficial effects of strains capable of producing extracellular polysaccharides (EPS), such as *Lactobacillus amylovora*, *Lactobacillus. plantarum*, *Lactobacillus. brevis*, and *Leuconostoc* spp. and *Weissella* species in expected volume and hardness can produce extracellular polysaccharides (Lynch et al., 2018). The reason is that EPS can enhance the quality of the gluten network (Chen et al., 2016; Suo et al., 2021) (Fig. 4).

3.4. Sourdough fermentation reduces consumer concern about whole-wheat products

Whole-wheat products are highly recommended for health reasons, but the presence of antinutritional factors such as phytic acid (InsP6) in WWF hinders mineral absorption in the body, although whether phytic acid is beneficial or harmful has been inconclusive. Phytic acid possesses potentially valuable properties. It can help prevent diabetes and regulate blood sugar levels by absorbing starch and sugar from food. Phytic acid activity also influences cholesterol formation and fat digestion (Sakandar et al., 2019). The enzyme responsible for phytate hydrolysis is inositol hexakisphosphatase (inositol hexakisphosphate phosphate hydrolase; EC 3.1.3.8/EC 3.1.3.26), which sequentially releases soluble inorganic phosphate, lower inositol phosphate, and inositol. Sourdough fermentation of whole-wheat dough shows low pH, high phytase, amylase, and xylanase activities (Baye et al., 2013; Cizeikiene et al., 2020; García-Mantrana et al., 2016; Leenhardt et al., 2005). In the study by Karaman et al. (2018), phytase active yeast and LAB isolated from sourdough were identified as phytase-positive species by FTIR, 16sRNA, and 26sRNA; moreover, phytic acid content was significantly reduced in LAB and bread with added yeast cultures. Sakandar et al. (2019) demonstrated that sourdough fermentation was much more effective than yeast fermentation in reducing the phytic acid content in whole-wheat bread (−62% and −38%, respectively). Typically, the most appropriate level of acidification ranges from pH 4.3 to pH 4.6, where the phytic acid content is reduced by more than 70%, and minerals such as calcium, sodium, magnesium, iron, and zinc become bioavailable (Arora et al., 2021). Additionally, *L. plantarum* and *L. brevis* exhibited the

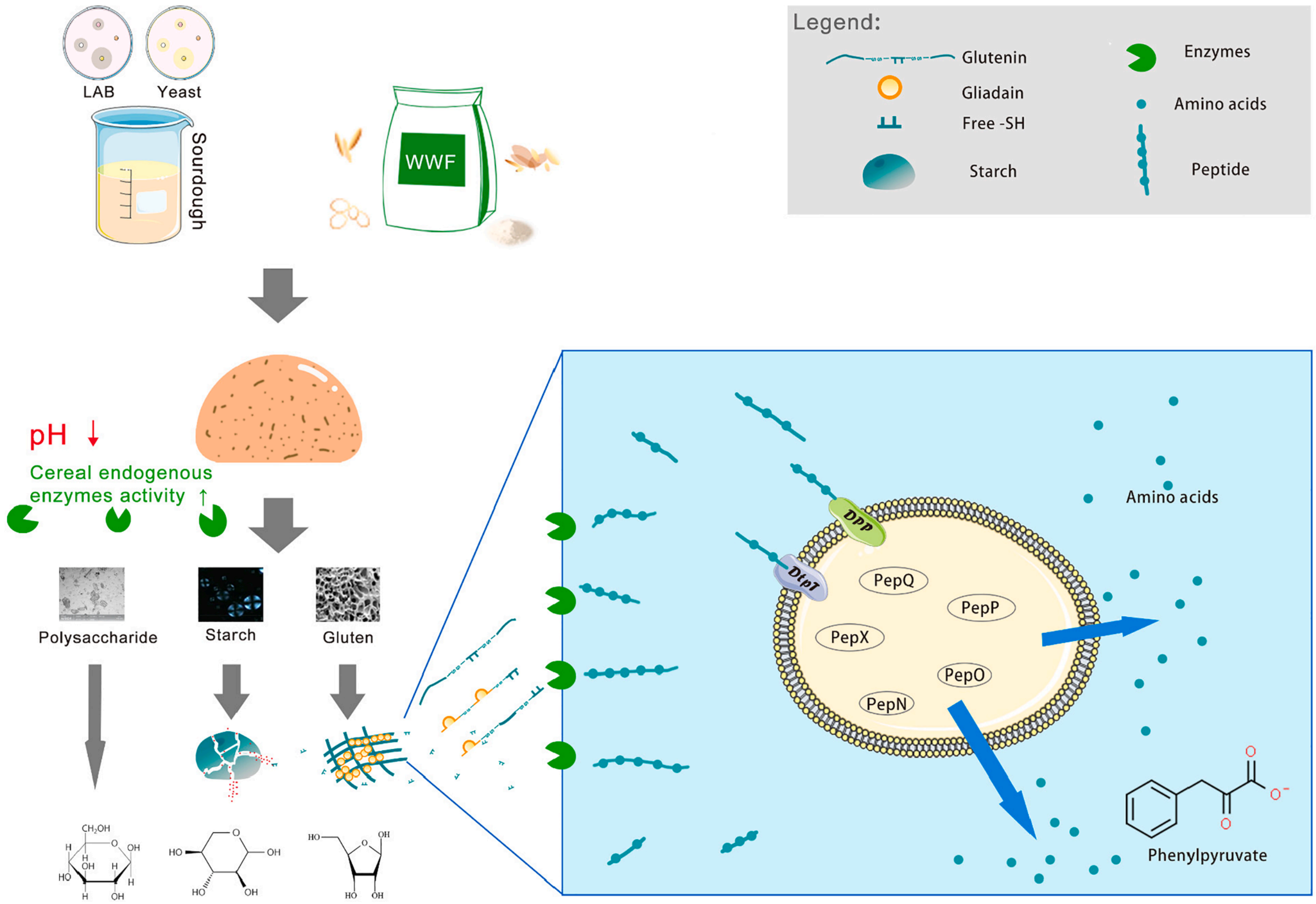

Fig. 4. Sourdough fermentation causes the hydrolysis of starch and protein in the dough.

highest phytase activity; the highest phytate degradation was observed in bread fermented at 25 °C (Yildirim & Arici, 2019). *Bifidobacteria* (specifically, *Bifidobacterium longum* and *Pseudobifidobacterium pseudobifidum*) also show high phytase activity (García-Mantrana et al., 2015; Palacios et al., 2008). Moreover, the maximum phytate reduction was determined in the culture combination of *S. cerevisiae* and *Pseudomonas pentose* (Karaman et al., 2018). However, whether the phytic acid degradation observed during sourdough fermentation is caused by phytase remains undetermined. A study concluded that increased levels of phytic acid, alkylresorcinol, and extractable phenolic acids (gallic, ferulic, vanillic, caffeic) do not seem to be attributable to LAB fermentation and phytase (Prückler et al., 2015). LAB in sourdough products and wild yeast in sourdough have been suggested to neutralize phytic acid, rendering yeast-based products more digestible (Hayta & Hendek Ertop, 2017). Despite inconclusive findings, the value of sourdough fermentation in reducing the disadvantages of phytic acid and increasing the bioavailability of minerals in whole-grain foods is emphasized.

In addition to phytic acid, raffinose, saponins, condensed tannins, and trypsin inhibitors are the main ANFs, the presence and content of which depend on the matrix (Arora et al., 2021). Raffinose is a predisposing factor for intestinal disorders, and condensed tannins and trypsin inhibitors suppress digestive enzymes, leading to the reduced digestibility of proteins and other nutrients. Although heat treatment completely deactivates trypsin inhibitors, heat resistance is exhibited by other ANFs, hence the need to apply other methods. In one study, acid fermentation of whole grains reduced the concentration of raffinose (62%–80%), tannin concentration (23%), trypsin inhibitors (23%–44%), and saponins (68%) (Montemurro et al., 2019). Combined pasteurization and yeast fermentation further reduced the residual concentrations of concentrated tannins (62%) and trypsin inhibitors (70%) (de Pasquale et al., 2020). Therefore, sourdough fermentation is the greenest, safest, and most sustainable alternative for degrading ANFs in whole-grain foods without adding exogenous substances.

Notably, some typical wheat diseases, such as wheat scab, have become a concern for farmers and scientists worldwide. Sick wheat is susceptible to bacterial and fungal infections and therefore faces the risk of excess fungal toxins. This poses a challenge for WWF, regardless of the process that led to fungal toxins. However, in addition to crop science and processing efforts to reduce mycotoxins, the use of sourdough fermentation in product preparation may help alleviate concerns about quality. In one study, a related strain of *Lactobacillus helveticus* FAM22155 was found to decompose aflatoxin B1 into four low-toxin organisms without a lactone ring structure during fermentation (Zhang et al., 2020). The judicious use of sourdough fermentation can be suitable in the degradation of aflatoxin B1 in wheat bran; the prerequisite is that the predominant LAB in the sourdough is identified to produce active enzymes against mycotoxins. The flour fractions of highly contaminated grain contain deoxynivalenol, *deoxynivalenol-3-glucoside*, and zearalenone. Strong mycotoxin removal can be achieved during long sourdough fermentation (Zadeike et al., 2020).

In addition, sourdough fermentation overcomes the increase in acrylamide that comes with baking bread; It is reported that some specific LABs (including *L. plantarum* PTCC 1896, *L. lactis* DSM 20017, *L. rhamnosus* DSM 20021, and *L. deuterium* DSM 20081) and yeast mixtures have this baking effect (Esfahani et al., 2017). The results showed that the acrylamide level in bread fermented with sourdough + yeast was considerably lower than that in pure yeast-fermented bread. Glucose metabolism and pH reduction are the most important indirect methods by which LAB can decrease acrylamide levels (Albedwawi et al., 2021). Meanwhile, yeast has shown a superior ability to remove acrylamide precursors (e.g., free asparagine) (Fredriksson et al., 2004). This result suggests that yeast fermentation with suitable LAB strains can be used to reduce acrylamide levels in whole-wheat bread. Sourdough fermentation also promotes the increase in antioxidant components in pasta products. LAB in sourdough (mainly *Lactobacillus plantarum*) is important for the release or production of antioxidant active substances, such as phenolics and active peptides (Fois et al., 2019; Muñoz et al., 2017; Ryu et al., 2019). Numerous types of lactobacilli enhance their intrinsic cellular antioxidant defenses by the secretion of antioxidant enzymes such as superoxide dismutase; meanwhile, some LAB promotes the reduction of oxidized glutathione to a monomer, a major non-enzymatic antioxidant, and a free radical scavenger (Gobbetti et al., 2019). Meanwhile, EPS produced by sourdough fermentation are other biomolecules synthesized by LAB that also exhibit antioxidant activity (Manini et al., 2016).

3.5. *Sourdough fermentation to improve the sensory quality of WWF products*

The sensory qualities of food are usually evaluated through the senses of sight, touch, taste, and smell. Whole-wheat products have a darker color, rougher texture, firmer texture, and a more complex flavor, compared with refined wheat products (Heiniö et al., 2016). Fermentation treatment effectively improves the specific volume and grain softness of wheat bran-enriched bread (Hemdane et al., 2016). Meanwhile, sourdough fermented WWF has demonstrated the potential for improving several unpleasant sensory properties (Prückler et al., 2015; Taccari et al., 2016). In a survey (Guerrini et al., 2019) conducted among bakers, the use of sourdough as a bulking agent for bread made from whole wheat was believed to improve the quality of the final product. Bread fortified with sourdough-fermented bran shows a higher specific volume, lower resilience, and cohesion, as well as higher firmness, gumminess, and chewiness than those of wheat bread made with baker's yeast (Pontonio et al., 2020a). Whole-wheat sourdough improved the quality of high-fiber bread quality and overcame the detrimental effect of bran on the specific volume of bread (Taccari et al., 2016). In addition, yeast fermentation improved the texture, flavor, nutritional value, and shelf life of bread; this study outlined the suitability of WWF for dough production, which encouraged further research on its application in the production of whole-wheat bread (Taccari et al., 2016). However, few studies have reported on improving the color of whole-wheat products by sourdough fermentation.

Traditionally used in processing WWF, sourdough fermentation is known to influence nutritional and sensory properties as well as stability. Flavor is one of the main factors determining the consumer acceptability of bread; thus, a large number of studies have been conducted to investigate the characteristics of volatile compounds in whole-wheat bread fermented with sourdough (Table 1). Recent studies have shown that sourdough produces far more compounds than pure yeast fermentation and that these organics significantly improve the quality, nutritional properties, and flavor of flour products (de Vuyst et al., 2016; Pételet al., 2017; Quattrini et al., 2019; Su et al., 2019). Volatile aroma compounds during sourdough fermentation are mainly derived from microbial and yeast metabolism, enzymatic or autoxidation of flour lipids, and Maillard reaction (Pételet al., 2017). Alterations in the flavor are mainly attributable to the following: i) intense protein hydrolysis in whole-wheat sourdough during prolonged fermentation due to the activation of cereal proteases at low pH, resulting in the production of amino acids; ii) release in whole-grain flour during fermentation of phenolic compounds; iii) more intense acidification in whole-grain flour than in refined flour; iv) synthesis of more flavor precursors and volatiles. In some studies, sensory analysis was applied to determine the effect of sourdough on bread flavor, whereas in others, isogenic strains with deletions in specific metabolic genes were used. Two approaches to sensory analysis are primarily used by researchers to determine the contribution of different LABs to the formation of flavor compounds: one is to start fermentation with a mixed or natural fermentor, characterize changes in both microorganisms and flavor compounds during fermentation, and finally identify the relationship between them by using statistical methods (e.g., correlation analysis) and the other is to start fermentation with a single-strain fermentor, determine the changes in the number of flavor compounds, and evaluate the correlation between them. The single-strain starting approach is more likely to exclude confounding factors and is therefore used more often in research (Liu, Li et al., 2020). In genetic research, studies have shown the effect of different species or strains of LAB on the formation of flavor compounds in dough and bread, in addition to the process by which sensory properties are conferred on breads (Axel et al., 2015; Francesca et al., 2019; Suo et al., 2021). Sourdough contains more aroma volatile compounds than pure yeast-fermented doughs. The main volatile aroma compounds are carboxylic acids, esters, alcohols, ketones, aldehydes, and heterocycles (Ripari, Cecchi, et al., 2016). In addition, the dominant volatile compounds produced by various processes of sourdough fermentation are often reported differently (Corona et al., 2016; Gänzle & Ripari, et al., 2016). LAB fermentation can also mask bitterness due to increased bran, which may be related to the degradation of phenolic acids and aldehydes (Prückler et al., 2015). Sourdough fermentation can also increase fruitiness (Spaggiari et al., 2020). However, excessive sourness and alcoholic taste are undesirable. Therefore, the use of yeast as a flavor enhancer requires carefully optimized fermentation conditions to provide moderate acidity and improved amino acid levels, as well as increased levels of certain volatile compounds to produce a balanced bread sensory profile.

Table 1
The flavor compounds involved in the sourdough fermentation process.

Type	Compounds	References
Alcohols	ethanol, methylpropanol, butanol, pentanol, propanol, hexanol, 2-butanol (tr), 2-hexanol, 3-methylbutanol, (E)-2-hexenol, heptanol, octanol (tr), 1-pentanol, 1-hexanol, 1-heptanol, 2-methylpentanol, 2-propen-1-ol, 2-methylbutanol, 1-octen-3-ol, 1-nonanol, 2-furanmethanol, 1,4-butanediol, 1-pentanol	Hansen & Schieberle, 2005; Pételet al., 2016; Saeed et al., 2017; Zhang et al., 2016
Aldehyde	hexanal, (E)-2-heptenal, acetaldehyde, benzaldehyde, nonanal, hexanal, (E)-2-octenal, (E)-2-nonenal, octanal, decanal, benzaldehyde, 3-methylbutanal	Pételet al., 2016; Zhang et al., 2019
Acid	octanoate, butanoic acid, formic acid, pentanoic acid, heptanoic acid, lactic acid	de Vuyst et al., 2017; Pételet al., 2016
Esters	ethyl acetate, ethyl lactate, ethyl propanoate, butyl acetate, 2-methylbutyl acetate, pentyl acetate, ethyl hexanoate, hexyl acetate, ethyl octanoate, 2-phenylethyl acetate, ethyl benzoate, ethyl decanoate, methyl salicylate, methyl acetate, γ-butyrolactone, γ-nonalactone	Cecchi & Ripari, 2018; Hansen & Schieberle, 2005; Martin-Garcia et al., 2021; Pételet al., 2016; Zhang et al., 2019
Others	3-methylhexana, phenol, 3-hydroxy-2-butanone, 2,3-butanedione, 6-methyl-5-hepten-2-one, 2-octanone, 2-pentylfurane	Martin-Garcia et al., 2021; Pételet al., 2016; Ripari et al., 2016; Zhang et al., 2016, 2019

3.6. *Potential of sourdough fermentation to enhance the shelf life of whole-wheat products*

Fungal contamination is a major cause of food spoilage. Consumers and factories expect food products to have a longer shelf life while reducing the addition of chemical preservatives. Numerous antifungal chemicals are used in the bread industry, such as propionate, and a large amount of revenue invested in these chemicals is not only unacceptable to consumers but also costs high. Sourdough bread is known to have a longer shelf life than that of sweet bread. The reason is that sourdough fermentation produces various types of antimicrobial compounds, such as acetic acid, which inhibit the growth of foodborne pathogens; mold caused by fungi is inhibited by antifungal agents (organic acids produced by LAB, *Lactobacillus royi*, etc.) (Sadeghi et al., 2019; Sakandar et al., 2019). The use of *Lactobacillus reuteri* isolates as protective leavening agents for whole-wheat yeast reduces phytate content and fungal mold in sourdough bread (Sadeghi et al., 2019). Another study showed that *L. plantarum* LB-1, F-3, and F-50 exhibited high antifungal activity among 20 tested LABs to extend the shelf life of flour products by 3–6 d (Sun et al., 2020). Moreover, acetic acid has the most significant and consistent antifungal activity, and the use of selected strains for yeast fermentation can produce acetic acid, potentially reducing the use of chemicals (Quattrini et al., 2019). Peptidase expression related to bioactive peptide formation and the conversion of free fatty acids to antifungal hydroxy fatty acids seem to be strain-specific features present in type I and type II acid dough (Black et al., 2013). Studies have constantly reported on possible antifungal properties exhibited by new LAB species, such as *Lactobacillus amylovorus* (Axel et al., 2015, 2016), *Lactobacillus paracasei* (Mantzourani et al., 2019), *Levilactobacillus hammesii* (Quattrini et al., 2019). Meanwhile, other metabolites of LAB with antifungal activity have been widely demonstrated, such as phenyl lactate, hydroxyphenyl lactate, benzoic acid, fatty acids, volatile compounds (e.g., diacetyl, acetoin), cyclic dipeptides, hydrogen peroxide, reuterin, and/or proteinaceous compounds (Salas et al., 2017; Crowley et al., 2013). Voulgari et al. (2010) have also found that extracellular antimicrobial substances were sensitive to protein hydrolases, suggesting that bacteriocins caused inhibitory activity. Numerous studies attribute the inhibitory effect on fungi to bacteriocins; however, bacteriocins are usually active only against closely related bacteria, and evidence that bacteriocins affects fungal growth is rarely reported. Most *in vitro* screening experiments for LAB antifungal activity have been performed using synthetic media such as the de Man, Rogosa, and Sharpe (MRS) agar media, but the isolation and purification of antimicrobial active substances have been a challenging task (Le Lay, 2016; Salas et al., 2017).

4. Strategies for improving sourdough-fermented whole-wheat products

4.1. Preferred strain of bacteria

The application of selected leavening agents for dough fermentation ensures stable LAB diversity and qualitative characteristics in the fermented dough. Probiotic properties and phytic acid degradation capacity have also been examined. Molecular characterization of yeast flora has been conducted. The use of yeast and bacterial combinations is recommended for sourdough preparation (Fekri et al., 2020). Co-culture of *L. plantarum* and *L. hammesii* enhances phenolic acid metabolism (Ripari et al., 2019). The application of selected starter cultures for sourdough propagation may ensure stable LAB diversity and defined properties of sourdough that affect quality (Cizeikiene et al., 2020). Screening of strains with high phytase and EPS production from cereal and non-cereal source LAB libraries as industrial fermentor cultures for whole-wheat product sourdough seems to be a feasible approach. Milanović et al., (2020) considered Lb. brevis LD66 and L. citreum PB220 as acceptable. Another study showed that the application of preferably thermophilic LAB (e.g., Lactobacillus delbrueckii ssp. Bulgaricus MI, L. rossiae GL14, and L. acidophilus DSM 20079) increased the porosity, elasticity, friability, and moisture content of whole-wheat bread but exerted no effect on the hardness and moisture content of whole-wheat bread (Cizeikiene et al., 2020). Screening of strains with high antimicrobial capacity, such as *Aspergillus* and *Eurotium* species, by *in vitro* and *in situ* techniques were the most dominant and resistant (Le Lay et al., 2016). Meanwhile, compounds with enhanced volatility can be obtained by using strains (Lancetti et al., 2020).

4.2. Focus on carbohydrate metabolism in the bran fraction during sourdough fermentation

Sugar metabolism in microorganisms during growth and reproduction has long drawn research interest because of its complexity and interesting properties. Sugar metabolism in LAB as the dominant bacterium in sourdough is important, particularly when the bran contains a large amount of non-starch polysaccharides. In addition to the hydrolysis of starch, the hydrolysis of the bran fraction of non-starch polysaccharides can be another pathway of a sugar source, which then affects the production of organic compounds in the dough system. The hydrolysis of maltose and sucrose by LAB is also significant in the production of glucose and fructose (maltose hydrolysis produces only glucose), which is the basis for further reactions (Fig. 5). Maltose metabolism preferentially conducted by maltose phosphorylase, the utilization of sucrose, and the use of fructose as an electron acceptor are common metabolic features of LAB (heterofermentation) and are not limited to sourdough isolates (Zheng et al., 2015). Therefore, a key question is the dose of fructose released via the hydrolysis of carbohydrates in the bran during whole-wheat dough fermentation and whether the release of fructose from the bran exerts a significant effect on the effect of dough fermentation, usually involving conversion to acetic acid and higher acid yields. Meanwhile, single-fructose/-glucose fermentation cannot produce ethanol, which can only be fermented by glucose in conjunction with fructose or other external electron acceptors (Prückler et al., 2015). In addition to its role as an electron acceptor, fructose partly metabolizes fructose and partly reduces it to mannitol via a heterogeneous fermentation pathway. Therefore, focusing on the effect on bran carbohydrate metabolism during sourdough fermentation can help clarify the ability of LAB to acidify bran and increase the source pathway of organic matter in whole-wheat dough.

4.3. Pre-fermentation technology

In modern wheat milling processes, roller milling systems allow the bran to be separated from the endosperm; therefore, bran is pretreated to achieve specific modifications without affecting the remaining grain components (Zhang et al., 2018). Solid-state fermentation of bran with LAB has been shown to reduce phytic acid, increase soluble active compounds, increase soluble arabinoxylan, and promote the formation of bran volatile components rich in microbial floral/fruity aromas (Spaggiari et al., 2020). The use of pre-fermented bran improved the nutritional composition, as well as increased the water content and specific volume of whole-wheat bread. Specifically, fermented bran increased antioxidant capacity, soluble non-starch polysaccharide content, free amino acid content, and protein digestibility; improved whole-wheat dough rheology; and reduced bread firmness (Messia et al., 2016; Pontonio et al., 2017; Tu et al., 2020). These results suggest that pre-fermentation can modify the technical function of milling by-products, thus exhibiting enhanced technical quality with respect to dough-holding capacity, bread specific volume, and crumb softness during storage. In addition, pre-fermentation reduces ANFs and enhances sensory properties.

4.4. Enhanced sourdough fermentation via integrated biotechnology

An integrated biotechnological approach has recently been proposed by Pontonio et al. (2020). Specifically, a combination of fermentation treatment (*Lactobacillus plantarum* and *Weissella confusa* strains) and enzyme treatment (xylanase) was applied to enable bran to improve its performance. Biochemical and nutritional analyses have indicated that fortified breads exhibit enhanced protein digestibility, reduced glycemic index, and enhanced sensory qualities. Therefore, the application of an

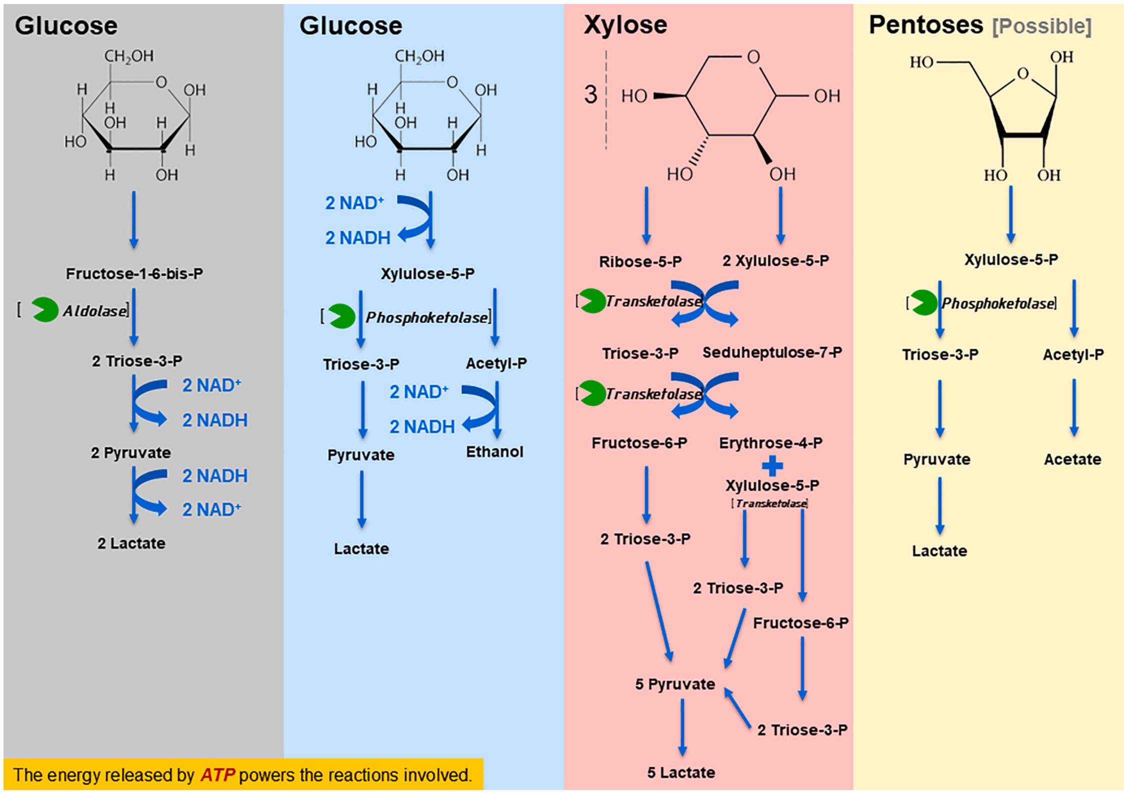

Fig. 5. Overview of metabolic processes of major carbohydrate.

integrated approach can significantly improve the quality of whole-wheat products and provide a promising strategy for their development.

5. Conclusions and prospects

Owing to its high dietary fiber and other health benefits, WWF has drawn considerable attention as a raw material for bread, biscuits, cake rolls, Chinese steamed breads, and other products. The use of sourdough can effectively improve the nutritional value and sensory properties (aroma, flavor, and texture) of whole-wheat products. It may also reduce consumer concerns about whole wheat products at the food preparation stage and the end products. For specific ingredients of WWF, precise breeding and cultivation of strains and production of type II sourdough show potential in promoting the industrialization of sourdough whole-wheat products. Type II sourdough is more conducive to establishing the manufacturing, transportation, and sales standards of sourdough whole-wheat products; however, type I sourdough is more conducive to ensuring microbial diversity in food in a specific area. The prominence of sourdough whole-wheat products enriching the table, improving diet structure, and improving human health has become the consensus of people globally. The mechanism of degradation/inhibition of toxic and harmful substances (e.g., antinutritional factors, fungal toxins, acrylamide formation, pesticide residues) by sourdough has also gained attention from the scientific community. However, more sourdough whole-grain products are still in the laboratory rather than on the supermarket shelves, indicating the need to expand and develop related research worldwide.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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