Trends in Food Science & Technology 113 (2021) 232–244

Contents lists available at ScienceDirect

Trends in Food Science & Technology

journal homepage: www.elsevier.com/locate/tifs

Challenges and opportunities for wheat alternative grains in breadmaking: *Ex-situ-* versus *in-situ*-produced dextran

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ARTICLE INFO

Keywords:
Exopolysaccharides
Dextran
Bread
Staling
Sourdough
Flavour

ABSTRACT

Background: The use of grains as an alternative to wheat in breadmaking has rapidly grown in the last few years, driven by the Sustainable Development Goals toward improving food security and promoting sustainable agriculture. Flours from legumes, pseudo-cereals, minor cereals and milling by-products, such as bran, are of particular interest. The production of partially substituted or wheat-free bread is, however, a challenging task in terms of texture and flavour attributes.

Scope and approach: The present review covers recent advances in the application of dextrans in improving dough rheology, baking performance and bread flavour characteristics. Emphasis has been given to *in situ* application of dextran via sourdough technology as a 'clean label' alternative to commercial hydrocolloid additives.

Key findings and conclusions: In-situ dextran production leads to bread with higher specific volume, softer crumbs and increased moisture content. Dextran also provides an anti-staling effect attributable to its ability to reduce water mobility and retard starch retrogradation. A structure–function relationship has suggested that dextran with high molecular weight and less branching is superior in enhancing bread quality. Furthermore, mild acidification favours the functionality of dextran in dough and bread systems, while intensive acidification results in adverse effects. Lactic acid bacterial strains belonging to the genus *Weissella* exhibiting mild acidification are therefore appreciated in regard to the utilisation of *in-situ* produced dextran. This review highlights the novel application of dextran as a flavour masking agent to minimise off-flavours (e.g. beany flavour, bitter taste, and aftertaste) originating from non-wheat grains, consequently improving the acceptability of the final products.

1. Introduction

The global action of diversifying food production in response to the growing population, changing diets, increasing urbanisation and rising malnutrition has encouraged extensive research into developing fortified or wheat-free breads. Crops possessing dense nutritional composition or nutraceutical properties have been exploited for that purpose (Boukid et al., 2019; Ohimain, 2015). Particularly in developing countries, where indigenous grain crops are promoted in industrial production to maximise their use in domestic food systems, thereby ensuring food security; this is the case in legumes and millets. However, incorporating flour from sources other than wheat in bread production represents a major technological challenge due to the absence of gluten, which results in dough viscoelastic and expansion restrictions (Ohimain, 2015). Among the strategies to overcome textural deficiencies, the use of hydrocolloids in these formulations is promising for achieving high-quality breads (Ferrero, 2017). Dextrans are bacterial exopolysaccharides (EPS) with a linear backbone of α-linked ᴅ-glucopyranosyl repeating units (Monsan et al., 2001). By water binding and mimicking the viscoelastic properties of gluten, dextrans act as hydrocolloids in breadmaking, which can be applied either *ex situ* as a purified bio-ingredient or *in situ* by using well-characterised dextran-producing lactic acid bacteria (LAB) in sourdough baking (Korcz & Varga, 2021; Lynch et al., 2017). The latter serves as a natural replacement for commercial hydrocolloids that meet consumers' demand for fewer or zero additives in food products.

Existing reviews have focused on the effect of exopolysaccharides in wheat and gluten-free breads (Galle & Arendt, 2014; Lynch et al., 2017;

Abbreviations: c*, critical overlap concentration; CMC, carboxymethyl cellulose; Da, Daltons; EPS, exopolysaccharides; HPMC, hydroxypropylmethyl cellulose; IMO, isomaltooligosaccharides; LAB, lactic acid bacteria; Mw, molecular weight; TTA, total titratable acidity.

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https://doi.org/10.1016/j.tifs.2021.05.003
Received 26 January 2021; Received in revised form 29 March 2021; Accepted 1 May 2021

Tieking & Gänzle, 2005). To the best of our knowledge, no report has specifically discussed the influence of dextran on properties of wheat, composite (i.e. mixtures of wheat and non-wheat flours) or wheat-free breads. Furthermore, there is a paucity of studies on flavour attributes of partially or completely substituted breads, although flavour is crucial in developing enriched breads with good consumer acceptability. This overview provides a comprehensive insight into the technological functionality of dextrans produced by LAB, with particular emphasis on modifications of dough rheology, bread textural properties, and staling rate. We also discuss the structure–function relationship of dextran in bread, which is essential for further applications of this biopolymer. Additionally, we summarise the latest findings on the influence of dextran on flavour perception of composite bread formulas.

2. Wheat and non-wheat flours in breadmaking

2.1. Wheat: a unique grain for bread and bakery products

Bread and grain-based products constitute the base and the largest section of the food pyramid and are an important part of the daily diet for millions of people worldwide (Rosell, 2011). According to the International Association of Plant Bakers (AIBI), the average bread consumption in Europe is approximately 59.4 kg/year per capita. American residents consume on average 39.3 kg of bread per year and a lower level is reported in South Africa (25.8 kg) and Asia (22 kg in Japan and 5.8 kg in China) (AIBI Bread Market Report, 2015, p. 28). Wheat flour is by far the most used flour in bread formulations, although in some regions of the world the use of rye flour is very high. Gluten proteins account for 80–90% of the total flour proteins from wheat. Gluten proteins consist of monomeric gliadins (soluble in 60–90% aqueous alcohol) and polymeric glutenins (alcohol insoluble) (Wieser, 2007). Gluten refers to the protein network built from covalent (disulphide bonds) and non-covalent (e.g. hydrogen bonds, ionic and hydrophobic bonds) interactions between gliadins and glutenins (Wieser, 2007). Gluten proteins are described as the environmental trigger of celiac disease, which is an autoimmune enteropathy of the small intestine in genetically predisposed individuals reaching a prevalence of approximately 1% worldwide (Lebwohl et al., 2015). The quantity and quality of gluten determine the dough viscoelastic properties, which play a predominant role in bread baking performance. The gliadins confer viscosity upon hydration and provide dough extensibility, whereas the glutenins contribute to dough elasticity (or resistance to extension) (Goesaert et al., 2005). Adequate extensibility allows the expansion of gas bubbles during fermentation and oven spring and sufficient elasticity is associated with resistance to deformation (or gas holding capacity), which together yield an aerated crumb bread structure (Dobraszczyk, 2004).

2.2. Needs and benefits of alternative flours

The current state of the Food and Nutrition Security projects that the world is misaligned to achieve the Sustainable Development Goals (SDG2) Zero Hunger target by 2030 (FAO, 2020). Five years after the global community pledged to end hunger, food insecurity and malnutrition, the number of people facing hunger/food insecurity is still rising. In 2019, about two billion people, i.e. 25.9% of the world's population, experienced hunger or lacked consistent access to nutritious and sufficient food (FAO, 2020). More than half of the food-insecure people live in Asia, while food insecurity is expanding the fastest in Africa. Furthermore, the COVID-19 pandemic has increased world undernourishment dramatically, and continues to exacerbate hunger and malnutrition. Food insecurity is not only a great threat to health and physical well-being, but impedes quality education and employment, spurring further mass migration. Currently, global food security is largely dependent on three cereals: wheat, rice and maize, which provide at least 40% of the world calories altogether. Wheat is the most traded cereal on international markets and its share in global food trade is still expanding (OECD/FAO, 2020). Notably, developing countries account for nearly 80% of all wheat imports with Egypt, Indonesia, Algeria, Brazil and the Philippines being the top five importers (OECD/FAO, 2020). To solve the food crisis and to achieve the Zero Hunger target, it is critical to implement industrial food transformations to reduce reliance on wheat.

In the baking industry, there is a trend toward fortifying or completely substituting wheat flour with nutrient-rich ingredients to produce health-enhancing or functional breads, such as high-protein, high-fibre, low-glycaemic-index carbohydrates and bioactive ingredient-intensive (e.g. vitamins, minerals, phenolic compounds, antioxidants) products. Within this framework, research has highlighted several wheat substitutes, including legumes (e.g. soya, faba bean, chickpea, lupin, cowpea), gluten-free cereals (e.g. sorghum, millets, oat), pseudo-cereals (e.g. amaranth, buckwheat, quinoa), oilseeds (e.g. sunflower, linseed), tubers (e.g. cassava, yam, potato) and cereal byproducts and side streams (e.g. bran and germ) (Ohimain, 2015).

Legumes have been utilised as organic fertilisers with low carbon and water footprints, which play an important role in reducing greenhouse gas emission (Maikhuri et al., 2016). Legumes are valuable ingredients for bread fortification and the benefit is twofold: (1) enhanced amino-acid balance due to the presence of lysine in legumes and sulphur-containing amino acids, e.g. methionine in wheat and (2) increased bread-protein content that serves as a potential alternative for animal-based protein (Boukid et al., 2019; Ohimain, 2015). Regular consumption of legumes was also linked to reduced diet-related chronic diseases, such as obesity, diabetes and cardiovascular diseases (Dhillon et al., 2016; Marventano et al., 2017; Rebello et al., 2014). Nevertheless, the presence of several antinutritional factors (e.g. trypsin inhibitors, lectins, phytic acid, tannins, saponins and raffinose) in legumes hampers their dietary utilisation, which has been reviewed extensively by Boukid et al. (2019).

Wholegrain pseudo-cereals, such as buckwheat (*Fagopyrum esculentum*), amaranth (*Amaranthus caudatus*) and quinoa (*Chenopodium quinoa*); starchy roots, such as cassava (*Manihot esculenta* Crantz); and minor cereals, such as sorghum (*Sorghum bicolor* L. Moench) and millets, have had a fundamental role in human civilisation but remain largely underutilised in current diets (Jackson et al., 2020; Mir et al., 2018; Taylor, 2019). These crops offer the advantage of tolerating drought and adapting to tropical climates where wheat cultivation does not thrive well. Currently, these crops are mostly used in localised trade and household consumption (Beta & Isaak, 2016). Their industrial utilisation, such as in bread making, is still limited due to the challenges in processing technologies. Promoting the industrial application of these indigenous crops may contribute to economic advancement of developing countries through the saving of foreign exchange on wheat importation and the development of local agriculture sector (Noorfarahzilah et al., 2014). Additionally, these crops have potential use in designing nutraceutical and functional foods with health benefits (Khan et al., 2019; Thakur & Kumar, 2019).

2.3. Textural and flavour challenges in breadmaking by non-wheat flours

The utilisation of non-wheat flours in bread making influences not only nutritional quality but technological and sensory properties. Bread made with composite flours containing 5–15% non-wheat flour exhibited acceptable technological and sensorial attributes (Ohimain, 2015). However, beyond 20% substitution of wheat flour, the appearance (shape and crust colour), loaf volume, crumb texture (cohesiveness and hardness), mouthfeel and shelf-life of breads were negatively affected, resulting in inadequate products (Kohajdová et al., 2013; Mariera et al., 2017; Mohammed et al., 2014). When wheat alternatives are introduced, gluten network formation is limited due to the different technological functionalities of the proteins and/or the interfering effect and water competition between fibres and gluten (Ferrero, 2017).

Numerous studies have been completed to overcome the drawback of the high-addition level of non-wheat flours on technological quality. Typically, the solution relies on the addition of vital gluten or texturing agents (e.g. hydrocolloids, emulsifiers, enzymes and chemical additives) that could mimic the gluten properties to form a cohesive and visco-elastic dough/batter, and thus to compensate the 'dilution' or absence of gluten associated with non-wheat flours (Ohimain, 2015). For example, carboxymethylcellulose (CMC, 6% flour basis) was used to increase the sensory quality of wheat-legume (up to 42% of chickpea/pea/soybean flour) composite breads (Angioloni & Collar, 2012). Emulsifiers (DATEM and distilled monoglycerides) were added to formulate wheat-millet (50:50) composite breads of acceptable quality (Schoenlechner et al., 2013). The positive effects of hydroxypropylmethylcellulose (HPMC) on crumb softness of gluten-free breads made from rice, maize, teff and buckwheat were also investigated (Hager & Arendt, 2013). Nevertheless, the use of these improvers could add to the cost of the final product and necessitate adding an ingredient label, which is often viewed negatively by consumers.

Coupled with the texture deficiencies, the production of composite or wheat-free breads is also challenged by lower consumer acceptance of the flavour. Flavour, a multisensory perception of smell, taste and chemical stimuli, is an essential quality trait that determines food choice (Prescott, 2015). Plant-based ingredients possess inherent flavour compounds and flavour precursors. The flavour of untreated flours is often moderate and bland. Upon food processing, a specific flavour of the product is formed, owning to the process-induced modifications of the flavour active compounds (Heiniö et al., 2015). For example, in leavened breads, the formation of flavour arises in part from yeast fermentation as well as from the baking process (Heiniö, 2014). The volatile compounds (e.g. aldehydes, ketones and alcohols) are responsible for the aroma as such, whereas non-volatile compounds (e.g. free fatty acids and lipids, phenolic compounds, amino acids, small peptides, free sugars and organic acids) directly impart the taste or indirectly act as flavour precursors (Heiniö et al., 2008, 2015).

Lipid degradation and fatty acid oxidation often generate off-flavours. For instance, the undesirable beany note is the main obstacle in introducing legume-enriched products to Western cultures. This flavour arises from the activation of endogenous lipoxygenases that catalyse the oxidation of polyunsaturated fatty acids, e.g. linoleic and linolenic acids (Roland et al., 2017). The primary oxidation products, hydroperoxides, are further degraded in enzymatic or chemical reactions forming volatile and non-volatile compounds that confer beany and rancid off-flavours. For instance, hexanal, *cis*-3-hexenal, *n*-pentylfuran, 2-(1-pentenyl)furan and ethyl vinyl ketone are identified major lipoxygenase-derived contributors to the beany flavour (Roland et al., 2017). These compounds are detected at low threshold values, and thus a small quantity of fatty acids is enough to develop strong beany flavour.

Lipid-rich plants, such as oat (~6%) and pearl millet (~7%), are extremely susceptible to lipid hydrolysis and cause rancid perception (Nantanga et al., 2008). Wholegrain or fibre-rich products are often described as having bitter and pungent flavour notes that reduce their acceptance (Heiniö et al., 2008, 2015). In wholegrain sorghum products, the off-taste, bitterness and astringency is mainly due to phenolic compounds and in particular the condensed tannins that are concentrated in the outermost bran layers (Kobue-Lekalake, 2009). Gluten-free quinoa bread was perceived as six-times bitterer and two-fold saltier than refined wheat bread, which is most likely associated with the presence of saponins and tannins (Gostin, 2019; Ruales & Naira, 1993). Additionally, a positive correlation between the perceived bitterness and the total phenolic content was found in wholegrain wheat bread (Challacombe et al., 2012). Both free and bound polyphenols, such as phenolic acids and flavonols (proanthocyanidins or tannins), contribute to the bitter and astringent tastes. However, the soluble/free polyphenols are considered more flavour-active than the bound fractions due to their higher dissolution in saliva (Heiniö et al., 2015). Taken together, textural and sensory profiles of non-wheat breads represent an obstacle to their widespread acceptance.

3. Sourdough in improving sensory and technological properties of bread

Sourdough fermentation is the one of the most ancient forms of bread-making and has retained its importance in contemporary bread production. Sourdough has been used as a leavening agent throughout human history, which has gradually been replaced by baker's yeast over the last 150 years (Catzeddu, 2011). Sourdough breads continue to play a crucial role in the market in much of Europe, especially in Germany, France, Spain and Italy. In northern Europe (e.g. Germany, the Baltic states and Russia) and the United States, sourdough is commonly used in rye breadmaking. The current artisanal and industrial practice employs sourdough as a baking ingredient to achieve dough acidification and improve bread. Sourdough is a mixture of flour and water fermented by LAB or in combination with yeasts, either spontaneous or inoculated (Hammes & Gänzle, 1998).

Over the past three decades, numerous studies focusing on wheat and rye flour have investigated the effect of sourdough on the flavour and texture of bread. It is well acknowledged that sourdough fermentation contributes to improved sensory quality, enhanced nutritional properties, increased loaf volume and prolonged shelf life (e.g. preventing spoilage and delaying staling) of baked goods (Arendt et al., 2007). Sourdough fermentation has also shown novel functional potential, such as salt reduction in baking products owing to the synthesis of flavouring free amino acids and derivatives (Belz et al., 2019), and sugar replacement by means of the formation of mannitol (Sahin et al., 2019). Furthermore, recent research has investigated the positive impact of sourdough fermentation on functional and nutritional properties of non-conventional flours (Coda et al., 2014; Gobbetti et al., 2019).

Sourdough fermentation is a safe and economic processing technique to decrease the antinutritional-contributing agents (e.g. trypsin inhibitor, phytate, tannins and raffinose-family oligosaccharides) and to improve the nutritional profiles (e.g. higher free amino acids concentrations, soluble fibre, γ-aminobutyric acid, total phenols and antioxidant activities) of legume flours (Coda et al., 2015; Curiel et al., 2015). Incorporation of fermented legumes reduced the predicted glycaemic index and improved the protein digestibility of the fortified wheat bread compared to non-fermented control (Coda et al., 2010, 2017; Peñaloza-Espinosa et al., 2011). Likewise, in pseudo-cereals and some minor cereals (e.g. millet and sorghum), the free amino acids, phenolic compounds and antioxidant activities increased during sourdough fermentation (Coda et al., 2010; Omoba et al., 2015; Wang et al., 2019; Zaroug et al., 2014). Wholegrain millet-, sorghum- and pseudo-cereal-based food products are known to have lower starch digestibility than refined wheat products due to their higher content of dietary fibre, resistant starch, polyphenols and so forth (Annor et al., 2017; Coda et al., 2014). The use of sourdough fermentation results in further reduction of the starch hydrolysis index compared to the non-fermented formulas (Coda et al., 2010; Wang et al., 2019; Wolter et al., 2014). The beneficial modifications mentioned above are attributed to a joint effect of acidification, endogenous cereal and/or microbial enzymes activity (e.g. phytase and proteases with optimal activity at pH 5.0–5.5 and 3.5–4.5, respectively) and other complementary mechanisms.

3.1. *Exopolysaccharides from sourdough lactic acid bacteria*

Sourdough is a rich natural resource of exopolysaccharide-producing LAB strains (Lynch et al., 2017). As a matter of fact, LAB form a variety of polysaccharides encompassing intracellular polysaccharides, e.g. glycogen, cell-wall polysaccharides, including peptidoglycan and lipoteichoic acids, and exocellular polysaccharides (Chapot-Chartier et al., 2011). The former two polysaccharides are an integral part of the bacterial cell. The exocellular polysaccharides are further categorised into capsular polysaccharides (CPS) that are covalently and tightly linked to the outer surface of the cell as a capsule, and EPS that are loosely associated with the cell surface or released into the surrounding medium as a slime (Madigan et al., 2006). EPS in their natural environment are involved in cellular recognition, protection of bacterial cell integrity under harmful conditions (e.g. desiccation, antibiotics or toxic compounds, osmotic stress, pH shifts), adhesion to surfaces and the formation of biofilms (Chapot-Chartier et al., 2011; De Vuyst & Degeest, 1999; Dertli et al., 2015; Looijesteijn et al., 2001). The chemical structure and physicochemical properties of EPS determine their commercial applications, ranging from the pharmaceutical, chemical and cosmetics industries to the food industry as well (e.g. thickening, gelling and stabilising agents) (Daba et al., 2021).

Exopolysaccharides from LAB can be classified into two groups on the basis of their structural features and biosynthesis mechanisms. Homopolysaccharides (HoPS) consist of a single type of monosaccharide either glucose, fructose or galactose. Heteropolysaccharides (HePS) composed of three to eight repeating units of varying monosaccharide combinations with D-glucose, D-galactose and L-rhamnose present in high frequency, with *N*-acetyl-aminosugars, glucuronic acid and non-carbohydrate substituents being less frequent (De Vuyst & Degeest, 1999). HePS exhibit a very large variation in their structural compositions and are not species specific (De Vuyst & Degeest, 1999). In contrast, HoPS have high structural similarity, which are subdivided into four categories as shown in Fig. 1 (Monsan et al., 2001; Ruas-Madiedo et al., 2002):

1. α-D-Glucans
    a. dextran: > 50% α-(1→6) main linkage with branching at positions 2, 3 and 4
    b. mutan: > 50% α-(1→3) with α-(1→6) side chains
    c. alternan: alternating α-(1→3) and α-(1→6) linkages
    d. reuteran: α-(1→4)/(1→6) linkages
2. β-D-Glucans, β-(1→3) backbone with β-(1→2) branching
3. β-D-Fructans
    a. levan: mainly composed of β-(2→6) linkages
    b. inulin type β-(2→1) linkages
4. Others
    a. polygalactan with a pentameric repeating unit of galactose
    b. glycogen-like α-(1→4) glucan.

HePS are synthesised via extracellular polymerisation of sugar-nucleotide repeating unit precursors that are formed in the cytoplasm, which is an energy-dependent process catalysed by intracellular glycosyltransferases (De Vuyst & Degeest, 1999). Most HoPS (α-glucans, inulin and levan) are produced by the action of extracellular glycansucrases, which is a relatively simple process without membrane translocation and requires the specific substrate sucrose. The cleavage of the glycosidic bond in sucrose provides the energy required for the reaction, which explains the higher yield of HoPS (1–10 g/L) than the energy-demanding HePS (0.15–0.6 g/L) (De Vuyst & Degeest, 1999). The biosynthesis of β-glucan and polygalactan HoPS is similar to HePS formation in that the polymer chain is assembled by glycosyltransferases within the cell and sucrose is not involved as a substrate (De Vuyst & De Vin, 2007; Werning et al., 2012).

HePS have found valuable application in the enhancement of rheology, texture, stability and mouthfeel of fermented dairy products (e.g. yogurt, fermented cream and milk-based desserts) and as a fat replacer for producing low-fat cheeses (Amatayakul et al., 2006; Duboc & Mollet, 2001). HoPS are mainly employed in baking products presumably due to their high yield and the dominance of HoPS-producing LAB in cereals (Galle & Arendt, 2014; Lynch et al., 2017). In this review, we focus on dextran since it is by far the most investigated HoPS in grain-based products and has attracted considerable attention from the food industry.

3.2. Production and physicochemical properties of dextran

3.2.1. Biosynthesis

Dextransucrase (sucrose: α-(1→6)-D-glucosyltransferase; E.C. 2.4.1.5) is the key enzyme that catalyses the biosynthesis of dextran from sucrose and is the sole industrial enzyme employed in the commercial production of dextran (Leemhuis et al., 2013). Dextransucrase is released from LAB of the genera *Weissella*, *Leuconostoc*, *Lactobacillus*, *Streptococcus* and *Pediococcus*. Commercial dextran is produced either by direct enzymatic synthesis using purified dextransucrase (cell-free

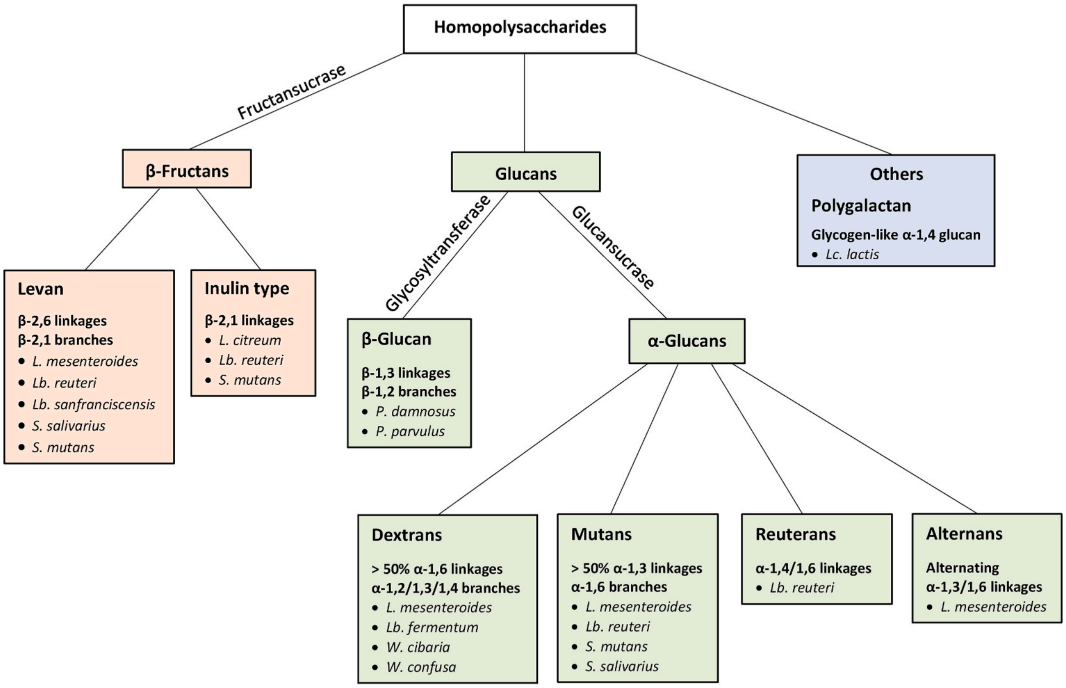

Fig. 1. Structural information of homopolysaccharides produced by lactic acid bacteria (W. *Weissella*, L. *Leuconostoc*, Lb. *Lactobacillus*, Lc. *Lactococcus*, P. *Pediococcus*, S. *Streptococcus*).

filtrate) and the substrate sucrose or by fermentative synthesis, i.e. the cultivation of *L. mesenteroides* strains in sucrose-containing medium (Leemhuis et al., 2013). The optimal conditions for dextransucrase activity have been extensively examined using cell-free extracts from *L. mesenteroides*, lying in the pH range of 5.0–6.5 and temperature range of 30–45 °C and preferably a small amount of calcium (e.g. 0.005%) (Ullrich, 2009). Increasing the sucrose content led to an increased yield of dextran, but it appeared to reduce the molecular weight (Mw) and increase the degree of branching (Hehre & Sugg, 1942; Kim et al., 2003).

The catalytic mechanism of dextransucrase is still not fully understood. A double-displacement mechanism has been elucidated, starting from the cleavage of the glycosidic bond of sucrose and the formation of a covalent glucosyl-enzyme intermediate with the release of a free fructose moiety (Leemhuis et al., 2013; Monsan et al., 2001). From this covalent glucosyl-enzyme intermediate, the ᴅ-glucosyl unit is transferred onto various acceptors. In the polymerisation of dextran, the glucosyl residues are added successively to the growing dextran chain to extend it. With respect to branch formation, the glucosyl or dextranyl residues are added to an exogenous dextran acceptor, yielding branched linkages (Robyt & Taniguchi, 1976). The presence of separate branching enzymes has also been investigated, such as α-(1→2) and α-(1→ 3) branching sucrases (Moulis et al., 2016; Passerini et al., 2015; Vuillemin et al., 2016). These branching sucrases and dextransucrase may work synergistically in catalysing the synthesis of branched linkages. Furthermore, the glucosyl units can be transferred onto acceptor sugars (e.g. maltose, isomaltose, lactose and ᴅ-fructose), leading to the formation of small molar mass oligosaccharides (Robyt & Eklund, 1983). Among those, the synthesis of glucooligosaccharides is of the utmost interest for potential applications in functional foods and health supplements (Kothari & Goyal, 2014). For example, the acceptor reaction with maltose leads to the formation of a linear series of isomaltooligosaccharides (IMOs) with a degree of polymerisation from 3 to 12 monomers, and a minor homologous series of α-(1→ 2)-branched IMOs (Shi et al., 2016; Shukla et al., 2014). IMOs serve as effective prebiotics that resist digestion in the upper gastrointestinal tract and are selectively fermented in the colon by beneficial bacteria, such as bifidobacteria and Lactobacilli; thus, they confer health-related benefits to the host (Glibowski & Skrzypczak, 2017).

3.2.2. *Structure and physicochemical characteristics*

Dextrans consist of variable degrees of branches depending on the origin of the dextransucrase. Most of the branches are short with only one or two glucose residues, while some are elongated and highly branched (Monsan et al., 2001). The most studied dextran is produced by *L. mesenteroides* NRRL B-512F, which is characterised by 95% α-(1→ 6) main linkages and 5% α-(1→3) side chains (Monsan et al., 2001). Dextrans produced by *Weissella* strains are particularly interesting—and they possess similar structures, i.e. a linear backbone with only 3–4% α-(1→3) branching (Maina et al., 2008; Shukla et al., 2014; Wang et al., 2019; Xu et al., 2018). Native dextrans exhibit a wide molecular weight distribution ranging from 10 to 10^6 kDa. Low Mw dextrans (40, 60 and 70 kDa) are widely utilised in the pharmaceutical industry as blood plasma substitutes and carriers in drug delivery, and in the manufacture of gel permeation chromatography (De Vuyst & Degeest, 1999; Kothari et al., 2014). Conversely, high Mw dextrans ($>10^3$ kDa) with few branches are preferred in the baking industry (Lacaze et al., 2007; Zhang et al., 2018).

Dextrans show great diversity in their physicochemical properties according to their molar mass and structure features. Some are readily soluble in water and polar organic solvents, such as dimethyl sulfoxide, formamide, ethylene glycol and glycerol (Belder, 2000). Some may present a certain degree of crystallinity or form aggregates in solutions (e.g. freeze-dried dextran) and requires heating to aid the dissolution. Linear dextrans often show higher water solubility than branched ones (Belder, 2000). Dextrans are insoluble in monohydric alcohols (e.g. methanol, ethanol and isopropanol) and ketones (e.g. acetone and 2-propanone). Generally, aqueous dextran solutions behave as Newtonian fluids at low concentration and non-Newtonian pseudoplastic fluids at high concentration. For instance, dextran produced by *W. confusa* A16 showed the characteristics of Newtonian viscosity in the concentration range 0.1–2% (*w/w*) (Wang et al., 2020). Dextran synthesised by *W. confusa* R003 exhibited Newtonian flow behaviour at concentrations below 2.5% (*w/v*), viscoelastic behaviour at 5% and gelling behaviour at 10% (Netsopa et al., 2018). Dextran formed by *L. mesenteroides* NRRL B-523 displayed viscoelastic behaviour at 25 g/L (Padmanabhan et al., 2003). With increasing concentration, dextran solutions transit from the dilute region to semi-dilute and concentrate domain. The transition from a dilute solution where individual polymer molecules are free to move to a semi-dilute solution where polymer chains interpenetrate and entangle with each other corresponds to the critical overlap concentration c*, which yields an abrupt increase in viscosity. c** marks the onset of the concentrated region, in which the coil size is independent of polymer concentration. Commercial dextrans with different molecular weights of 200, 500 and 2000 kDa exhibit a c* of 6%, 4% and 3.2% (*w/w*), and a c** of 22%, 15% and 12%, respectively (Pinder et al., 2006). Notably, the rheological properties of dextran solutions are not significantly affected by pH, ionic strength or salt concentration since they are neutral polymers (Kothari et al., 2014).

3.2.3. *In-situ production versus ex-situ added pure dextran*

Dextran can be produced by certain LAB during sourdough fermentation, which provides a convenient and economical way for its applications in baking products. The addition of dextran-enriched sourdough, usually at 10%–60% (dough basis), has consistently been reported to improve bread quality, such as a higher specific volume and softer crumbs (Galle et al., 2012b; Katina et al., 2009; Wang et al., 2018; Wolter et al., 2014). The *in-situ*-produced functional dextran is a natural alternative to commercial hydrocolloids, such as HPMC and xanthan gum, which does not necessitate rigorous toxicological testing and labelling of the product package (De Vuyst & Degeest, 1999). Furthermore, dextran and, particularly, the simultaneously formed small Mw glucooligosaccharides have been demonstrated to have health-enhancing benefits due to their potential as prebiotics (e.g. the *Bifidobacterium*-stimulating effect in an *in vitro* model) and the possible role in pathogen inhibition (Amaretti et al., 2020; Lynch et al., 2017; Olano-Martin et al., 2000; Tingirikari et al., 2014).

Apart from being produced *in situ*, dextran has been used directly in food processing as a pure ingredient in previous studies (Rühmkorf et al., 2012; Zhang et al., 2018). In fact, dextran has a long history of clinical use (e.g. plasma volume expansion and eyes drops) and as food packaging materials (Belder, 2000). Dextran does not appear to be included in the lists of permitted food additives in the United States (FASEB, 1975). However, dextran produced from *L. mesenteroides* was approved by the European Commission in 2001 as a bread-improver additive with levels restricted to a maximum of 5% in the end product. Dextran as an ingredient has the advantage of employing well-defined dextran with desirable molar mass, structure and amount in food processing. This manner is more controlled compared to *in-situ* formation, which can be affected by fermentation conditions (e.g. dough yield, fermentation time and temperature, pH and sucrose content) and composition of substrate, such as buffering capacity and the presence of a maltose acceptor that results in isomaltooligosaccharide formation and reduced yield of dextran (Galle & Arendt, 2014; Immonen et al., 2020; Katina et al., 2009; Schwab et al., 2008). However, the *ex-situ* addition of dextran in food products may not deliver the same multifunctionality as the *in-situ* production. In addition, the industrial production of dextran includes a first fermentation with sucrose-rich medium followed by purification and fractionation, which is characterised by high production cost and low yield. The organic solvent used during the processing steps is also a concern regarding pollution and recuperation issues.

3.2.4. *Viscosity as an indicator of in-situ dextran production*

In a fermented flour matrix, dextrans act as a thickening agent, leading to a more viscous sourdough. For example, the viscosity of dextran-enriched wheat sourdoughs fermented by *W. confusa* E392 was nearly five-fold higher than the control sourdoughs (Katina et al., 2009). The thickening effect was also demonstrated in dextran containing sorghum, millet and waste-bread (blends of recycled wheat breads and water) sourdoughs fermented by *W. confusa* A16 (Immonen et al., 2020; Wang et al, 2019, 2020). The amount of dextran, however, was not exactly proportional to the viscosity of sourdoughs. Dextrans synthesised by different strains seem to show different intrinsic ability in increasing viscosity in a given matrix. For example, faba-bean sourdough fermented by *W. confusa* E3403 containing 0.9% (flour basis) of dextran showed comparable viscosity to that fermented by *L. pseudomesenteroides* DSM 20193 with 3.6% dextran (Wang et al., 2018). It has been stated that, besides dextran concentration, the intermolecular legume protein–dextran interactions may also play an important role in thickening (Xu et al., 2017, 2018). The general recognised factors that influence the viscosity-enhancing capacity of dextran are molecular weight, degree and length of side chains, and number of intermolecular bonds (Lacaze et al., 2007; Rühmkorf et al., 2012). By and large, viscosity measurement is an indicative and useful method in screening dextran-producing LAB to confirm the production of this biopolymer (Wang et al., 2019; Xu et al., 2017).

4. Functionality of dextran in improving bread quality

4.1. *Dough rheology parameters*

The rheological properties of dextran-containing bread doughs have been determined (Table 1). A proper dough for breadmaking must have sufficient strength to prevent collapse, diffusion and losses of gas bubbles—and is able to extend without rupturing during gas expansion (Mir et al., 2016). Numerous fundamental and empirical rheological test methods, such as farinograph, Kieffer extensograph, dynamic oscillation, rheofermentometer, alveograph, and TA (Texture Analyser) texture analysis, have been utilised to measure the dough properties, which are usually related to quality indicators of the end products.

In general, the influence of *in-situ* produced dextran on dough rheological properties depends on the flour characteristics, the type and amount of dextran synthesised (or the strains employed), and the utilisation dosage of sourdoughs in bread doughs. As an example, the dough strength of bread doughs made from gluten-free quinoa and teff flours containing dextran-enriched sourdoughs (20% dough basis) was significantly increased compared to control, but decreased in sourdough-containing buckwheat, sorghum and wheat bread doughs (Wolter et al., 2014). In wheat- and gluten-free sorghum bread doughs, the addition of 10–20% dextran-enriched sourdough fermented by *W. cibaria* MG1 led to a lower complex modulus G* (total resistance to deformation) and a higher phase angle δ (phase shift between stress and strain), indicating a tendency toward more viscous behaviour (Galle et al., 2012a,b). The inclusion of dextran-enriched sourdough generated a significant increase in gas production (i.e. the maximum height of gaseous release and the total volume of gaseous release) during dough proofing compared to control. In another study, the higher proofing performance of wheat dough was also obtained upon the use of 40% dextran-enriched sourdough fermented by *W. confusa* QS813 (Tang et al., 2018). However, contrary to the results of Galle et al. (2012a, b), an increase in dough elasticity, namely increased elastic modulus (G') and reduced tan δ (loss tangent, the ratio of the loss modulus to storage modulus), was observed with dextran incorporation.

In regard to dextran producers, the effect of two different dextrans produced *in situ* by *L. pseudomesenteroides* DSM 20193 and *W. confusa* E3403 on dough rheological characteristics of composite formulations based on wheat–faba bean flours (30:70) was compared (Wang et al., 2018). The farinographic curve of composite flour doughs showed significant improvement (e.g. a higher water absorption and dough consistency) with both dextrans. The incorporation of the two dextran-enriched sourdoughs also demonstrated a similar trend of dough softening (increased δ). However, the maximum resistance to extension ($R_{\max}$) and dough strength value (A_{tot}) were improved only when dextran-enriched sourdough fermented by *W. confusa* E3403 was used. This might be linked to the acidity level of the matrix as explained in section 4.4. The doughs exhibiting stronger resistance to extension and higher strength at the moment of rupture correspond to higher bread volume and softer crumbs. The incorporation of dextran formed *in situ* by *W. confusa* A16 also showed similar increments in farinograph water absorption and extension parameters ($R_{\max}$ & A_{tot}) in millet–-wheat composite formulations (50:50) (Wang et al., 2019). A significant decrease in dough stickiness after kneading and proofing was observed when dextran was added, indicating better dough handling properties.

The effect of *ex-situ*-added dextrans on dough rheology has also been explored in different bread doughs. For instance, supplementing refined and wholemeal wheat flour doughs with purified dextran at different concentrations (0.5%, 1.0%, 2.5%, 5% flour basis) resulted in a linear increase of farinograph water absorption while gas retention capacities during yeast fermentation decreased with dextran presence at most dosage levels (Zannini et al., 2014). The effect of added commercial dextrans (0.1% flour basis) with different molecular weights (T10, T70, T250, T750 and T2000) on sourdough-containing wheat dough rheology was also studied (Zhang et al., 2018). Sourdough doughs with added dextran demonstrate increased elastic (G') and viscous (G'') moduli compared to doughs without dextran, and high Mw dextran (T2000) exhibits the maximum increase. Several factors pertaining to *ex situ* dextran addition (Mw in combination with weak acidification) that influence wheat dough viscoelastic properties were further investigated in a recent study (Zhang et al., 2019). The G' decreased and tan δ increased with solely dextran addition, leading to a less elastic and more viscous dough than the control. In contrast, under weakly acidic conditions, dextran significantly increased the dough elasticity (higher G' and lower tan δ). The authors concluded that mild acidification was fundamental to dextran-induced enhancement of wheat dough elasticity. In a follow-up study, modifications in the physicochemical properties of the gluten network in the presence of high Mw dextran were demonstrated (Zhang et al., 2020). A trend toward higher β-sheets and lower β-turn contents in the secondary structure of the gluten proteins was observed upon dextran inclusion in a mildly acidic environment, resulting in a strengthened gluten network with higher coherence and more elastic-like behaviour.

4.2. *Bread textural properties: structure–function relationship*

The positive effects of dextran on dough rheological properties correlate with improvements in bread textural properties. Bread-specific volume, crumb softness and staling rate have been the most extensively studied characteristics. Positive effects were generally reported at dextran utilising levels ranging from 0.1% to 2% (flour basis) in wheat-flour matrix (Di Cagno et al., 2006; Galle et al., 2012a; Katina et al., 2009; Wolter et al., 2014; Zannini et al., 2014). In composite formulations prepared from faba-bean–wheat (30:70), millet–wheat (50:50), and sorghum–wheat (50:50) flours, increased specific volume (13–21%), reduced crumb hardness (12–53%) and delayed staling were also observed with the addition of dextran (0.9–1.6% flour basis) (Wang et al., 2018, 2019, 2020). Furthermore, dextran-enriched breads showed a higher moisture content and slower moisture loss during storage. A trained sensory panel described the sorghum-wheat bread containing dextran as more elastic, foldable, moist, cohesive, soft and smooth compared to control breads. Regarding gluten-free breads made from sorghum, buckwheat, teff and quinoa, a similar trend of reduced crumb hardness and slower staling was shown with supplemented dextran (0.1–0.3% flour basis), but no changes in loaf specific volume were observed (Galle et al., 2012b; Schwab et al., 2008; Wolter et al., 2014).

Table 1
Dough rheological properties and textural quality of dextran-enriched breads.

Type of flour	Dextran producer	Dextran Mw and yield	Application dose (% flour basis)	Dough property	Bread characteristic	References
Wholegrain wheat, refined wheat (bakers' flour, biscuit flour)	Unknown	Mw: 5000–40000 kDa	Purified ingredient (0.5, 1, 2.5, and 5% to bread)	Farinograph water absorption increased with increased dextran dosage. Gas retention capacities reduced at most dosage levels.	Loaf volume improved in refined flours with 0.5% dextran. Softer crumb over 5 days of storage. Reduced cell wall thickness of crumb.	Zannini et al. (2014)
Wheat	Unknown	T10, T70, T250, T750, and T2000 (Mw: 10, 65, 255, 750, 1500–2800 kDa)	Purified ingredient (0.1% to sourdough bread)	Increased elastic (G') and viscous (G'') moduli values. Hindered starch pasting (lower peak viscosity, breakdown and setback).	Decreased specific volume. Retarded staling rate (except for T70).	Zhang et al. (2018)
Wheat	Unknown	T2000 (Mw: 1500–2800 kDa)	Purified ingredient (0.1% to sourdough bread)	Lower elastic modulus (G') and higher tan δ values with dextran presence alone. Increased elastic modulus (G') and decreased tan δ values when dextran was added with sourdough.	Increased specific volume. Reduced staling rate. Improved crumb softness.	Zhang et al. (2019)
Wheat	*Leuconostoc mesenteroides* B512	Mw: 2000 kDa	Purified ingredient (0.5% *w/w* to chemically acidified gluten dough)	Hindered glutenin polymerisation with dextran addition. Under mild acidic condition, dextran increased β-sheet and decreased β-turn proportions of gluten proteins, leading to a more coherent and elastic gluten network,		Zhang et al. (2020)
Wheat	*W. cibaria* MG1	Mw: 3000000 kDa 5.8 g/kg SD	Sourdough with *in-situ* produced dextran (10% and 20% to bread)	Decreased complex modulus $\|G^*\|$, increased phase angle δ, higher H`m (height of gaseous release) and V_t (total volume of gaseous release).	Increased specific volume. Reduced crumb hardness over 5 days of storage. Positive effects more pronounced at 20% addition.	Galle et al. (2012a)
Gluten-free sorghum	*W. cibaria* MG1	Mw: 3000000 kDa 8 g/kg SD	Sourdough with *in-situ* produced dextran (10% and 20% to bread)	Decreased complex modulus $\|G^*\|$, increased phase angle δ. Increased gas release parameters (H`m and V_t).	Bread volume unaffected. Decreased crumb hardness. Slower staling rate. 20% addition was more effective than 10%.	Galle et al. (2012b)
Wheat, gluten-free buckwheat, quinoa, sorghum and teff	*W. cibaria* MG1	Buckwheat (4.2 g/kg SD) Sorghum (1.1 g/kg) Quinoa (3.2 g/kg) Teff (0.9 g/kg)	Sourdough with *in-situ* produced dextran (20% to bread)	The dough strength values increased in quinoa and teff doughs, but decreased in buckwheat, sorghum and wheat doughs.	Bread volume unaffected. Crumb porosity increased. Crumb firmness and staling rate reduced in buckwheat, teff and wheat breads. Water activity not changed.	Wolter et al. (2014)
Wheat	*W. confusa QS813*	Mw: 160000 kDa 18.45 g/kg SD	Sourdough with *in-situ* produced dextran (40% to steamed bread)	Increased agglomeration of glutenin macropolymer and particle size. Increased water absorption. Increased gas production (higher H`m and Vt). Increased elastic modulus (G') and reduced tan δ	Increased bread specific volume and decreased crumb hardness. Delayed bread staling. More uniform and fine crumb structure.	Tang et al. (2018)
Faba bean-wheat composite flour (30:70)	*W. confusa* E3403 *L. pseudomesenteroides* DSM 20193	Mw: 4379 kDa *L. pseudomesenteroides:* 13 g/kg SD *W. confusa:* 18.7 g/kg SD	Sourdough with *in situ* produced dextran (43% to bread)	Increased farinograph dough consistency and water absorption. Reduced elastic modulus (G') and increased phase angle δ. Increased Kieffer parameters (maximum resistance to extension and dough strength value) only with *W. confusa* dextran.	Increased specific volume and crumb softness with *W. confusa* dextran. Dextran-enriched *L. pseudomesenteroides* sourdough negatively affected bread texture and volume.	Wang et al. (2018)
Pearl millet-wheat composite flour (50:50)	*W. confusa* A16	Mw: 3300 kDa 12.6 g/kg SD	Sourdough with *in-situ* produced dextran (59% to bread)	Increased farinograph water absorption. Increased maximum resistance to extension and dough strength.	Increased bread volume. Decreased crumb firmness. Slower moisture loss and delayed staling.	Wang et al. (2019)

(*continued on next page*)

Table 1 (*continued*)

Type of flour	Dextran producer	Dextran Mw and yield	Application dose (% flour basis)	Dough property	Bread characteristic	References
				Reduced dough stickiness after kneading and proofing.		

W. Weissella, *L. Leuconostoc*, Mw = molecular weight, SD = sourdough.

The mechanisms behind the dextran functionality in bread systems are partially unclear. In wheat and composite flour matrices, the high water-binding capacity and intermolecular interactions (e.g. hydrogen bonding or steric interactions) between dextrans and the gluten proteins affect the network structure; the rheological behaviour of dough is also affected (Ross et al., 1992). The resultant greater dough strength and gas-retention capacity contribute to a higher bread volume, which potentially explains why the volume improvement in 100% or partially substituted wheat breads was no longer observed in gluten-free formulations. In the context of *in-situ* application, it should also be noted that the fructose accumulated during dextran synthesis may stimulate yeast metabolism and consequently CO_2 production (Galle et al., 2012a, b). However, the effect of the monosaccharides released from sucrose metabolism on bread volume and textural quality is controversial and requires further investigation (Wang et al., 2020). Furthermore, the effect of IMO produced together with dextran on bread textural properties remains poorly understood.

The beneficial influence on bread texture attributes appears to be a function of the structure and concentration of the dextrans. Dextrans bearing linear chains were shown to be more effective in increasing specific loaf volume than dextrans with a higher degree of branching (Lacaze et al., 2007). The linear polymer chains may line up and interact through hydrogen bonding or other molecular interactions, which assists the gluten network in the wheat-containing system. Furthermore, dextrans with high Mw and α-(1→3)-linked side chains exhibited superior moisture retention in breads compared to dextrans with smaller Mw and branching at position *C*4 (Rühmkorf et al., 2012). The varied water-binding capacity of dextrans was attributed to their different polymer conformations. The texture-improving effect of dextran has been related positively to its molecular weight (Zhang et al., 2018). Dextrans with high molar mass have a stronger delaying effect on the wheat-bread firming process. Moreover, a positive dose-response effect of dextran addition on bread texture was reported (Wang et al., 2020).

4.3. Dextran as an anti-staling agent

Bread stales during storage, leading to significant food waste and huge economic losses all over the world (Fadda et al., 2014). Staling, commonly recognised as dry and hard crumb or loss of freshness, is mainly attributed to starch retrogradation and moisture migration (i.e. macroscopic migration from crumb to crust and molecular redistribution between starch and gluten) (Gray & Bemiller, 2003). Starch retrogradation refers to the transformation from an amorphous state to a more ordered structure after gelatinisation, which begins with fast crystallisation of amylose within few hours (short-term retrogradation) followed by slow recrystallisation of amylopectin side chains upon storage from several days to weeks (long-term retrogradation) (Goesaert et al., 2005; Miles et al., 1985). Amylopectin retrogradation is often accompanied by an increased degree of crystallinity with the formation of B-type crystalline polymorphs and decreased water mobility due to incorporation into the crystal lattice (Gray & Bemiller, 2003).

Dextrans have been shown to retard starch retrogradation and stabilise the breads against staling in both wheat and composite flour systems. The inhibitory effect on starch recrystallisation of wheat bread depends on the molar mass of the dextrans (Zhang et al., 2018). Bread supplemented with high Mw dextran (T2000) showed the lowest retrogradation enthalpy value (differential scanning calorimetry (DSC) assays) and the least amount of B-type crystallites formed after seven days of storage. Lower water mobility was also observed in the presence of high Mw dextran, evidenced by less water molecules incorporated into the amorphous starch using low-field nuclear magnetic resonance (LF-NMR) assays (Zhang et al., 2019). The authors also noted that dextran hindered the swelling and gelatinisation of starch granules, thereby decreasing the amount of amylose leaching and inhibiting short-term retrogradation. The decreased starch-water uptake and gelatinisation might be owed primarily to the associations between the dextran and starch molecules (Lynch et al., 2017).

A similar starch retrogradation deferring phenomenon was observed in composite millet-wheat bread containing dextran, which showed significantly decreased retrogradation enthalpy and endothermic peak temperature values after one and four days of storage (Wang et al., 2019). The anti-staling mechanism of dextran is likely related to: (1) its high water retention capacity that prevents water redistribution; (2) a decrease in the formation of B-type crystals by interactions with gelatinised starches, thereby interrupting the intermolecular alignment; and (3) interference of the starch–gluten interactions, which has previously been shown to accelerate the staling of bread (Biliaderis et al., 1997; Fadda et al., 2014; Zhang et al., 2018).

4.4. Effects of sourdough acidification on the functions of in-situ produced dextran

When produced *in situ*, a synergistic effect between dextran and sourdough acidification has been observed. Sourdough acidification affects the dough structural components, such as gluten proteins and starch, and in turn alters bread properties in both direct and indirect ways. Under acidic pH, the gluten proteins present a net positive charge due to the protonation of their carboxylic side chains, which contributes to increased water uptake and solubility (Arendt et al., 2007). The increased intramolecular electrostatic repulsion fosters the unfolding of gluten proteins and exposure of their hydrophobic regions. This results in disentanglement of the gluten network and leads to dough softening (Clarke et al., 2004). Acidification is also responsible for the activation of proteolytic enzymes, such as endogenous flour proteases, that display optimal activity at pH 4 (Kawamura & Yonezawa, 1982). A slightly disentangled or partially-hydrolysed gluten network would benefit from gas expansion, leading to a higher specific volume and less crumb hardness. A mildly acidic environment favours the activity of α-amylase, which degrades the crystallisable amylopectin side chains, leading to retarded starch retrogradation (Goesaert et al., 2009).

Sourdough acidification is indeed essential to the technological functionality of dextran in bread. Dextran and mild acidification showed synergetic improvement of bread volume and crumb softness as well as inhibition of starch retrogradation and bread staling. A positive effect on the gluten network was observed only when dextran was added under mildly acidic conditions (Zhang et al., 2020). Dextran itself tends to weaken the gluten network by interfering with the formation of intermolecular and intramolecular disulphide bonds (gluten protein cross-linking), while mild acidification decreases this intervention (Zhang et al., 2020). Mild acidification and dextran combination also enhance the thermal stability of the gluten network. The acidic conditions probably induce interactions between dextran and gluten–starch associations, which lead to increased dough elasticity and stability (Zhang et al., 2019). In addition, increased solubility of gluten proteins due to mild acidification may reinforce their intermolecular interactions, such as hydrogen bonding with dextran.

Nevertheless, intensive acidification would counteract the beneficial effect of *in-situ*-produced dextran (Wang et al., 2018). Intensive acidification results in over degradation or depolymerisation of gluten proteins and a highly weakened gluten network, which negatively affect bread textural properties. In the faba-bean matrix, dextran-enriched sourdough fermented by *L. pseudomesenteroides* DSM 20193 demonstrated a high level of acidification measured as total titratable acidity (TTA) of 18.5 mL NaOH 0.1 M/10 g of dough, leading to decreased dough strength and bread volume and increased crumb firmness compared to control bread (Wang et al., 2018). When free fructose is present, heterofermentative LAB, such as *Leuconostoc* strains, reduce fructose to mannitol by mannitol dehydrogenase activity with concomitant oxidation of NADH to NAD^+ (Wisselink et al., 2002). This induces the conversion of acetyl-phosphate to acetate and a further increase in sourdough acidity. Importantly, most *Weissella* strains do not use fructose as an electron acceptor to support acetate formation. For this reason, the dextran-producing *Weissella* spp. have received great attention in sourdough bread applications, which exhibit mild acidification (e.g. TTA 6–10 mL as measured in wheat, faba-bean, millet, and sorghum sourdoughs) and are capable of producing sufficient dextrans *in situ* with high molar mass and linear chain structure that are ideal for improving dough rheological properties and bread textural quality (Galle et al., 2012a; Katina et al., 2009; Wang et al., 2018, 2019, 2020).

5. Novel applications of dextran for flavour masking

5.1. Changes in flavour induced by sourdough

The effectiveness of sourdough in improving the flavour of wheat and rye breads has been well established in the literature (Katina, 2005, p. 92). Sourdough bread is often richer in flavour and more aromatic than regular wheat bread, which is increasingly appreciated by consumers. The flavour profile of sourdough bread is determined by the type of flour used as well as the processing steps, such as sourdough fermentation, Maillard and caramelisation reactions and lipid oxidation (Fig. 2). In sourdoughs, the composition of flavour compounds is strongly dependent on the enzymatic and microbial metabolic activities, including the formation of acids (primarily lactic and acetic acids and to lesser amount citric and malic acids), the synthesis of flavour precursors (e.g. free amino acids), and the production of volatile flavour compounds (e.g. alcohols, aldehydes, esters, ketones and sulphur) (Pétel et al., 2017). The ratio of lactic to acetic acid is an important factor affecting bread flavour and shelf-life. Lactic acid is perceived as a fermented sour taste associated with dairy products that confers yogurt or milky-like flavour to bread (Belz et al., 2019). Whereas acetic acid imparts a vinegar-like and slightly astringent flavour to the bread (Lotong et al., 2007). Acetic acid also possesses strong anti-microbial activity against fungal growth and rope-forming bacteria, which prevents spoilage and extends shelf-life of bread products (Gerez et al., 2009). Thus, a combination of both the acids is typically desirable. The primary degradation of cereal proteins by the activity of endogenous flour proteases results in the liberation of polypeptides, which are further broken down into small-sized peptides and free amino acids by intracellular peptidases of LAB (Gänzle et al., 2008). Amino acids together with simple aldose or ketose sugars are flavour precursors involved in Maillard reactions, which form a great variety of volatile compounds upon heating, such as pyrazines, pyrroles, furans, sulphur-containing compounds and lipid degradation products (Salim-ur-Rehman et al., 2006). These compounds contribute to the typical and powerful flavour of bread crust, namely the roasted/toasted, caramelised and sweet notes (Heiniö et al., 2015). The small molar mass peptides contribute to the bitter taste in cereal products and are therefore less appreciated by consumers (Heiniö et al., 2015).

The addition of sourdough in breadmaking does not always improve the aroma and taste, as it largely depends on the endogenous flour components, the fermentation conditions and the proportion of sourdough used (Meignen et al., 2001). For instance, the addition of 42% (dough basis) faba-bean sourdoughs produced over a long fermentation period (24 h) that possessed high acidity (TTA up to 13.5 mL) significantly increased the intensity of the musty taste and aftertaste of the composite faba-bean-wheat breads (Varis, 2017, p. 85). Similarly, the inclusion of 59% (dough basis) sorghum sourdoughs (TTA 7.4 mL) fermented for 24 h resulted in a higher intensity of bitter taste and aftertaste of the composite sorghum-wheat breads (Wang et al., 2020). Gluten-free buckwheat, quinoa, sorghum and teff sourdough breads were perceived as mouldy and grassy, which was liked less by consumers (Wolter et al., 2014). The intense off-flavours in the resultant sourdough breads are attributed to the biochemical changes during sourdough fermentation including: (1) intensive acidification; (2) intensive proteolysis liberating bitter-tasting small peptides and amino acids; and (3)

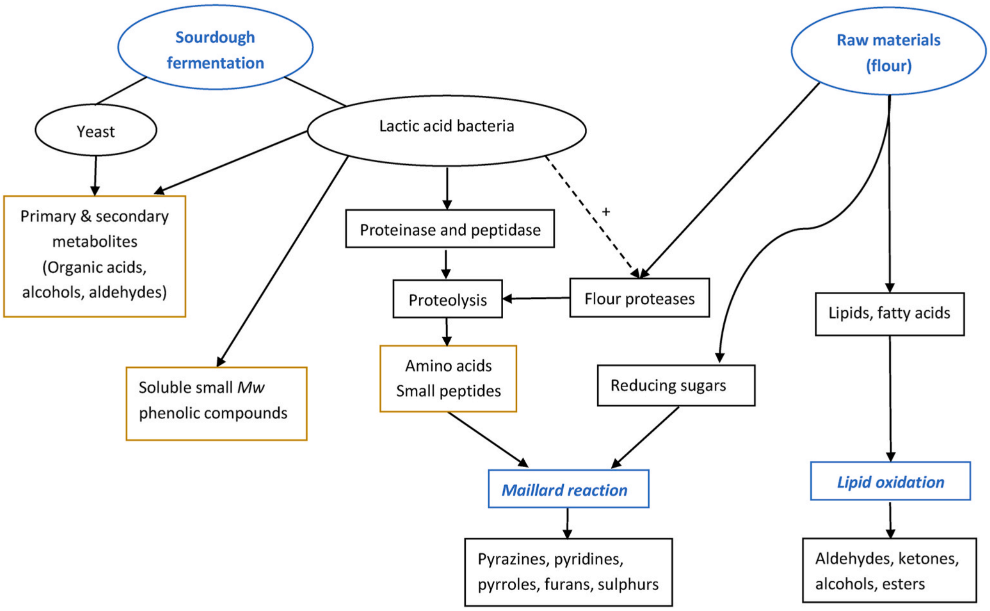

Fig. 2. The generation of flavour compounds in sourdough bread.

release of small Mw polyphenols, which offer a strong, bitter taste by hydrolytic enzymes, such as endogenous flour and/or bacterial esterases (Heiniö et al., 2015; Wang et al., 2020). The undesirable flavours present in these formulations may be masked by sweeteners or flavouring agents in a large quantity (Heiniö et al., 2015; Selvamuthukumaran & Pathak, 2019), which may have a detrimental impact on health and is against consumer and policy demand for sugar-reduced products.

5.2. *Effects of dextran on flavour–texture interactions*

Aroma and taste are key elements in flavour perception. Aromas can be sniffed and detected by the receptors in the nose (orthonasal olfaction), which help set our flavour expectations (Spence, 2020). They are also released and delivered through the top of the throat to the nasal cavity (retronasal olfaction), which is constitutive of flavour. Taste compounds are dissolved in saliva and perceived by the specific taste detectors located on the plasma membrane of taste receptor cells in the oral cavity (Fábián et al., 2015). Flavour sensation is closely related to oral texture, namely how food is broken down inside the mouth. Oral food processing imparts structural modifications to the food and confers dynamic flavour perception, which starts from food injection, mastication (mechanical size reduction), salivation (moistening and enzymatic interactions), bolus formation and ultimately swallowing (Lawless & Heymann, 2010). Tastants from a fluid food are dissolved and diluted directly into saliva, while the taste stimuli of solid food are progressively sensed during chewing. Food breakdown upon chewing fosters the release of flavours to the surrounding saliva or vapour phase, which are subsequently transported to the taste receptor cells and the olfactory receptors, respectively. The flavour perception of solid foods is largely influenced by the availability of its flavour compounds to the receptor cells (Overbosch et al., 1991). The breakage function leads to variable degrees of food particle size reduction, mainly determined by the fracture characteristic (or chemical composition) of the food matrix (Voon et al., 1986). The particle size distribution during oral processing further affects the flavour release kinetics, namely the diffusion rate and surface area exposed for the exchange of flavour compounds in saliva, which consequently affect the levels of flavour stimuli accessing the oral and nasal sensors (Feron & Salles, 2018).

The addition of polysaccharide hydrocolloid texturing agents (e.g. xanthan gum, alginate, carrageenan, pectin, starch, CMC and HPMC) modifies the rheology (flow behaviour) and textural properties of the food systems and consequently alters the flavour release (Tournier et al., 2007). The studies cited in this review highlight that an increase in polysaccharide concentration leads to a decrease in perceived flavour intensity. In solution, the declined flavour intensity only occurs at polysaccharide concentrations above its critical overlap concentration (c*), which coincides with a sharp increase in viscosity (Baines & Morris, 1987; Cook et al., 2002; Hollowood et al., 2002). For gel systems, the decrease in perceived flavour intensity is linked to a higher gel strength with an increased polysaccharide content (Costell et al., 2000; Koliandris et al., 2008; Lundgren et al., 1986). It must be noted that the texture–flavour interactions clearly depend on the nature of the flavour compounds and the type of polysaccharide used (Arancibia et al., 2013; Cook et al., 2018; Troszyńska et al., 2010).

The impact of dextran polysaccharide on flavour perception of bakery products has been investigated only in few recent studies. For instance, the dextran-enriched (0.27% bread basis) faba-bean sourdough composite bread was perceived as less intense in pea odour, crumb/crust odour, musty odour and taste and aftertaste compared to faba-bean sourdough bread without dextran and composite control bread (Varis, 2017, p. 85). Similarly, the dextran-enriched (0.56% bread basis) sorghum sourdough composite bread showed lower intensities of sour odour and taste, bitter taste and aftertaste than its dextran-negative counterpart (Wang et al., 2020). The produced dextran seemed to be primarily responsible for the flavour masking effect since the two sourdough breads had identical levels of sour- and bitter-related flavour compounds, such as lactic/acetic acid and polyphenolic compounds. This hypothesis was further collaborated by following the perceptual changes in model wheat breads containing purified dextran of varying concentrations from 0.12% to 0.96% (bread basis) using a sensory scaling assay (magnitude estimation) (Wang et al., 2020). A trained sensory panel ($n = 17$) verified the suppressing effect of dextran on sour and bitter off-flavours in chemically-acidified breads and caffeine-containing breads, respectively. Moreover, the flavour masking effect of dextran in bread was shown to be concentration dependent. The masking phenomenon seemed to take place at dextran concentrations higher than its c*. Above c*, a reduction in flavour intensity with increased polymer content was observed. Below this value, the flavour perception remained unchanged.

5.3. *Mechanisms of the flavour-masking effect of dextran*

The underlying mechanism of flavour masking by polysaccharides in food matrices is an on-going debate. Three phenomena have been proposed (*vide infra*): (1) physical structure modification of the matrix that influences the diffusion and release of flavour compounds; (2) molecular interactions between polysaccharides and flavour stimuli; and (3) the mucoadhesion property of polysaccharides.

Physical state: The addition of polysaccharides improves the viscosity or stability of the food system, leading to slower diffusion and migration of flavour molecules to the matrix–saliva or matrix–air interface to activate downstream messengers. In solution, the increased viscosity is due to the entangled polysaccharide network restricting mixing and consequently less flavours are dissolved in saliva for sensation (Koliandris et al., 2008). Regarding breads, the oral texture (e.g. crumb elasticity and cohesiveness) was significantly changed when dextran was added at high concentrations, which may generate a different breakage function upon chewing and consequently altered flavour release (Wang et al., 2020). Bread with high levels of dextran has a more cohesive and softer texture. When a crumb is chewed and mixed with saliva, a properly sized bolus with high apparent viscosity is formed, which provides a high retention capacity of flavour molecules. In contrast, bread with or without a small amount of dextran shows a more brittle or crumbly structure, which generates greater surface area for flavour release following intensive breakage during chewing. Another possibility could be that the high water binding capacity of polysaccharides limits water migration in the food matrix and thereby suppresses flavour perception (Hollowood et al., 2002).

Molecular level: There are various types of molecular interaction between polysaccharides and volatile compounds, including hydrogen bonding, hydrophobic interactions, apolar van der Waals interactions (London dispersion forces), steric interactions or molecular inclusion, depending on the structure (e.g. ionic groups and chain length) and surface area of the macromolecules (Braudo et al., 2000; Lubbers et al., 2007; Rutschmann & Solms, 1990; Samavati et al., 2012; Yven et al., 1998). Unlike the studies on aroma compounds, few studies have evaluated the interactions between non-volatile compounds and polysaccharides. Therefore, future research should focus on tastant–dextran binding for a better understanding of their impact on taste release.

Mucoadhesion: The surface of the tongue is covered by a mucosal membrane. Many polysaccharides adhere to the mucosal surfaces through intermolecular interactions (e.g. hydrogen bonding, van der Waals forces, covalent bonding and hydrophobic interactions) and the penetration of polymer chains (Cook et al., 2017). The mucoadhesive nature enables their recent widespread use in the pharmaceutical industry, such as drug formulations and in food products, to modulate the retention and perception of flavour (Cook et al., 2017, 2018). Mucoadhesion has been shown to contribute to the retention of tastants on taste buds and slow down the release of the aroma compounds (Mälkki et al., 1993). Polysaccharides differ in their mucoadhesive strength and show a different controlling effect in aroma release and perception (Cook et al., 2018). In this regard, future work is necessitated to evaluate the mucoadhesive properties of dextran and its corresponding influence on flavour modulation.

6. Conclusions

A wealth of recent research clearly highlights that the *in-situ*-produced dextrans by sourdough fermentation are natural, effective and versatile bread improvers. The formation of dextran *in situ* enables the development of appealing composite or wheat-free breads with acceptable texture and flavour attributes, which is considered a great option to increase the use of alternative grains in bakery products. Remarkably, besides the structure and concentration of the dextran polymers, the acidification levels of the applied matrix determine their functional performance in dough rheology and bread characteristics. In a mildly acidic environment, high Mw dextran induces positive changes to the viscoelastic behaviour and extensional properties of dough, leading to improved textural quality and prolonged shelf-life of bread. On the other hand, intensive acidification counteracts the beneficial effects of dextran. The underlying mechanisms of action and the molecular interactions between dextrans and the structural dough components, such as gluten and starch, warrant further clarification. Importantly, using dextrans to mask the undesirable flavours derived from non-wheat ingredients and the processing steps is a novel and attractive solution—and represents a key area for future research.

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