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Gas cell stabilization by aqueous-phase constituents during bread production from wheat and rye dough and oat batter: Dough or batter liquor as model system

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Abstract

Proper gas cell stability during fermentation and baking is essential to obtain high-quality bread. Gas cells in wheat dough are stabilized by the gluten network formed during kneading and, from the moment this network locally ruptures, by liquid films containing nonstarch polysaccharides (NSPs) and surface-active proteins and lipids. Dough liquor (DL), the supernatant after ultracentrifugation of dough, is a model system for these liquid films and has been extensively studied mostly in the context of wheat bread making. Nonwheat breads are often of lower quality (loaf volume and crumb structure) than wheat breads because their doughs/batters lack a viscoelastic wheat gluten network. Therefore, gas cell stabilization by liquid film constituents may be more important in nonwheat than in wheat bread making. This manuscript aims to review the knowledge on DL/batter liquor (BL) and its relevance for studying gas cell stabilization in wheat and nonwheat (rye and oat) bread making. To this end, the unit operations in wheat, rye, and oat bread making are described with emphasis on gas incorporation and gas cell (de)stabilization. A discussion of the knowledge on the recoveries and chemical structures of proteins, lipids, and NSPs in DLs/BLs is provided and key findings of studies dealing with foaming and air–water interfacial properties of DL/BL are discussed. Next, the extent to which DL/BL functionality can be related to bread properties is addressed. Finally, the extent to which DL/BL is a representative model system for the aqueous phase of dough/batter is discussed and related to knowledge gaps and further research opportunities.

KEYWORDS
batter liquor, bread, dough liquor, gas cell, lipids, nonstarch polysaccharides, proteins

Abbreviations: A–W, air–water; AX, Arabinoxylan; BL, Batter liquor; DAG, Diacylglycerol; DGDG, Digalactosyldiacylglycerol; DL, Dough liquor; dm, Dry matter; FFA, Free fatty acid; MAG, Monoacylglycerol; MGDG, Monogalactosyldiacylglycerol; MW, Molecular weight; NA(L)PE, N-acyl(lyso)phosphatidylethanolamine; NPL, Nonpolar lipid; NSP, Nonstarch polysaccharide; PC, Phosphatidylcholine; PE, Phosphatidylethanolamine; PhL, Phospholipid; PI, Phosphatidylinositol; PL, Polar lipid; TAG, Triacylglycerol; UF, Ultracentrifugation; WE-AX, Water-extractable arabinoxylan; WU-AX, Water-unextractable arabinoxylan.

1 | INTRODUCTION

Bread is an important staple food. In many parts of the world, most of it is made from wheat (*Triticum aestivum* L.) flour with a straight-dough process that typically starts by mixing flour, water, yeast (*Saccharomyces cerevisiae*), and salt (and in some cases other minor ingredients such as redox agents and enzymes) into viscoelastic dough (Delcour & Hoseney, 2010). The dough is then placed in a fermentation cabinet and baked in an oven. The loaf volume, crumb structure, and texture of bread, which are the quality parameters that are focused on in the present paper, to a large extent depend on the total number and size distribution of gas cells formed during dough formation and on how these gas cells are stabilized during dough fermentation and baking. In wheat bread making, hydrated gluten proteins develop into a continuous, viscoelastic network that in the early stages of fermentation provides structural support to expanding gas cells and thereby stabilizes them (van Vliet et al., 1992). It has been suggested that this network toward the end of fermentation no longer completely surrounds gas cells as it regionally ruptures when dough expands (Gan et al., 1990). In such regions, proteins, surface-active lipids, and nonstarch polysaccharides (NSPs) dissolved in a liquid film surrounding the gas cells supposedly take over their stabilization (Gan et al., 1995). These liquid films are believed to be part of the aqueous phase of dough.

Today's consumers are increasingly interested in consuming a variety of bread products. Examples of such product types are nonwheat and mixed cereal breads. To some of these, health or nutritional benefits are ascribed. These may relate to the fact that (partially) substituting wheat (*Triticum aestivum* L.) by, for example, rye (*Secale cereale* L.) or oat (*Avena sativa* L.) flour increases bread dietary fiber (Andersson et al., 2009; Dini et al., 2012; Hüttner & Arendt, 2010) and lysine (i.e., an essential amino acid) (Delcour & Hoseney, 2010; Dewettinck et al., 2008) contents. In addition, breads from gluten-free cereals such as pure oats can be consumed by individuals with celiac disease only if all earlier celiac disease-related symptoms are alleviated and the patient has been on a gluten-free diet for a minimum of 6 months (Cohen et al., 2019; La Vieille et al., 2016). However, nonwheat breads have poorer loaf volume and crumb structure than wheat bread because they lack the typical wheat gluten network in their doughs or batters. Hence, it can be reasoned that gas cell stabilization by dough or batter aqueous-phase constituents may be even of greater importance in nonwheat than in wheat bread making. Interesting in this regard is that most nonwheat cereal flours contain even higher levels of aqueous-phase-soluble constituents than wheat flour (Janssen, 2020).

An approach that has been adopted for investigating the properties of the wheat dough aqueous-phase constituents involves isolating at least a fraction of it by ultracentrifugation (UF). The supernatant obtained in this way is generally referred to as "dough liquor" (DL). Such DL is considered representative for the aqueous phase of dough (Baker et al., 1946; MacRitchie, 1976) and consists primarily of proteins, lipids, arabinoxylan (AX), β-D-glucan, and mono-, di-, and oligosaccharides (Janssen, 2020; Primo-Martín et al., 2006; Salt et al., 2006; Turbin-Orger, Della Valle, et al., 2015). Since 1946, 32 studies have been published in which DL was isolated from wheat dough. In contrast, only four publications (Janssen et al., 2021; Janssen, Wouters, Linclau, et al., 2020; Janssen, Wouters, Meeus, et al., 2020; Janssen, Wouters, Pauly, et al., 2018) exist in which DL was separated from rye dough or "batter liquor" (BL) was isolated from oat batter. In most of the above studies, the aim was to explore the gas cell stabilizing potential of DL/BL constituents by assessing their foaming behavior, bulk viscosity (η_{bulk}), and air–water (A–W) interfacial properties.

Against the above background, the present manuscript aims to comprehensively and critically review the current knowledge on DL/BL and its relevance when studying gas cell stabilization in wheat, rye, and oat bread making. In Section 2 of this review, the main unit operations in wheat and nonwheat (i.e., rye and oat) bread making are described with emphasis on the principles governing gas incorporation and gas cell (de)stabilization. This knowledge is crucial to comprehend at which stage(s) in the bread making process and by which mechanisms dough/batter aqueous-phase constituents contribute to gas cell stability. In Section 3, the history of the use of UF as a tool to separate the aqueous phase of dough/batter is first addressed. Then, literature data on the recoveries and chemical structures of proteins, lipids, and NSPs found in wheat and rye DLs as well as in oat BL are discussed in detail. This is essential for obtaining in-depth understanding of the flour constituents/dough ingredients likely to be recovered in DL/BL as well as of the role they may play in wheat, rye, and oat bread dough/batter gas cell stabilization. To this end, mechanisms by which proteins and surface-active lipids can stabilize A–W interfaces are highlighted prior to providing a thorough discussion on the most important findings in the available literature dealing with the foaming and A–W interfacial properties of DL/BL. In Section 4, the relation between DL/BL functionality and bread properties is addressed. Finally, the validity of DL/BL as a model system for studying gas cell stabilization in bread making is discussed and related to critical knowledge gaps as well as perspectives for further research that could shed even more light on the mechanisms by which gas cells in bread making are stabilized. Fully grasping these mechanisms will contribute to optimizing the

production and quality of wheat, nonwheat, gluten-free, and mixed cereal breads.

2 | GAS INCORPORATION AND GAS CELL (DE)STABILIZATION DURING BREAD PRODUCTION

2.1 | Wheat bread making

The three main phases of the wheat bread making process are (1) dough mixing, (2) fermentation, and (3) baking. Each of these are here discussed with a focus on the mechanisms by which gas is incorporated and gas cells are (de)stabilized.

2.1.1 | Mixing

Dough is formed by mixing and kneading its ingredients. The action of the mixer ensures proper hydration of the gluten proteins and starch granules of the flour used. In an optimally mixed dough, gluten proteins occur as a continuous network consisting of films or sheets as the main structural element (Amend & Belitz, 1991), whereas starch granules remain discontinuous and act as filling agent (Bloksma, 1990). Interaction between starch granules and gluten proteins in wheat flour dough is mediated by its puroindolines (i.e., small globular proteins) and polar lipids (PLs) (remnants from the amyloplast lipid membrane in which starch granules are synthesized) at the surface of starch granules (Pauly et al., 2013). Although starch certainly co-determines dough rheology (Amemiya & Menjivar, 1992; Larsson & Eliasson, 1997), gluten protein provides dough with viscoelastic character and suitable bread making properties. Gliadins and glutenins, which make up the gluten fraction of the wheat proteins, each play a different role herein. In this manuscript, the term "gluten–starch matrix" is used for describing the bulk phase of dough as a whole, whereas the term "gluten network" is used for referring to a specific characteristic of gluten proteins in dough.

Glutenins play a key role in forming the three-dimensional gluten network during dough development and bestow elasticity and strength on dough (Belton, 1999; Ewart, 1972; Veraverbeke et al., 1998). Very important in this context are the oxidation of free thiol groups of glutenin polymers and thiol-disulfide exchange reactions between such polymers, eventually resulting in a very high molecular weight (MW) network of interconnected glutenin subunits (Ooms & Delcour, 2019). The elastic properties of this gluten network can according to Belton (1999) be ascribed to an interplay between "loop" regions, in which glutenin–glutenin interactions are favored, and "train" regions, in which glutenin–water interactions are favored. Hydrogen bonding dynamics in these loop-and-train regions during dough mixing supposedly provide the gluten network with the ability to be extended without breaking (Belton, 1999).

Gliadins impart viscous flow properties to dough. They are noncovalently incorporated in the dough glutenin network (Shewry et al., 2000) and thereby reduce the degree to which glutenin–glutenin interactions occur (Cornec et al., 1994; Khatkar et al., 1995). Indeed, the gliadin-to-glutenin mass ratio is an important parameter for the bread making quality of wheat flour as it significantly affects dough rheology (Veraverbeke & Delcour, 2002).

Gliadins and glutenins have isoelectric points of 7.8 and 5.8, respectively (Lambrecht et al., 2017). Thus, at the pH of freshly mixed (5.8) and fermented (4.8) doughs (Jayaram et al., 2013), gliadins are positively charged, whereas glutenins carry little if any charge. Hence, the contribution of electrostatic repulsive forces between two gliadin molecules can be expected to be greater than those between two glutenin molecules. In the authors' view, this difference may have two important consequences for the behavior of gliadins and glutenins in dough. First, gliadin molecules may become more soluble over the course of fermentation. That the solubility of aqueous gliadin dispersions increases from approximately 30% at pH 6.0 to 90% at pH 4.0 (Thewissen et al., 2011) seems to support this reasoning. Second, the lower extent of electrostatic repulsion between glutenins may increase their tendency to take part in network formation during dough mixing, although other glutenin characteristics such as their composition (e.g., ratio of high- to low-MW glutenin subunits), structure (e.g., degree of branching), and polymer size distribution must be considered as well (Veraverbeke & Delcour, 2002).

Dough mixing results in redistribution of most wheat flour lipids from the surface of starch granules to gluten proteins (Chung & Tsen, 1975; Gerits et al., 2013; Janssen, Wouters, Pareyt, et al., 2018; Olcott & Mecham, 1947). The extent to which redistribution of lipids impacts the rheology of dough is still under debate but not the focus of the present work.

An important event during dough mixing is the incorporation of air, a phenomenon first addressed by Baker (1941) and Baker and Mize (1937, 1941, 1946). These researchers showed that it coincides with dough formation and that the type and pressure of the gas present during mixing have a pronounced effect on dough development. Gas cells are physically entrapped in the gluten–starch matrix once dough is sufficiently coherent. The two major constituents of air, that is, nitrogen and oxygen, are present in a ratio of 3.7 to 1. Although the solubility of oxygen in water is twice

that of nitrogen (Kaye & Laby, 1911), the majority of it is gradually consumed by yeast or used by flour endogenous lipoxygenases for unsaturated lipid oxidation (Decamps et al., 2016). The remaining oxygen is used by other endogenous enzymes such as ascorbic acid oxidase (when the dough recipe comprises ascorbic acid) or consumed in the oxidation of protein-free thiol groups (Decamps et al., 2016). This implies that a few minutes after mixing, the gas cells in dough primarily contain nitrogen. Experimental evidence for the depletion of oxygen over the course of dough mixing has been provided by Joye et al. (2012) using luminescence spectroscopy. The total number and size distribution of gas cells in dough at the end of mixing are important prerequisites for obtaining bread with a desirable crumb structure (Scanlon et al., 2008; Shimiya & Nakamura, 1997; van Duynhoven et al., 2003). This relates to the fact that the only way to form new gas cells after dough mixing is by redividing the existing ones in a unit operation called punching (see Section 2.1.2) (Delcour & Hoseney, 2010). Thus, the gas cells formed during mixing are the only ones into which carbon dioxide can diffuse during fermentation once the dough aqueous phase is saturated with carbon dioxide (see Section 2.1.2). However, the contribution of the initial dough gas cell population is expected to be limited when multiple punching steps are applied throughout fermentation (see Section 2.1.2).

In recent years, noninvasive techniques (i.e., X-ray computed microtomography [Babin et al., 2006; Bellido et al., 2006; Koksel, Aritan, et al., 2016; Trinh et al., 2013] and ultrasound measurements [Koksel, Scanlon, et al., 2016; Koksel, Strybulevych, Page, et al., 2017; Leroy et al., 2008; Scanlon et al., 2008] or a combination of both [Koksel, Strybulevych, Aritan, et al., 2017]) have allowed concluding that the gas cell size distribution in freshly mixed dough is characterized by a (positively skewed) lognormal function. Babin et al. (2006) measured an average gas cell radius of 90 μm for yeast-leavened dough a few minutes after mixing. Considerably lower average gas cell radii (55 μm [Bellido et al., 2006] and 52 μm [Trinh et al., 2013]) have been reported for nonyeast-leavened dough. Also for nonyeast-leavened dough, Leroy et al. (2008) and Koksel, Aritan, et al. (2016) observed median gas cell radii of 14 and 22 μm, respectively. Whether this difference in gas cell radius in freshly mixed yeast-leavened and nonyeast-leavened dough is relevant is difficult to assess as, to the best of our knowledge, only Babin et al. (2006) have provided data on the gas cell radii in yeast-leavened dough a few minutes after mixing. In addition, the mixing conditions in terms of water levels, mixer types, and mixing times and the types of flour used above differed from each other, which also may have influenced the average initial gas cell radius. The number of gas cells per volume unit in nonyeast-leavened dough has been estimated as 56,540 cells/cmş (Bellido et al., 2006) and 120,000 cells/cmş (Trinh et al., 2013). However, the actual number may be considerably higher, as recent high-resolution X-ray computed microtomography measurements indicated numbers between 1350k and 2100k cells/cmş for nonyeast-leavened dough (Koksel, Aritan, et al., 2016). Even though Bellido et al. (2006) reported considerably lower numbers for dough than Koksel, Aritan, et al. (2016), the ratios of total gas cell to total dough volume in both studies (i.e., 10% and 11%, respectively) were similar. Moreover, these volume densities agree well with those reported by Babin et al. (2006) (10%) for yeast-leavened dough a few minutes after mixing and by Leroy et al. (2008) (12%) for nonyeast-leavened dough. It thus seems that—a few minutes after mixing—gas makes up 10% to 12% of the total volume of dough irrespective of whether yeast is present or not.

Evidently, the size distribution and total number of gas cells in dough depend on several parameters.

The first factor that impacts dough aeration is the pressure applied during mixing (Campbell et al., 1998; Chin et al., 2004; Martin et al., 2004; Trinh et al., 2013). Dough mixed under higher mixer headspace pressure (200 kPa) tends to contain more gas than when mixed under lower such pressure (13 kPa) (Campbell & Martin, 2012; Chiotellis & Campbell, 2003). Trinh et al. (2013) compared doughs mixed either at a constant headspace pressure of 100 kPa or in a headspace pressure regime in which the initial pressure of 100 kPa was reduced to 50 kPa over the course of mixing. In the latter case, the number of gas cells per unit volume and mean gas cell volume were 25% and 50%, respectively, lower than in the former case. In each of these studies, the mixer was connected to separate vacuum and compressed air lines that allowed (i) mixing at pressures above or below atmospheric pressure and (ii) adjusting the mixer headspace pressure over the course of mixing (Dimitrova et al., 2001).

A second parameter is the total work or energy input during mixing. According to Chin and Campbell (2005), it depends not only on the dimensions and geometry of the mixer, but also on mixing time and mixing speed. They indeed observed that "increasing the work input" either by increasing the mixing speed at constant mixing time or by increasing the mixing time at constant mixing speed increases the amount of gas incorporated. Also, when a "constant work input" was delivered with either a higher mixing speed and a shorter mixing time or by a lower mixing speed and a longer mixing time, the former lead to more gas incorporation in dough (Chin & Campbell, 2005) likely because the existing gas cells experienced greater shear forces and thus broke up more easily into multiple smaller ones (Wilde, 2012). The latter would imply that higher mixing speeds result in doughs with smaller gas

cells even if this was not reported on in the study by Chin and Campbell (2005).

A third factor is the type of flour used and how it is mixed into dough. Interestingly, doughs prepared from either low- or high-protein flour mixed at the same speed incorporate similar amounts of gas, but less energy input is required to reach maximum aeration in the former than in the latter doughs (Chin & Campbell, 2005).

A fourth factor that plays a role in the aeration of dough is viscosity. At a given mixing speed, the impact of the shear forces exerted on the dough and thus on the gas cells therein is higher when the viscosity is higher. As a result, doughs of high viscosity generally have more and smaller gas cells than doughs of low viscosity as more gas cells are divided into multiple smaller cells as mixing proceeds in the former case (Mills et al., 2003; Wilde, 2012).

Finally, it has been suggested that the size distribution of gas cells in dough also depends on the presence of surface-active constituents that can either spontaneously adsorb at gas cell A–W interfaces (Bloksma, 1981; Kokelaar & Prins, 1995) or be forced upon them due to the mixing action (Örnebro et al., 2000). In this view, such constituents lower σ of newly formed A–W interfaces, which implies that less energy is needed to create them (see Section 3.4.1). During dough mixing, this then facilitates formation of new cells to which carbon dioxide can diffuse during fermentation. However, there is no direct evidence that surface-active constituents are involved in the aeration of dough. In this context, it has been argued that the viscosity of the gluten–starch matrix is too high for soluble surface-active constituents to diffuse to and adsorb at gas cell A–W interfaces (Örnebro et al., 2000). That including sodium stearoyl lactylate in a dough recipe does not change the total volume of gas incorporated in it seems to support this reasoning (Campbell et al., 2001). Last but not least, that isolated gluten protein powders (Balla et al., 1998; Eliasson & Lundh, 1989; Lundh et al., 1988), aqueous alcohol solutions of gliadin (Wannerberger et al., 1997), dilute acid solutions of glutenin (Tao et al., 1989), and flour particles (Eliasson et al., 1991; Lundh et al., 1988) can be spread at A–W interfaces in model system experiments has led to the suggestion that the intensive mechanical treatment during mixing may spread or deposit both soluble and insoluble flour constituents at gas cell A–W interfaces (Örnebro et al., 2000). However, to the best of our knowledge, there is no direct experimental evidence for similar behavior in doughs.

2.1.2 | Fermentation

In bread making, fermentation is typically carried out at 30°C and 90% relative humidity, the latter to prevent the dough surface from drying out. During fermentation, yeast mainly releases ethanol and carbon dioxide (Delcour & Hoseney, 2010), but also organic acids (Rezaei et al., 2015) and aroma compounds (Aslankoohi et al., 2016; Struyf et al., 2017).

Carbon dioxide is arguably the most important compound produced by yeast during bread fermentation. Its production does not result in immediate expansion of gas cells. Indeed, it is released in the aqueous phase of dough and dissolves therein, where it is in equilibrium with carbonic acid. Its impact on the pH of the dough is smaller than that exerted by succinic acid and other organic acids (Jayaram et al., 2013). Once the water phase is saturated with carbon dioxide molecules, they diffuse into the gas cells incorporated during the mixing stage. From this moment onward, gas cells expand.

Ethanol can impact gas cell stabilization by affecting the rheology of dough (see section "Strain hardening by the viscoelastic gluten network") (Jayaram et al., 2013), presumably by altering protein–protein (Lambrecht et al., 2016) and/or protein–starch interactions (Robertson et al., 2011). However, this effect is expected to be relevant only at advanced stages of fermentation as freshly mixed dough contains hardly any ethanol. In addition, ethanol solutions have considerably lower σ than pure water. Thus, ethanol may compete with surface-active constituents (see section "Interfacial stabilization by liquid films containing surface-active constituents") for adsorption at the A–W interface (Dussaud et al., 1994). Furthermore, it may induce changes in protein conformation and thereby in its surface activity (Pace et al., 2004; Wouters et al., 2017).

With regard to organic acids, particularly the release of succinic and acetic acid produced by yeast cells decreases the pH of dough during fermentation (Jayaram et al., 2013; Rezaei et al., 2014). Indeed, a strong pH decrease was observed when nonyeast-leavened dough was prepared with an aqueous succinic (Jayaram et al., 2013; Rezaei et al., 2014, 2015) or acetic (Rezaei et al., 2014, 2015) acid solution or when yeast-leavened dough was prepared with ampicillin (an antibiotic that prevents the bacterial production of lactic acid but leads to a similar yeast metabolite pattern as in dough prepared without ampicillin) (Jayaram et al., 2013). No such pH decrease was observed when nonyeast-leavened dough was prepared with a saturated carbon dioxide solution (at pH 4.0) instead of water (Jayaram et al., 2013). The yeast-mediated pH decrease may affect the charge of gluten proteins (see Section 2.1.1) and thus potentially also their engagement in intermolecular interactions, which in turn can alter dough rheology (Meerts, Cervera, et al., 2018). Dough aqueous-phase proteins and possibly also some lipids may be affected in a similar way (Pauly et al., 2014), which in turn may have an impact on their behavior at the A–W interface (see Section 3.4.1).

In a typical straight-dough process, the first fermentation phase is typically followed by dough punching, molding, and proofing. Punching refers to the mechanical pressing of dough (Delcour & Hoseney, 2010). Although punching releases carbon dioxide, it still positively contributes to the gas cell distribution in dough as it breaks up and thus redistributes preexisting gas cells into multiple smaller ones (Delcour & Hoseney, 2010; Shimiya & Nakamura, 1997). It also redistributes fermentable sugars (Delcour & Hoseney, 2010). Punching is followed by molding and proofing. In pan bread production, molding involves rolling the punched dough into a cylindrical shape, after which its outer parts are carefully folded inward and the dough is placed in a baking tin (Delcour & Hoseney, 2010). Proofing is the final step during which the molded dough can rise before it is baked in the oven.

2.1.3 | Baking

After proofing, the dough is baked. In the oven, pronounced and almost immediate expansion of the dough takes place. This expansion is commonly referred to as the "oven spring" and the result of four phenomena (Delcour & Hoseney, 2010). First, yeast activity and thus carbon dioxide production increase with temperature until yeast cells lyse at around 55°C. Second, gases in the dough expand as temperature increases. Third, the solubility of carbon dioxide in water decreases when temperature increases. Thus, carbon dioxide increasingly diffuses into gas cells as temperature increases. Fourth, the vaporization of both water and ethanol induced by the temperature increase also contributes to the overall dough expansion. The oven rise stops at about 72°C (He & Hoseney, 1991) and partially coincides with dough solidification and thus with the setting of the crumb structure. In bread making, starch gelatinization starts at about 60 to 65°C (Delcour & Hoseney, 2010; Nivelle et al., 2019). As part of the process, starch granules absorb large amounts of water and swell extensively, amylopectin crystals melt, and amylose leaches and thus solubilizes into the extra granular space, which results in a highly viscous paste (Delcour & Hoseney, 2010). At least part of the leached amylose molecules associate with lipids (preferentially with free fatty acids [FFAs] [Janssen, Wouters, Pareyt, et al., 2018]) to form so-called "amylose–lipid inclusion complexes" (Conde-Petit et al., 2006; Kugimiya et al., 1980; Nivelle et al., 2019). Starch swelling and gelatinization are accompanied by substantial water binding by its biopolymers and cause water loss from gluten (Bosmans et al., 2012; Bushuk, 1966; Tolstoguzov, 1997). In addition, heating promotes oxidative crosslinking and sulfhydryl-disulfide interchange reactions in gluten proteins (Guerrieri et al., 1996; Li & Lee, 1998). Although glutenin polymerizes already at 60 to 70°C (Schofield et al., 1983), temperatures exceeding 90°C are required for gliadins to become incorporated in the gluten network (Lagrain et al., 2008).

In summary, both starch gelatinization and gluten polymerization are involved in transformation of the gas discontinuous "foam-like" structure of dough into the gas continuous "sponge-like" structure of bread. Indeed, at this point in the process, gas cells are opened, the structure sets, and carbon dioxide is released from the dough/bread. It is thus imperative for obtaining a high-quality bread that gas cells are sufficiently stable until the moment at which the structure sets.

Especially proofing (Lassoued et al., 2007; van Duynhoven et al., 2003) and oven spring are crucial phases in the context of gas cell stability as it is during these phases that gas cells come in close contact with each other. Gas cell destabilization during these phases leads to a reduction of their numbers and an increase in their mean diameter, phenomena that can be considered equivalent to the "coarsening" of a foam structure, and thus results in a heterogeneous gas cell distribution (Babin et al., 2006; Turbin-Orger et al., 2012; van Duynhoven et al., 2003) and/or in a lower bread volume (due to a loss of gas from dough). Such coarsening can occur via coalescence (i.e., the merging of gas cells) or disproportionation. In what follows, these mechanisms are discussed.

2.1.4 | Gas cell destabilization mechanisms

Disproportionation

"Disproportionation" or "Ostwald ripening" encompasses a net diffusion of gas from smaller to larger gas cells (Garrett, 1993). The Young–Laplace equation relates the pressure difference across an interface (i.e., ΔP, the so-called Laplace pressure) to its shape or curvature. In turn, the curvature of interfaces is defined by their principal radii (R_1 and R_2) as well as by the surface tension (σ) (see section "Surface activity" for a more detailed description of this concept) acting on them (Damodaran, 2005) (Figure 1a). Smaller gas cells experience a greater Laplace pressure than larger ones (Figure 1a). As a point of reference, perfectly spherical gas cells in dough (for which R_1 and R_2 hence are equal) with a σ of 50 mN/m and radii of 50 or 200 μm experience Laplace pressures of 2000 and 500 Pa, respectively.

A consequence of the Young–Laplace equation, at least in common foams, is that gas molecules from smaller cells more readily dissolve in the continuous phase and from there diffuse into larger cells in which the Laplace pressure is lower (Garrett, 1993). When discussing bread dough

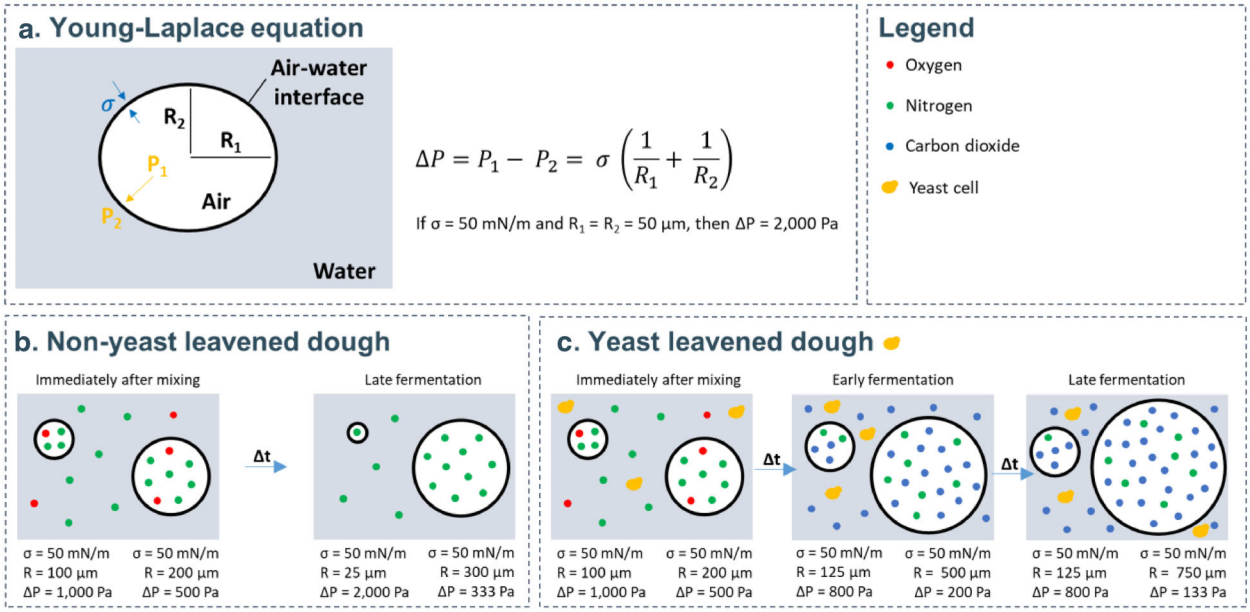

FIGURE 1 (a) Graphical illustration of the Young–Laplace equation that relates the pressure difference between the inside and outside of the curved interface (ΔP) (i.e., the Laplace pressure) of an air bubble in water to its curvature. The latter depends on the radius of the air bubble in the x (R_1) and y (R_2) directions as well as on the surface tension (σ) acting on the air–water interface. Schematic representation of the authors' view on the occurrence of gas cell disproportionation in (b) nonyeast-leavened dough and (c) yeast-leavened dough over the course of fermentation. In panels b and c, gas cells are considered to be perfect spheres (implying that $R_1 = R_2$ in the Young–Laplace equation) and σ is assumed to be independent of the gas cell radius. The latter assumption is based on the fact that the dough aqueous phase contains an excess of surface-active constituents (Wilde, 2012) that would instantly occupy newly formed gas cell interfacial area

foams, nonyeast-leavened and yeast-leavened doughs are distinguished, as their gas cell and dough aqueous-phase compositions are different.

That disproportionation can occur in nonyeast-leavened dough was first suggested by Shimiya and Yano (1988). With optical microscopy, they observed that larger gas cells increased in volume at the expense of smaller ones. This was later also shown by Koksel, Aritan, et al. (2016) and Koksel, Strybulevych, Aritan, et al. (2017). With X-ray computed tomography and ultrasound measurements, they observed a twofold decrease in the total number of gas cells with a radius lower than 16 μm (i.e., the detection limit of the setup), implying that small gas cells shrank and eventually disappeared (Figure 2a). As a result, the median gas cell radius increased when the dough was rested for a period of 190 min (Koksel, Aritan, et al., 2016; Koksel, Strybulevych, Aritan, et al., 2017) (Figure 2b).

Shimiya and Nakamura (1997) reported a higher number of gas cells with a diameter lower than 50 μm in fermented yeast-leavened dough than in nonyeast-leavened dough (rested for a period equivalent to the fermentation time of the yeast-leavened dough). Over the course of a 160-min fermentation process, these small gas cells in yeast-leavened doughs neither expanded nor shrank (Shimiya & Nakamura, 1997). That they did not grow may be because of the lower Laplace pressure in the larger gas cells (Kumagai et al., 1991; Shah et al., 1998; Shimiya & Nakamura, 1997) and that they did not shrink may, as suggested by van Vliet et al. (1992), to an extent have been related to the presence of a strongly viscoelastic film at their A–W interfaces. However, one would expect such viscoelastic film to prevent shrinkage of gas cells also in nonyeast-leavened doughs. As noted above, this does not seem to be the case.

That disproportionation seems more pronounced in nonyeast-leavened than in yeast-leavened doughs (Shimiya & Nakamura, 1997) most likely relates to differences in gas cell and dough aqueous-phase composition in both cases. In nonyeast-leavened doughs, no carbon dioxide is produced. Hence, gas cells in such doughs consist of nitrogen and oxygen. As oxygen is more rapidly consumed (see Section 2.1.1), a few minutes after mixing already gas cells primarily consist of nitrogen. When the dough gas cell size distribution is heterogeneous, Laplace pressure differences provoke diffusion of nitrogen molecules from smaller to larger gas cells (Figure 1b).

In yeast-leavened doughs, carbon dioxide is continuously released into the dough aqueous phase. When it is saturated with it, excess carbon dioxide molecules diffuse into the gas cells formed during mixing. One could argue that carbon dioxide only diffuses into larger gas cells, given the lower Laplace pressure therein than in smaller gas cells. This would imply that smaller gas

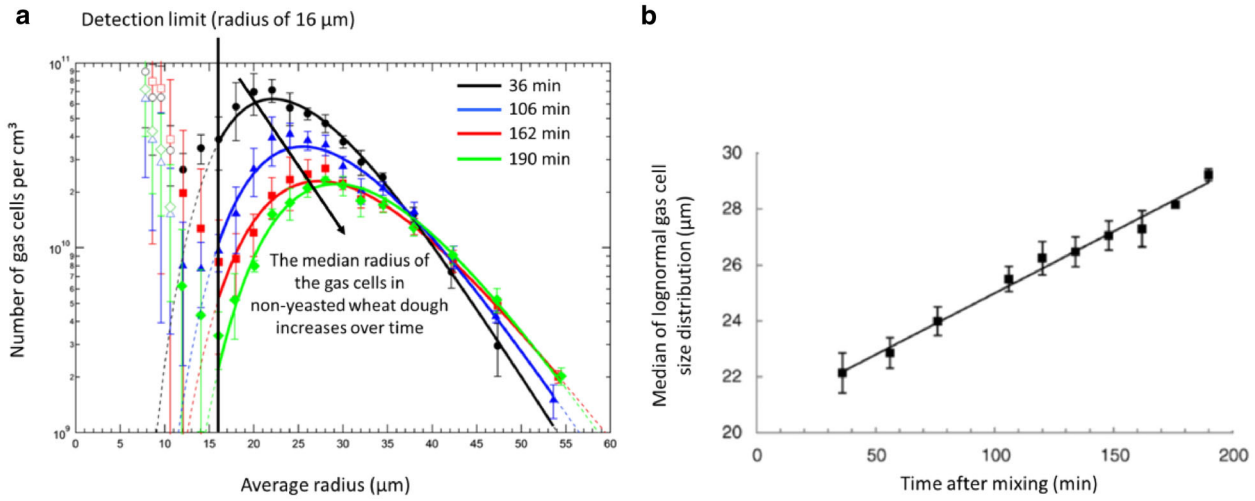

FIGURE 2 (a) Evolution of the gas cell size distribution (black circles, 36 min; blue triangles, 106 min; red squares, 162 min; green diamonds, 190 min) in nonyeast-leavened wheat dough as a function of mixing time and the respective fitted lognormal probability density functions (striped lines). (b) Evolution of the median of the fitted lognormal gas cell size distribution in nonyeast-leavened wheat dough as a function of mixing time. That the median gas cell radius increases over time implies that disproportionation occurs in nonyeast-leavened wheat dough. Reproduced with permission from Koksel, Aritan, et al. (2016)

cells contain no carbon dioxide. If this were the case, behavior as in nonyeast-leavened doughs would be expected, that is, these small gas cells would disappear as nitrogen molecules diffuse from smaller to larger gas cells, driven by their Laplace pressure difference. However, no shrinkage of smaller gas cells seems to occur in yeast-leavened doughs (Shimiya & Nakamura, 1997). Although additional experimental evidence is required to confirm that smaller gas cells in yeast-leavened doughs do not shrink during fermentation, observations by Shimiya and Nakamura (1997) imply that—at least in the early stages of fermentation—carbon dioxide does diffuse into both smaller and larger gas cells (Figure 1c). Over the course of fermentation, larger gas cells then expand while smaller gas cells do not (Shimiya & Nakamura, 1997). Thus, carbon dioxide produced by yeast during later fermentation seems to preferentially diffuse into larger gas cells. It remains to be investigated why such an effect seems to take place in advanced stages of fermentation. Possibly, the increasingly larger difference in Laplace pressure between smaller and larger gas cells plays a role in this. In the early stages of fermentation, the difference in Laplace pressure between smaller and larger gas cells could be insufficient to completely prevent carbon dioxide diffusion into smaller gas cells. As the Laplace pressure difference increases (due to expansion of the larger gas cells), the preferential diffusion of carbon dioxide into larger gas cells becomes more pronounced, now (almost) completely preventing diffusion of carbon dioxide in the smaller gas cells (Figure 1c). Irrespective of the above, the scenario whereby smaller gas cells remain small while larger ones continuously expand due to preferential diffusion of yeast-produced carbon dioxide to the latter because of Laplace pressure differences still—as is the case for disproportionation—leads to a greater heterogeneity in gas cell distribution of the foam structure of yeast-leavened dough (Kumagai et al., 1991; Shah et al., 1998; Shimiya & Nakamura, 1997). Immediately after mixing, a homogeneous distribution of gas cells in many instances is desirable, as it results in uniform expansion of these gas cells during fermentation and, after baking, in a homogeneous crumb structure. Evidently, the crumb structure desired depends on the type of bread and on regional preferences. For instance, a standard tin loaf requires the bread dough to have numerous, small gas cells, whereas a French baguette dough is typically characterized by fewer, larger gas cells (Wilde, 2012).

Coalescence

Coarsening of the foam-like structure of dough occurs when smaller gas cells merge into larger ones. This phenomenon is generally known as "coalescence." In regular foams, the distance between gas cells and thus their susceptibility to coalescence depends on the rate at which the liquid in the films separating them drains (Haas & Johnson, 1967). The very high viscosity of wheat dough prevents the aqueous phase from draining (Mills et al., 2003; Wilde, 2012). Hence, when the gluten network provides gas cells with physical support and thus stability, no coalescence is expected. This for the most part seems to be the case, as will be discussed below (see section "Strain hardening by the viscoelastic gluten network"). However, during

proofing (see Section 2.1.2) and oven rise (see Section 2.1.3), the gluten network may regionally rupture because of its substantial extension as a result of gas cell expansion. In such case, gas cells would be separated only by a liquid film (Gan et al., 1990) (see section "Interfacial stabilization by liquid films containing surface-active constituents"). From this moment onward, liquid drainage can be expected to occur at a rate that largely depends on the η_{bulk} of the fluid in these films. Such drainage evidently decreases the distance between gas cells and may even lead to coalescence. The extent to which coalescence occurs mostly depends on the composition and stability of the gas cell A–W interfaces. The gas cell stabilizing mechanisms in bread making, that is, strain hardening by the gluten network and interfacial stabilization by liquid film constituents, are discussed in the next section.

2.1.5 | Gas cell stabilization mechanisms

Strain hardening by the viscoelastic gluten network

The degree to which gas cells are stabilized in bread making first and foremost depends on the viscoelastic flow properties of dough. Hydrated gluten proteins provide dough with the ability to "strain harden" under extension (van Vliet et al., 1992), which means that the stress needed to deform dough increases more than proportionally when it is subjected to larger strains. A result of strain hardening of gluten proteins is that thinning of dough films between neighboring gas cells as a result of their expansion occurs where said films have the greatest thickness (Figure 3c1). This mechanism promotes uniform expansion of gas cells and thereby counteracts coalescence and disproportionation (van Vliet et al., 1992). A measure for strain hardening is typically obtained by monitoring the extensional viscosity of dough as a function of its deformation. This deformation can be applied either in one (uniaxial) or two (biaxial) directions.

In experimental studies, uniaxial deformation of dough is typically imposed with a Kieffer dough and gluten extensibility rig (Kieffer et al., 1998; Dunnewind et al., 2002) or an extensional viscosity fixture coupled to a standard rheometer (Meerts, Cervera, et al., 2018; Meerts et al., 2017a, 2017b; Meerts, Vaes, et al., 2018; Meerts, Van Ammel, et al., 2017; Meeus et al., 2019; Melis, 2019), whereas compression between two lubricated plates (Janssen et al., 1996; Kokelaar et al., 1996; Sliwinski, Kolster, et al., 2004; Sliwinski, van der Hoef, et al., 2004; Turbin-Orger et al., 2016; van Vliet et al., 1992) or bubble inflation devices (Chin et al., 2005; Dobraszczyk & Roberts, 1994; Sroan et al., 2009) allows subjecting dough to biaxial deformations. However, it is likely that strain hardening not always effectively succeeds at stabilizing gas cells throughout fermentation and baking.

Interfacial stabilization by liquid films containing surface-active constituents

Gan et al. (1990) flash froze wheat doughs prepared from either white flour or whole meal in liquid nitrogen at different time points during fermentation and investigated their internal structure with cryo-scanning electron microscopy. At advanced stages of fermentation, some gas cells were not completely surrounded by the gluten–starch matrix (Gan et al., 1990). Prior to sublimation of surface ice under vacuum, ice crystals were observed near gas cell A–W interfaces. After sublimation, a ruptured gluten network was observed (as schematically illustrated in the transition from C1 to C2 in Figure 3) (Gan et al., 1990). During fermentation and baking, gluten strands can rupture. As already mentioned above, during baking, water is redistributed from gluten proteins to starch granules as the latter gelatinize (Bosmans et al., 2012; Bushuk, 1966; Dreese et al., 1988; Tolstoguzov, 1997; Willhoft, 1971). Indeed, considerably more water is associated with the starch fraction in bread crumb (77%) than in freshly mixed dough (46%) (Bushuk, 1966). Although it has been argued that water redistribution from gluten to starch makes the gluten network more susceptible to fracturing (Babin et al., 2006), to the best of our knowledge direct experimental evidence for this hypothesis has not yet been brought forward. Interestingly, despite local discontinuities in the gluten network around gas cells, the dough still retains its gas and even continues to expand (Gan et al., 1990). Thus, Gan et al. (1990) reasoned that besides strain hardening of the gluten network an additional barrier provides gas cells with stability even when not completely enveloped by said network. It has been proposed that this barrier in essence is a liquid film that has been named a "liquid lamella" and contains surface-active constituents (Figure 3c2) (Gan et al., 1990, 1995). Rupture of these liquid films would of course lead to gas cell coalescence (Figure 3d). A critical remark is that the above reasoning is based on cryo-scanning electron microscopy evidence for which the sample preparation is often rather destructive and leads to artifacts (e.g., rupturing of the gluten network). Still, that surface-active constituents may occur at dough gas cell A–W interfaces had already been suggested earlier (Bloksma, 1990; Larsson, 1983; MacRitchie, 1976; MacRitchie & Gras, 1973; Parker et al., 1990), although no direct experimental evidence was put forward at that time.

Over the past two decades, further evidence has supported the concept that gas cells in dough are stabilized by liquid films containing surface-active constituents.

Dubreil et al. (2002) located fluorescently labeled puroindoline-a (i.e., a small globular protein

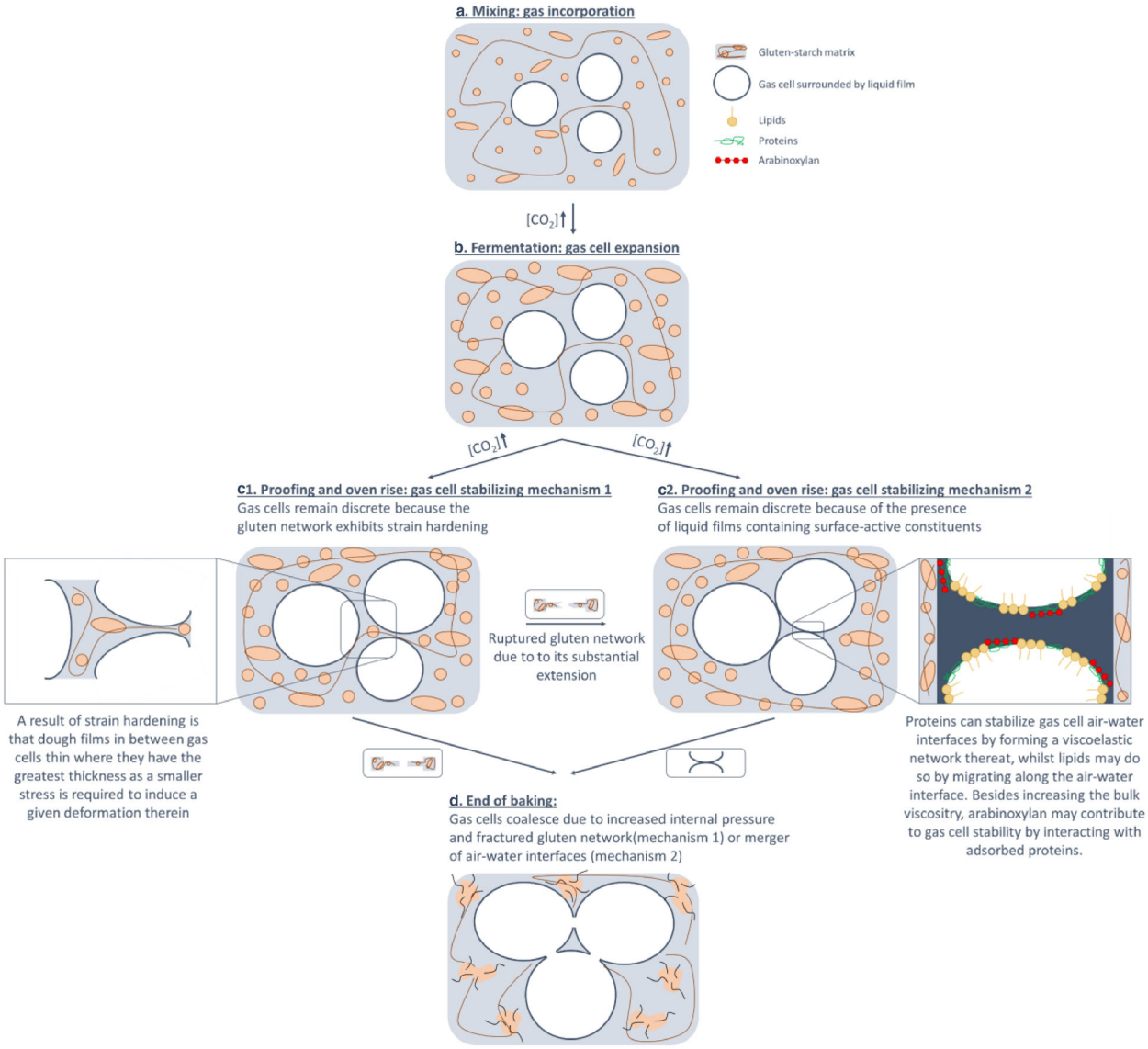

FIGURE 3 Schematic representation of the presumably simultaneously occurring gas cell stabilization mechanisms in bread making. Gas cells are incorporated during dough mixing (a) and in the early stages of fermentation physically stabilized by the gluten network (b). Later on, two scenarios may occur. In scenario 1, during proofing and oven rise, the gluten network exhibits strain hardening, which promotes uniform expansion of gas cells and thereby stabilizes them (c1). As such, gas cells remain stable until they merge at the end of baking when the crumb structure sets (d). In scenario 2, during proofing and oven rise, the gluten network ruptures regionally due to substantial extension. It is believed that at this point in time, surface-active proteins and lipids and arabinoxylans dissolved in liquid films surrounding gas cells take over their stabilization (c2). This liquid film supposedly stabilizes gas cells until at the end of baking gas cell air–water interfaces merge (d)

endogenously present in some wheat flour types) and phospholipids (PhLs) in nonyeast-leavened wheat dough using confocal scanning laser microscopy. Although lipids seemingly covered parts of the gas cell A–W interfacial areas, puroindoline-a was only present in the bulk phase of the dough (Dubreil et al., 2002) (Figure 4a1). In contrast, when dough prepared from defatted flour was supplemented with fluorescently labeled puroindoline-a, the latter seemed to occupy most gas cell A–W interfacial areas (Dubreil et al., 2002) (Figure 4a2). In a similar confocal laser scanning microscopy experiment, Li et al. (2004) localized fluorescently labeled gliadins, glutenins, PhLs, and FFAs in yeast-leavened wheat dough. Although glutenins and FFAs apparently were only present in the bulk phase of the dough, gliadins (Figure 4b1) and PhLs (Figure 4b2) seemed to also occur at gas cell A–W interfaces (Li et al., 2004).

Although magnetic resonance imaging has been successfully used for accurately quantifying dough density changes during fermentation (Bonny et al., 2004; De Guio et al., 2009; Goetz et al., 2003; Rouillé et al., 2005; Takano et al., 2002; van Duynhoven et al., 2003), the resolution

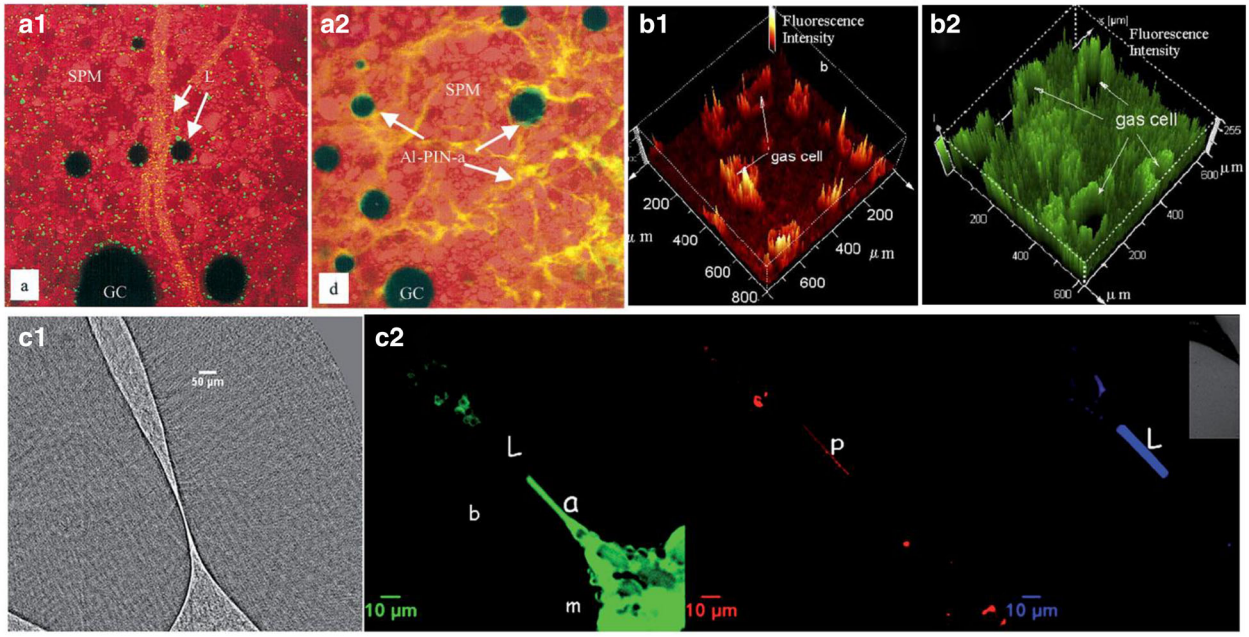

FIGURE 4 Microscopic evidence supporting the concept that liquid films containing surface-active constituents stabilize gas cells in dough. (a) Confocal scanning laser microscopy images of nonyeast-leavened wheat dough (denoted by "SPM") prepared with (a1) nondefatted flour and (a2) defatted flour supplemented with fluorescently labeled puroindoline-a (denoted by "PIN-a"). In image A1, phospholipids appear green and yellow, whereas in image A2, green and yellow colors indicate the locations of puroindoline-a in dough. Gas cells are denoted by "GC." (b) Confocal scanning laser microscopy images of yeast-leavened wheat dough containing fluorescently labeled gliadins (b1) and phospholipids (b2), illustrating their possible occurrence at gas cell air–water interfaces. (c1) Two-dimensional confocal scanning laser microscopy scan of yeast-leavened wheat dough demonstrating that after 125 min of fermentation gas cells are enclosed by dough films with an average thickness lower than 5 μm. (c2) Confocal scanning laser microscopy image of such dough film in which water (denoted by "a"), proteins (denoted by "P"), and lipids (denoted by "L") are stained green, red, and blue, respectively. Reproduced with permission from Dubreil et al. (2002) (a), Li et al. (2004) (b), and Turbin-Orger, Babin, et al. (2015) (c)

and restriction to two dimensions are insufficient to estimate the relative importance of the gluten network and the abovementioned liquid films for gas cell stabilization. Elsewhere, X-ray computed microtomography has allowed observing that part of the gas cells during proofing and oven rise are stabilized by films with an average thickness lower than 15 (Babin et al., 2006) or 5 (Turbin-Orger, Babin, et al., 2015; Turbin-Orger et al., 2012) μm (Figure 4c1) (i.e., the spatial resolutions of the corresponding X-ray setups used). As these films did not contain (swollen) starch granules, which according to Babin et al. (2006) have an average diameter of about 30 μm, it has been argued that they are composed of liquid containing soluble flour constituents such as proteins and lipids (Babin et al., 2006; Turbin-Orger, Babin, et al., 2015; Turbin-Orger et al., 2012). Confocal scanning laser microscopy evidence for the presence of water, proteins, and lipids in the abovementioned 5-μm-thick films was provided by Turbin-Orger, Babin, et al. (2015) and is shown in Figure 4c2. However, it seems that these 5-μm-thick films represent extended gluten strands covered with surface-active constituents.

In summary, despite the indirect evidence discussed above there is still no direct experimental proof that gas cells in bread doughs are surrounded and thus possibly stabilized by liquid films containing surface-active constituents. An alternative approach to test this hypothesis is to investigate the properties of wheat DL. Baker et al. (1946) were the first to ultracentrifuge wheaten dough and coined the term DL for the collected supernatant. As noted above, such DL is considered representative for the aqueous phase of dough. The state-of-the-art regarding the properties of DL will be discussed in-depth in Section 3.

In the next section, the incorporation of gas and stabilization of gas cells in rye and oat bread making are briefly discussed.

2.2 | Rye and oat bread making

Rye (Chen & Bushuk, 1970) and oat (Peterson, 2016) flour have lower prolamin and glutelin levels than wheat flour (Delcour et al., 2012). Moreover, rye (Meeus et al., 2019) and oat (Hüttner et al., 2010) prolamins and glutelins lack the ability to form a strong viscoelastic protein network that wheat gluten proteins form. As a consequence, hydrating and mixing rye flour results in poorly

extensible dough (Verwimp et al., 2006; Weipert, 1997), whereas hydrating and mixing oat flour creates a cake-like batter (Hüttner et al., 2010; Renzetti et al., 2010). Hence, the protein network in rye doughs and oat batters provides gas cells with less structural support during mixing, fermentation, and early baking than is the case in wheat dough. Even more so, rye doughs (Meeus et al., 2019) and certainly also oat batters do not display strain hardening. Therefore, it can be expected that gas cells in yeast-leavened rye doughs and oat batters are more susceptible to coalescence (see section "Coalescence") than those in wheat dough, which then leads to more pronounced coarsening of the foam structure. Indeed, rye (Angioloni & Collar, 2011; Buksa, Nowotna, et al., 2013; Pauly & Delcour, 2018) and oat (Angioloni & Collar, 2011; Hager et al., 2012; Pauly & Delcour, 2018; Renzetti et al., 2008) bread loaves have lower volume and/or crumb with larger and more heterogeneously distributed gas cells than wheat bread. For rye bread, it has been argued that the formation of protein–water-extractable AX (WE-AX) complexes contributes to gas cell stabilization as they increase the viscosity of dough (Buksa, 2016; Buksa et al., 2016). To the best of our knowledge, no efforts have been made to unravel the mechanisms by which gas cells in oat bread making are stabilized. Given that rye and oat flours do not form a viscoelastic protein network, it can be argued that gas cell stabilization by liquid films containing surface-active constituents is more important in nonwheat (and mixed cereal) bread making than in wheat bread making. The gas cell stabilizing potential of aqueous-phase-soluble constituents in rye doughs and oat batters will be addressed in detail in Section 3.

3 | UF AS A TOOL TO STUDY THE ROLE OF DOUGH/BATTER AQUEOUS-PHASE CONSTITUENTS IN WHEAT, RYE, AND OAT BREAD MAKING

3.1 | Historical development

As noted above (see Section 1), at least in 32 studies the aqueous phase has been isolated from wheat dough by UF, whereas a mere four studies are available in which DL/BL was obtained from rye dough or oat batter. Table 1 shows a comprehensive overview of the conditions used for dough making and subsequent UF in these studies. It also lists the aqueous-phase constituents and their investigated properties. Mauritzen and Stewart (1965, 1966) reported on the impact of including redox agents in wheat bread dough formulas on the composition of DL. MacRitchie (1976) established that a gravitational force of 100,000 × g for 50 min suffices to separate the dough's soluble phase from its insoluble phase. In addition, he was the first to assess the foaming properties of wheat DL and suggested that lipids in the aqueous phase play a role in gas cell stabilization. Sahi (1994), possibly encouraged by the microscopy images published by Gan et al. (1990) (see section "Interfacial stabilization by liquid films containing surface-active constituents"), for the first time examined the A–W interfacial properties of wheat DL constituents. Also in the 1990s and early 2000s, the impact of water content (Larsson & Eliasson, 1996a), mixing time (Larsson & Eliasson, 1996b), and addition of different ingredients (Larsson, 2002; Larsson & Eliasson, 1996b) on DL composition was researched. UF was also used to assess the contribution of hydrated gluten proteins to dough rheology (Georgopoulos et al., 2004, 2006; Kuktaite et al., 2005). Later on, the protein (Gan & Schofield, 1998; Salt et al., 2005; Sancho et al., 2008) and lipid (Gerits et al., 2015; Janssen, Wouters, Linclau, et al., 2020; Melis, 2019; Salt et al., 2018) compositions of wheat DLs as well as their foaming properties (Liu et al., 2020; Pauly et al., 2014; Turbin-Orger, Della Valle, et al., 2015), bulk viscosity (η_{bulk}) (Liu et al., 2020; Pauly et al., 2014; Turbin-Orger, Della Valle, et al., 2015), and A–W interfacial properties (Melis, 2019; Min et al., 2020; Primo-Martín et al., 2006; Salt et al., 2006, 2018; Turbin-Orger, Della Valle, et al., 2015) were studied. Recently, Janssen, Wouters, Pareyt, et al. (2018), Janssen, Wouters, Linclau, et al. (2020), and Janssen, Wouters, Meeus, et al. (2020) performed several in-depth studies of the contributions of various DL/BL constituents to the foaming, η_{bulk}, and A–W interfacial properties of wheat and rye DLs and oat BL.

3.2 | Phase separation of wheat and rye DL and oat BL during UF

UF of wheat dough typically yields five distinct phases (Larsson & Eliasson, 1996a, 1996b): (1) a liquid phase, in some cases with a thin oil layer on top of it (Mauritzen & Stewart, 1965; Pauly et al., 2014; Salt et al., 2006), (2) a gel phase, (3) a gluten protein phase, (4) a starch phase, and (5) unseparated dough.

In most studies (Table 1), phases 1 and 2 together are denoted by the term "DL." Exceptions to this are that in the studies of Mauritzen and Stewart (1965, 1966), Turbin-Orger, Della Valle, et al. (2015), Salt et al. (2018), Liu et al. (2020), and Min et al. (2020), the above phases 1 and 2 were subjected to a second centrifugation step to discard the lipids. Although both approaches have merit, in our view these lipids are to be considered as an integral part of DL/BL as they accompany the dough/batter aqueous phase and thus apparently are not strongly bound to the protein–starch matrix (see Section 2.1.1). Above a certain wheat dough water absorption, the amount of phase 1 increases

TABLE 1 Overview of the studies in which the aqueous phase of wheat or rye dough (i.e., wheat or rye dough liquor [DL]) or oat batter (i.e., batter liquor [BL]) was isolated by ultracentrifugation

Reference	Dough formula(s) apart from water	DL/BL isolation conditions	DL posttreatment	DL constituent investigated- Assessed feature	DL functional aspect investigated- Used concentration
Wheat flour					
Baker et al. (1946)	Flour, NaCl, yeast	No dough rest 40,000 rpm, 20′, 30°C	n/a	Protein - Level - Sulfhydryl content	Bulk viscosity - n/c
Mauritzen and Stewart (1965)	Flour, NaCl Flour, NaCl, KIO_3 Flour, NaCl, cysteine Flour, NaCl, *N*-ethylmaleimide Flour, NaCl, Na_2SO_3	45′ dough rest 105,000 × g, 70′, 30°C	Dialysis Centrifugation	Protein - Level Carbohydrates - Hexose content - Pentose content	Bulk viscosity - n/c
Mauritzen and Stewart (1966)	Flour, NaCl Flour, NaCl, KIO_3 Flour, NaCl, cysteine Flour, NaCl, *N*-ethylmaleimide Flour, NaCl, Na_2SO_3	45′ dough rest 105,000 × g, 70′, 30°C	Dialysis Centrifugation	Protein - Level - Sulfhydryl content - Disulfide content	n/a
MacRitchie (1976)	Flour Partially defatted flour	No dough rest 10,000 to 407,000 × g, 50′	Freeze-drying	Protein - Level Lipid - Level	Foaming properties - n/c
Sahi (1994)	Flour	No dough rest 100,000 × g, 75′, 30°C	Freeze-drying Defatting	Protein - Level Lipid - Level	Surface tension decrease - 10 mg dm DL/mL Surface shear modulus - 10 mg dm DL/mL
Larsson and Eliasson (1996a)	Flour	No dough rest 100,000 × g, 60′, 25°C	n/a	n/a	n/a
Larsson and Eliasson (1996a)	Flour Flour, AA Flour, lecithin Partially defatted flour	No dough rest 100,000 × g, 60′, 25°C	n/a	n/a	n/a
Gan and Schofield (1998)	Partially defatted flour, NaCl	No dough rest 100,000 × g, 60′, 4°C	Dialysis Centrifugation Freeze-drying	Protein - Level - MW distribution	n/a
Dubreil et al. (2002)	Flour	No dough rest 100,000 × g, 75′, 30°C	Freeze-drying PIN addition	n/a	Foaming properties - 8 mg dm DL/mL

(Continues)

TABLE 1 (Continued)

Reference	Dough formula(s) apart from water	DL/BL isolation conditions	DL posttreatment	DL constituent investigated- Assessed feature	DL functional aspect investigated- Used concentration
Courtin and Delcour (2002)	Flour, NaCl, sugar, yeast, AA Flour, NaCl, sugar, yeast, AA, xylanase	No dough rest 95′ dough fermentation 155′ dough fermentation 10,000 × g, 15′, 4°C	Boiling Freeze-drying Centrifugation	n/a	Bulk viscosity - n/c
Larsson (2002)	Flour Flour, lactic acid Flour, NaCl	No dough rest 100,000 × g, 60′, 25°C	n/a	n/a	n/a
Kuktaite et al. (2003)	Flour, water	No dough rest 100,000 × g, 60′, 25°C	n/a	Protein - Level - MW distribution	n/a
Sahi (2003)	Flour Flour, fat Flour, DATEM	No dough rest 100,000 × g, 75′, 30°C	Freeze-drying	Protein- Level FAMEs - Level	Surface tension decrease - 10 mg dm DL P/mL Surface shear modulus - 10 mg dm DL P/mL
Mills et al. (2003)	Flour, NaCl, AA	30′ dough rest at 25°C 200,000 × g, 30′, 30°C	n/a	n/a	Surface tension decrease - 0.1 to 1.0 mg dm DL P/mL Surface dilatational modulus - 0.1 to 1.0 mg dm DL P/mL
Watanabe et al. (2003)	Flour Flour, fat	No dough rest 100,000 × g, 90′, 25°C	n/a	n/a	n/a
Georgopoulos et al. (2004)	Flour	No dough rest 100,000 × g, 60′, 25°C	n/a	n/a	n/a
Kuktaite et al. (2005)	Flour	30′ dough rest 100,000 × g, 60′, 25°C	n/a	n/a	n/a
Salt et al. (2005)	Flour Partially defatted flour Flour, NaCl Flour, NaCl, AA	90′ dough rest at 30°C 200,000 × g, 30′, 30°C	Dialysis	Protein - MW distribution - Species identification	n/a
Georgopoulos et al. (2006)	Flour Partially defatted flour	No dough rest 100,000 × g, 60′, 25°C	n/a	n/a	n/a
Salt et al. (2006)	Flour Partially defatted flour Flour and NaCl Flour, NaCl, AA	90′ dough rest at 30°C 200,000 × g, 30′, 30°C	Freezing (−20°C)	Protein - Level - MW distribution Carbohydrates - Presence	Surface tension decrease - 0.1 to 19 mg dm DL P/mL Surface dilatational modulus - 0.1 to 19 mg dm DL P/mL

(Continues)

TABLE 1 (Continued)

Reference	Dough formula(s) apart from water	DL/BL isolation conditions	DL posttreatment	DL constituent investigated- Assessed feature	DL functional aspect investigated- Used concentration
Primo-Martin et al. (2006)	Flour, NaCl Flour, NaCl, DATEM Flour, NaCl, xylanase Flour, NaCl, lipase	60′ dough rest at 30°C 150,000 × g, 60′, 20°C	n/a	Protein - Level - MW distribution - Secondary structure Lipid - Level - Class identification	Surface tension decrease - 0.9 mg dm DL P/mL Surface dilatational modulus - 0.9 mg dm DL P/mL
Sancho et al. (2008)	Flour, NaCl, AA	30′ dough rest at 30°C 200,000 × g, 30′, 30°C	Dialysis Freezing (−20°C)	Protein - MW distribution - Species identification	n/a
Patel et al. (2012)	Flour, Flour, AA Flour, α-amylase Flour, AA, α-amylase Flour, improver mix	No dough rest 131,000 × g, 60′, 23°C	n/a	n/a	n/a
Toole et al. (2013)	Flour	No dough rest 200,000 × g, 30′, 25°C	n/a	n/a	n/a
Pauly et al. (2014)	Flour Flour, NaCl Flour, NaCl, sugar Flour, NaCl, sugar, yeast Partially defatted flour Partially defatted flour, NaCl, sugar Partially defatted flour, NaCl, sugar, yeast	No dough rest 126′ rested at 23°C 126′ fermented at 30°C 165,000 × g, 60′, 20°C	Freeze-drying Freezing (−20°C)	Protein - Level - Recovery PINs - Level - Recovery AX - Level - Recovery	Bulk viscosity - 1.2 mg dm DL P/mL Foaming properties - 1.2 or 0.3 mg dm DL P/mL
Gerits et al. (2015)	Flour, NaCl, sugar, yeast, Flour, NaCl, sugar, yeast, DATEM Flour, NaCl, sugar, yeast, lipase	126′ dough fermentation at 30°C 165,000 × g, 60′, 20°C	Freeze-drying	Lipid - Level - Class identification	n/a
Turbin-Orger, Della Valle, et al. (2015)	Flour, NaCl, yeast Flour, NaCl, sugar, yeast Flour, NaCl, fat, yeast Flour, NaCl, sugar, fat, yeast Flour, NaCl, bran, fat yeast	No dough rest 35,000 rpm, 90′, 30°C	Centrifugation	Protein - Level Lipid - Level Carbohydrates - AX content - AGP content	Bulk viscosity - Native concentration Surface tension decrease - Native concentration Foaming properties - 1/10 dilution

(Continues)

TABLE 1 (Continued)

Reference	Dough formula(s) apart from water	DL/BL isolation conditions	DL posttreatment	DL constituent investigated- Assessed feature	DL functional aspect investigated- Used concentration
Hemdane et al. (2016)	Flour, NaCl, sugar, yeast, bran	120′ dough fermentation at 30°C 50,000 × g, 30′, 7°C	n/a	Enzymes - α-Amylase activity - Endoxylanase activity	n/a
Salt et al. (2018)	Flour, NaCl	90′ dough rest at 30°C 200,000 × g, 30′, 30°C	Centrifugation	Lipid - Level - Species identification	Surface tension decrease - Native concentration - 0.1 to 10 mg dm DL/mL Surface dilatational modulus - 0.1 to 10 mg dm DL/mL Foaming properties - n/c
Melis (2019)	Flour, NaCl, sugar, yeast Flour, NaCl, sugar, yeast, lipase	126′ dough fermentation at 30°C 165,000 × g, 60′, 20°C	Freezing (−80°C)	Protein - Level - Recovery Lipid - Level - Recovery - Class identification	Surface tension decrease - native concentration - 1/1 dilution - 1/4 dilution Surface dilatational modulus - Native concentration - 1/1 dilution - 1/4 dilution
Liu et al. (2020)	Flour, bran Flour, bran, xylanase Flour, bran, glucose oxidase	40′ dough rest at 34°C 180,000 × g, 90′, 25°C	Cooling (4°C, 90′)	Protein - Level - Recovery Lipid - Level Carbohydrates - AX content - AX recovery - Sulfhydryl content - MW distribution	Bulk viscosity - 1/3 dilution Foaming properties - 1/8 dilution
Min et al. (2020)	Flour, NaCl	90′ dough rest at 30°C 200,000 × g, 30′, 30°C	Centrifugation	Lipid - Species identification	Surface tension decrease - Native concentration Surface dilatational modulus - Native concentration

(Continues)

TABLE 1 (Continued)

Reference	Dough formula(s) apart from water	DL/BL isolation conditions	DL posttreatment	DL constituent investigated- Assessed feature	DL functional aspect investigated- Used concentration
Wheat, rye, and oat flour					
Janssen, Wouters, Pauly, et al. (2018)	Flour, NaCl, sugar, yeast	126′ dough fermentation at 30°C 165,000 × g, 60′, 20°C	Freeze-drying Freezing (−20 or −80°C)	Protein - Level Lipid - Level - Class identification Carbohydrates - AX content - β-D-Glucan content	Bulk viscosity - 5.00 mg protein/mL Foaming properties - 5.00 mg protein/mL Surface tension decrease - 5.00 mg protein/mL Surface dilatational modulus - 5.0 mg protein/mL
Janssen, Wouters, Linclau, et al. (2020)	Flour, NaCl, sugar, yeast	126′ dough fermentation at 30°C 165,000 × g, 60′, 20°C	Freeze-drying Freezing (−20°C) Defatting Lipid reconstitution	Protein - Level Lipid - Level - Species identification Carbohydrates - AX content - β-D-Glucan content	Surface tension decrease - 1.50 or 5.00 mg protein/mL Surface dilatational modulus - 5.00 mg protein/mL Surface shear modulus - 1.50 mg protein/mL
Janssen, Wouters, Meeus, et al. (2020)	Flour, NaCl, sugar, yeast	126′ dough fermentation at 30°C 165,000 × g, 60′, 20°C	Freeze-drying Freezing (−20°C) Defatting Xylanase addition β-D-Glucanase addition	Protein - Level Lipid - Level Carbohydrates - AX content - β-D-Glucan content	Bulk viscosity - Native concentration - 1.50 mg protein/mL Foaming properties - 5.00 mg protein/mL Surface tension decrease - 5.00 mg protein/mL Surface dilatational modulus - 5.00 mg protein/mL Surface shear modulus - 1.50 mg protein/mL
Janssen et al. (2021)	Flour, NaCl, sugar, yeast	126′ dough fermentation at 30 °C 165,000 × g, 60′, 20°C	Freeze-drying Freezing (−20°C) Xylanase addition β-D-Glucanase addition	Protein - Level Lipid - Level Carbohydrates - AX content - β-D-Glucan content	Thin film drainage dynamics- Native concentration • Wheat DL and oat BL - 1.50 mg protein/mL • Wheat DL - 1.00 mg protein/mL • Oat BL - 0.50 mg protein/mL • Rye DL

Note: The term "native concentration" refers to the dm concentration in the supernatant of dough after ultracentrifugation.

Abbreviations: AA, ascorbic acid; AGP, arabinogalactan peptide; AX, arabinoxylan; DATEM, diacyl tartaric esters of monoacylglycerols; DL, dough liquor; dm, dry matter; ELISA, enzyme-linked immunosorbent assay; FAME, fatty acid methyl ester; MW, molecular weight; n/a, not applicable; n/c, not communicated; P, protein; PIN, puroindoline.

quasi linearly with the water content (Larsson & Eliasson, 1996a; Sahi, 2003). This implies that once starch granules, gluten protein, and water-unextractable AX (WU-AX) and maybe some other water-unextractable constituents are fully hydrated and not capable of retaining additional water, the remaining water is recovered as wheat DL. Of interest is that the amount of phase 1 decreases when the wheat dough recipe includes lecithin (i.e., a mixture of PhLs). This is probably because it causes an inferior separation of gluten and starch during UF (Larsson & Eliasson, 1996b). That partial prior defatting of wheat flour improves the phase separation of starch and gluten supports this statement (Larsson & Eliasson, 1996b).

As to nonwheat DL/BL, a relatively lower amount of water is recovered in wheat DL than in rye DL and oat BL (Janssen, 2020). However, it should be noted that more water is used to produce rye doughs and oat batters than in wheat dough making (Janssen, 2020).

In what follows, the impact of changes in dough recipe and DL isolation conditions on the composition of the resulting DL is discussed.

3.3 | Chemical compositions of wheat and rye DL and oat BL

3.3.1 | Dry matter and water recoveries of DL/BL

The total amount of DL recovered from wheat dough depends on the dough formula (Larsson, 2002; Pauly et al., 2014; Sahi, 2003) and the dough resting time prior to UF (Pauly et al., 2014). For instance, Sahi (2003) for nonyeast-leavened wheat flour–water doughs observed that a higher dough water absorption leads to a higher recovery of dry matter (dm) in DL. Including salt in nonyeast-leavened wheat flour doughs increases the recovery of DL (Larsson, 2002; Pauly et al., 2014). This total DL recovery further increases when the formula contains both salt and sugar (Pauly et al., 2014). Evidently, when part of the recipe, sugar and salt are recovered in DL and increase DL yield. However, at the same time, the DL also contains more water (Pauly et al., 2014). This may be because salt (Danno & Hoseney, 1982; Van Steertegem et al., 2013) and sugar (Ponte, 1990) alter gluten and starch water binding properties. A further observation is that when nonyeast-leavened doughs prepared from wheat flour, water, and salt are allowed to rest for 120 min after mixing, significantly more water and dm is recovered in DL than when such doughs are ultracentrifuged immediately after mixing (i.e., without resting for 120 min) (Pauly et al., 2014). This indicates that during dough resting some water is released, which then may solubilize additional quantities of dough constituents. This water release may be caused by action of flour endogenous hydrolytic enzymes such as amylases, xylanases, and peptidases. Interestingly, the total amounts of DL recovered from otherwise identical nonyeast-leavened and yeast-leavened doughs (containing sugar and salt) are similar after resting and fermentation of dough for a same amount of time (Pauly et al., 2014). As yeast during fermentation consumes sugars, less dm is recovered in DL from yeast-leavened and fermented dough than in DL from its nonyeast-leavened and rested counterpart (Pauly et al., 2014). That the total recovered DL amounts in both cases are similar thus implies a higher recovery of water in the former DL (Pauly et al., 2014). However, as noted above (see Section 2.1.2) yeast produces ethanol that when dissolved in the aqueous phase of dough likely at least partially is recovered as DL. This may contribute to the higher amount of water recovered in DL from yeast-leavened and fermented dough than in DL from its nonyeast-leavened and rested equivalent (Pauly et al., 2014). That ethanol is present in aqueous extracts of yeast-leavened wheat dough containing sugar and salt (Jayaram et al., 2014) seems to support this reasoning. Fermentation of dough alters the composition of its aqueous phase. Hence, bread doughs should be rested/fermented for an appropriate time prior to UF if one is to assess the potential of dough aqueous-phase constituents to stabilize gas cells during proofing and baking.

Recoveries of dough dm in DL from yeast-leavened wheat dough vary between 3.0% and 7.6% (Turbin-Orger, Della Valle, et al., 2015), whereas those of yeast-leavened rye dough and oat batter dm are 10.4% and 4.7%, respectively (Janssen, 2020). However, it should be mentioned that (i) the recipes of these doughs/batters were different which—as mentioned above—may have had an impact on the total amount of dm recovered, and that (ii) dm recoveries reported for DL/BL from yeast-leavened doughs/batters should be interpreted carefully. Indeed, yeast converts sugar and thus dm into carbon dioxide and ethanol. Thus, the total amount of dm originating from sugars in yeast-leavened dough is expected to be lower than that in freshly mixed dough.

The dm of DL/BL and thus likely also of the dough aqueous phase consists mainly of proteins, lipids, AX, β-D-glucan, and mono-, di-, and oligosaccharides (Janssen, 2020; Primo-Martín et al., 2006; Salt et al., 2006; Turbin-Orger, Della Valle, et al., 2015). It most likely also contains minor levels of minerals and vitamins (Belitz et al., 2009). As proteins, lipids, and NSPs are the most important constituents in the context of dough gas cell stability (see Section 3.4), their recoveries and chemical structures are discussed in more detail. To the best of our knowledge, the dough/batter dm recoveries of monosaccharides, disaccharides, and oligosaccharides (such as dextrins and

xylo-oligosaccharides derived from damaged starch and AX, respectively) in DL/BL have not yet been reported in literature.

3.3.2 | DL/BL proteins

Protein recovery of DL/BL

Cereal flour proteins are typically classified according to a protocol originally proposed by Osborne (1907). This protocol is based on sequential extraction of proteins in different media and distinguishes

(i) albumins, which are extractable in water,
(ii) globulins, which are extractable in dilute salt solution (e.g., 0.4 M NaCl),
(iii) prolamins, which are extractable in aqueous alcohol solutions (e.g., 60% to 70% [v/v] ethanol),
(iv) glutelins, which are extractable in a dilute acid (e.g., 0.05 M acetic acid) or base (e.g., 0.05 M KOH), and
(v) a residual fraction (Belitz et al., 2009).

As this classification is based on sequential extractions, there is a certain overlap between the different fractions. Proteins typically make up about 10% to 12% of dm of bread-making wheat flour (Goesaert et al., 2005) and consist of 15% to 20% albumins and globulins and a total of 80% to 85% prolamins (called gliadins) and glutelins (called glutenins) (Delcour et al., 2012). The latter primarily consists of high-MW glutelins and polymeric albumins and globulins (called triticins) (Goesaert et al., 2005). The protein level of rye flour (about 7% of dm) is generally lower (Belitz et al., 2009; Buksa, Ziobro, et al., 2013; Verwimp et al., 2004). In addition, rye flour contains a much higher level of albumins (typically 34%) and globulins (typically 11%) than of prolamins (typically 19%) and glutelins (typically 9%) (Chen & Bushuk, 1970). The latter two together are called secalins. Hüttner et al. (2011) found the protein levels in six oat cultivars to vary from 10.6% to 16.5% of dm. Oat flour proteins consist of 9% to 20% albumins, 50% to 60% globulins, 4% to 14% prolamins (called avenins), and 21% to 27% glutelins (Peterson, 2016). The latter fraction primarily consists of polymeric globulins (Robert et al., 1985). Thus, rye and oat flours contain relatively more aqueous-phase extractable proteins than wheat flour.

Reported flour protein recoveries in wheat DL vary between 4.0% (of whole meal wheat flour protein) (Liu et al., 2020) and 10.3% (of wheat flour protein) (Janssen, 2020). Janssen (2020) argued that the much higher levels of albumins and globulins in rye flour (see above) explain the much higher recovery of proteins in rye DL (39.6% of rye flour protein) than in wheat DL (10.3% of wheat flour protein). In spite of the high level of albumins and globulins in oat flour (see above), the level of proteins recovered in oat BL in the same study was low (3.1% of oat flour protein) (Janssen, 2020), likely because the oat kernels used had been heat treated (i.e., kilned) prior to milling. Kilning oat kernels indeed induces protein denaturation and aggregation, leading to partial loss of solubility (Runyon et al., 2015).

Sahi (2003) for nonyeast-leavened wheat flour–water doughs reported that a higher dough water absorption causes more proteins to be recovered in DL. The inclusion of salt in the recipe of nonyeast-leavened wheat flour–water doughs considerably increases the DL protein recovery (Pauly et al., 2014). No further increase in dm protein recovery is observed when only sugar or both sugar and yeast are added to a formula containing wheat flour, water, and salt (Pauly et al., 2014). The increased DL protein recovery in the presence of salt can likely be ascribed to increased solubility of globulins and to altered intermolecular interactions between gluten proteins during dough development due to shielding of some of their charges (primarily those of gliadins, see Section 2.1.1) (He et al., 1992; Miller & Hoseney, 2008). Such shielding causes gluten proteins to hold less water (Larsson, 2002), which then may solubilize additional quantities of albumins and globulins. It has been reported that gliadins can be extracted with water from nonyeast-leavened wheat flour–water dough when salt is included in the formula (Sato et al., 2015; Ukai et al., 2008). This would suggest that salt ions increase the solubility of not only globulins but also and likely to a lesser extent prolamins in the dough aqueous phase and thus potentially also in DL. In addition, a greater portion of prolamins could be expected to dissolve in the aqueous phase of dough in the presence of PLs. Indeed, some flour/yeast PLs (e.g., phosphatidylcholines [PCs]) by binding to prolamins during dough mixing (see Section 2.1.1) may decrease their hydrophobicity and thus their tendency to dissolve in the dough aqueous phase.

Identification of DL (foam) protein species

Salt et al. (2005) identified 42 albumin and/or globulin proteins in DL from nonyeast-leavened wheat doughs by mass spectrometry. The most abundant proteins were β-amylase (61.4 kDa), serpin (40.0 kDa), tritin (28.8 kDa), and members of the α-amylase/trypsin inhibitor family (14.4 kDa). Of interest is that, irrespective of whether salt was included in the formula or not, neither puroindolines (14 to 15 kDa) nor prolamins were detected in wheat DL. In the same study (Salt et al., 2005), the protein composition of foam produced from DL was investigated. Tritins and α-amylase/trypsin inhibitors were present in lower and higher concentrations, respectively, in wheat DL foam than in DL itself (Salt et al., 2005). Later, Pauly et al. (2014) investigated whether fermentation impacts the

protein composition of wheat DL and foams produced from it. Using capillary electrophoresis, proteins with molecular masses similar to those reported by Salt et al. (2005) were identified. Inclusion of salt, sugar, and yeast in the formula caused an increase in the concentration of α-amylase/trypsin inhibitors in DL (Pauly et al., 2014). In addition, the concentration of protein in foams prepared from DLs seemed to increase over time as liquid drained from the films between adjacent gas cells (Pauly et al., 2014). This indicates that proteins indeed adsorbed at gas cell A–W interfaces (see section "DL/BL A–W interfacial properties") (Pauly et al., 2014). In contrast to Salt et al. (2005), Pauly et al. (2014) found the concentrations of α-amylase/trypsin inhibitors in a DL solution prior to whipping and in the obtained foam to be similar. Also contrasting with the findings of Salt et al. (2005) is that Pauly et al. (2014) found that wheat DL contains puroindolines and that they are enriched in foam from DL from fermented wheat dough. Earlier, Sancho et al. (2008) compared the proteomes of DLs isolated from nonyeast-leavened doughs prepared from flour of four wheat cultivars, each grown under hot/dry or cool/wet regimes. Although some minor differences were noted, the overall impact of cultivar and growth conditions on the DL protein population seemed to be limited (Sancho et al., 2008).

3.3.3 | DL/BL lipids

Lipid recovery of DL/BL

Cereal flour lipids are generally classified either as starch lipids, which—as their name implies—occur inside starch granules, or as nonstarch lipids (Morrison, 1981). In this review manuscript, the focus is on the latter. The former are only released from starch granules at elevated temperatures (Janssen, Wouters, Pareyt, et al., 2018; Morrison, 1981) and thus are considered functionally inert at the dough stage of bread making. The term "lipids" hereafter refers to the nonstarch lipid fraction of flour. Interested readers are referred to Melis and Delcour (2020) for detailed information on wheat starch lipids. Lipids make up 2.0% to 3.0% (Melis & Delcour, 2020), 1.0% to 2.7% (Verwimp et al., 2004; Zeringue & Feuge, 1980), and about 7.0% (Chung & Ohm, 2000; Pauly & Delcour, 2018; Price & Parsons, 1979) of wheat, rye, and oat flour dm, respectively.

Melis (2019) reported flour lipid recoveries of 0.84% and 1.07% (both expressed on wheat flour lipid basis) in DL isolated from yeast-leavened dough prepared from flour of two wheat cultivars. A considerably higher wheat DL lipid recovery (2.61% of wheat flour lipids) was reported by Janssen (2020). They also noted that much more lipid is recovered in rye DL (13.4% of rye flour lipids) and oat BL (18.7% of oat flour lipids) than in wheat DL (2.61% of wheat flour lipids) and argued that this lower wheat DL lipid recovery may to an extent relate to the binding of lipids to gluten proteins during dough mixing (see Section 2.1.1) (Janssen, 2020). To what extent protein–lipid interactions occur during rye dough and oat batter making has—to the best of our knowledge—not been studied.

Identification of DL/BL (foam) lipid classes

The lipid population of wheat (Gerits et al., 2015; Janssen, Wouters, Linclau, et al., 2020; Melis, 2019; Salt et al., 2018) and rye (Janssen, Wouters, Linclau, et al., 2020) DL and oat (Janssen, Wouters, Linclau, et al., 2020) BL consists of a heterogeneous mixture of nonpolar lipids (NPLs) and PLs. The predominant NPL classes in these liquors are triacylglycerols (TAGs), diacylglycerols (DAGs), monoacylglycerols (MAGs), and FFAs, whereas monogalactosyldiacylglycerols (MGDGs), digalactosyldiacylglycerols (DGDGs), *N*-acyl phosphatidylethanolamines (NAPEs), *N*-acyl lysophosphatidylethanolamines (NALPEs), and PCs are the most abundant PL classes (Gerits et al., 2015; Janssen, Wouters, Linclau, et al., 2020; Melis, 2019; Salt et al., 2018). Turbin-Orger, Della Valle, et al. (2015) found that the lipid population of wheat DL consists of 67% TAGs, 29% FFAs, and 4% PLs. In contrast, Janssen, Wouters, Linclau, et al. (2020) reported that PLs represent about 19% of the lipids in wheat DL. In the same study, higher (26%) and lower (8%) PL levels were measured for rye DL and oat BL lipids, respectively, than for wheat DL (Janssen, Wouters, Linclau, et al., 2020). Nonetheless, it seems that most lipids recovered with DL or BL are nonpolar.

Turbin-Orger, Della Valle, et al. (2015) observed that inclusion of rapeseed oil in a wheat dough recipe increases the amount of lipids and of FFAs in particular in DL isolated therefrom. Furthermore, Salt et al. (2018) compared the levels of lipids other than NAPE and NALPE in DL and foam prepared therefrom. Lipid enrichment in the foam fraction largely resulted from increased levels of extractable FFAs and—although to a lesser extent—of TAGs, DAGs, and phosphatidylinositols (PIs) (Salt et al., 2018). That the obtained DL foams contained much lower DGDG, MGDG, and phosphatidylethanolamine (PE) levels than their parent DLs is rather surprising as it is generally believed that PLs readily adsorb at A–W interfaces (see section "Surface rheology"). Min et al. (2020) recently reported that increased expression of a quantitative trait locus for bread loaf volume on chromosome 7A of an isogenic wheat line pronouncedly increased the concentration of the most abundant MGDG and DGDG species in flour and DL.

Yeast lipids

Apart from high levels of ergosterol NPLs and sphingolipid PLs and trace amounts of DAGs, TAGs, and

phosphatidylserines, lipids of (wild-type) *S. cerevisiae* yeast strains consist of about 20.3% PI, 14.9% PE, and 14.3% PC. The most prominent acyl group combinations of *S. cerevisiae* PI are 16:0/16:1 (31%) and 16:0/18:1 (31%), of PE 16:1/16:1 (47%) and 16:1/18:1 (41%), and of PC also 16:1/16:1 (49%) and 16:1/18:1 (38%) (Ejsing et al., 2009). Interestingly, each of these lipid species has been detected in DL isolated from yeast-leavened wheat and rye doughs (Janssen, Wouters, Linclau, et al., 2020). However, it should be noted that prior lysis of yeast cells may be required for their lipids to be released in the dough aqueous phase (and thus in DL) and that (partial) lysis may have occurred during UF. Finally, BL from yeast-leavened oat batters only contains trace amounts of PI 16:0/16:1 (Janssen, Wouters, Linclau, et al., 2020), implying that the majority of *S. cerevisiae* PhLs are not recovered in oat BL.

Impact of lipases on DL lipid recovery and lipid composition

The molecular structure of lipids in bread making can be modified in situ by including lipases in the recipe, that is, lipid degrading enzymes catalyzing the hydrolysis of (phosphodi)ester bonds of glycero(phospho)lipids. Based on their selectivity, three types of lipases are generally distinguished (Melis & Delcour, 2020):

(i) TAG lipases catalyze the hydrolysis of ester bonds of TAGs and in doing so release DAG and an FFA. They also hydrolyze DAGs into an FFA and an MAG and MAGs into an FFA and glycerol.
(ii) Phospholipases A_1 and A_2 catalyze the cleavage of the ester bond of PhLs at the *sn*-1 and *sn*-2 positions, respectively, and thereby liberate a lysophospholipid and an FFA. Phospholipases specifically hydrolyzing lysophospholipids are denoted as "lysophospholipases." Their action releases FFAs and glycerol derivative.
(iii) Galactolipases as their name implies catalyze the hydrolysis of galactolipids. They release FFAs and lysogalactolipids. Further hydrolysis of the latter produces FFAs and glycerol derivatives.

It is important to note that most lipases have broad substrate specificity and hydrolyze a wide range of lipid classes depending on the lipase dosage and the applied conditions (Melis & Delcour, 2020 and references therein).

Primo-Martín et al. (2006) observed no change in the DL dm lipid level when the recipe of a nonyeast-leavened wheat dough contained lipases acting either on both PLs and NPLs or (primarily) on TAGs. In contrast, Gerits et al. (2015) observed a pronounced increase of the DL dm lipid level when isolated from yeast-leavened doughs prepared from recipes containing an optimal dose (i.e., corresponding to the most pronounced relative increase in bread loaf volume) of either a phospholipase or a lipase acting on both PLs and NPLs. For both lipases, the increase in DL lipid level not only resulted from higher levels of extractable FFAs and lysolipids but also from higher levels of extractable PLs endogenously present in the flour. The latter in their view was caused by emulsification of these endogenous PLs by enzymatically released lysolipids (Gerits et al., 2015). A rather similar observation with regard to the DL dm lipid level has been made by Melis (2019) for a yeast-containing dough recipe containing a lipase acting on both PLs and NPLs. It is rather striking that in contrast to the findings of Gerits et al. (2015) most PL classes were not detected in lipid extracts of DLs isolated from lipase containing doughs (Melis, 2019).

3.3.4 | DL/BL nonstarch polysaccharides

AX is the most abundant NSP in wheat and rye flours and makes up 1.3% to 2.7% (Gebruers et al., 2008) and about 5.0% (Pauly & Delcour, 2018; Vinkx & Delcour, 1996) of their respective flour dm weights. About 40% of rye flour AX is WE-AX (Vinkx & Delcour, 1996), which is more than generally the case for wheat flour (25% to 33% of AX) (Meuser & Suckow, 1986). Both WE-AX and WU-AX populations have a great structural heterogeneity, with molecules varying considerably in MW, degree of substitution (as assessed by the arabinose-to-xylose ratio), and substitution pattern (Cleemput et al., 1993, 1995; Gebruers et al., 2008).

In contrast to what is the case for wheat and rye flour, β-D-glucan is the most abundant NSP in oat flour. Based on analysis of four oat cultivars, Papageorgiou et al. (2005) reported contents between 2.1% and 3.9% of flour dm. Much as is the case for AX, β-D-glucan can be divided into WE molecules and those that are not (Wood, 2010). Both represent heterogeneous populations varying in MW and molar ratios of cellotriosyl and cellotetraosyl units (Lazaridou & Biliaderis, 2007).

Evidently, the AX and β-D-glucan populations in DL are WE.

Pauly et al. (2014) and Janssen (2020) reported wheat flour total AX recoveries of 19.3% and 19.4%, respectively, in DL from yeast-leavened and fermented dough containing salt and sugar. Much less AX was recovered in wheat (19.4% of wheat flour total AX) DL and oat (8.5% of oat flour total AX) BL than in rye (43.0% of rye flour total AX) DL (Janssen, 2020). Furthermore, the β-D-glucan recovery in rye DL (53.3% of rye flour total β-D-glucan) was higher than in wheat DL (18.1% of wheat flour total β-D-glucan) and oat BL (18.5% of oat flour total β-D-glucan) (Janssen, 2020). Finally, Turbin-Orger, Della Valle, et al. (2015) noted

that DLs isolated from different wheat dough formulas also contain arabinogalactan peptide. The latter are extractable from flour with water (Loosveld et al., 1998; Van den Bulck et al., 2005) and typically make up 0.3% of wheat flour dm (Loosveld et al., 1998), 0.2% of rye flour dm (Van den Bulck et al., 2005), and 0.005% of wholemeal oat dm (Göllner et al., 2011).

Including salt in the recipe of nonyeast-leavened wheat flour dough pronouncedly increases the recovery of AX in wheat DL (Pauly et al., 2014). No further increase in DL total AX recovery was noted when also sugar was included in the recipe (Pauly et al., 2014). Interestingly, the recovery of total AX in DL from yeast-leavened and fermented dough is considerably higher than that in DL from its nonyeast-leavened counterpart rested for the same time period (Pauly et al., 2014). This may be because expansion of gas cells and extension of the gluten network cause more AX to be recovered in DL.

The above illustrate that wheat DL is a complex mixture of constituents, of which proteins, lipids, and NSPs are arguably the most important in the context of gas cell stabilization. The mechanisms by which they may do so are discussed below.

3.4 | Role of wheat and rye DL and oat BL constituents in gas cell stabilization

3.4.1 | Surface-active constituents: Proteins and lipids

Surface activity

Most proteins and amphiphilic lipids can diffuse to and adsorb at gas cell A–W interfaces. Proteins contain both hydrophobic and hydrophilic amino acids, whereas surface-active lipids such as FFAs and PLs consist of one (in the case of FFA) or more hydrophobic hydrocarbon chains and a hydrophilic functional group. Upon adsorption, proteins and lipids lower σ of the A–W interface. Proteins have higher MWs than lipids and diffuse more slowly to A–W interfaces. Once adsorbed, they occupy larger areas thereat than lipids do. The latter implies that (i) proteins are surface-active at lower concentrations than lipids (i.e., a single protein molecule reduces σ of an A–W interface to a lower value than a single lipid molecule), and that (ii) a given A–W interfacial area can contain more lipid than protein molecules. As a point of reference, lipid- and protein-stabilized A–W interfacial films generally have equilibrium σ values between 42 and 22 mN/m and 57 and 47 mN/m, respectively, whereas pure water has a σ value of approximately 72 mN/m (Bos & van Vliet, 2001).

Surface rheology

Proteins and lipids can further stabilize A–W interfaces by increasing their stress carrying capacity and thus their ability to withstand deformations.

Once proteins adsorb at an A–W interface, they partially unfold, orient their more hydrophobic regions toward the air phase, mutually interact, and develop a strong viscoelastic film (Murray, 2007) (Figure 5a). Such continuous protein film provides a degree of physical stability to gas cells and can slow down or even prevent merging of neighboring gas cells by exerting steric hindrance and/or electrostatic repulsion.

In contrast, lipids form a weak viscoelastic fluid monolayer at A–W interfaces, the structure of which depends on the orientation of the hydrocarbon chains of the adsorbed lipid molecules thereat. This in turn largely depends on their concentration at the A–W interface, the length of fatty acid chains, and number of *cis* unsaturated carbon–carbon bonds (Kaganer et al., 1999; Krog, 1981).

Three types of lipid monolayers are generally distinguished: gaseous (Figure 5b1), liquid expanded (Figure 5b2), and liquid condensed (Figure 5b3). *Cis* double bonds in free or esterified FFAs as well as short acyl chains hinder the close packing of lipid molecules at interfaces and promote the formation of gaseous and liquid expanded monolayers (Kaganer et al., 1999; Krog, 1981). It has been argued that liquid condensed monolayers at A–W interfaces are stronger physical barriers against gas cell coalescence (Krog, 1981; Lucassen-Reynders, 1993; MacRitchie, 1976) or disproportionation (Krog, 1981; Quoc et al., 2002; Tcholakova et al., 2011) than liquid expanded or gaseous monolayers. Gaseous monolayers are presumably not present at dough gas cell A–W interfaces directly after mixing or in the early stages of fermentation as sufficient surface-active lipids and proteins are present in the dough aqueous phase to occupy all A–W interfacial area[1] (Melis & Delcour, 2020). They may, however, be present at dough gas cell A–W interfaces during proofing and oven rise as during these phases gas cells rapidly expand. As a result, the total A–W interfacial area that needs to be stabilized increases rapidly as well. Furthermore, when the surface concentration of lipids is locally reduced by deformation-induced flow of liquid at interfaces (e.g., when gas cells expand during fermentation), adsorbed lipids are inclined to restore this concentration gradient and generate counteracting Marangoni stresses that decrease the rate of surface convection (Manikantan & Squires, 2020). The magnitude of this gradient and the related Marangoni forces depends on the nature of the lipids involved. Lipids that

[1] According to Wilde (2012), there may be 50 times more protein in the aqueous phase of dough than needed to stabilize its gas cell A–W interfaces.

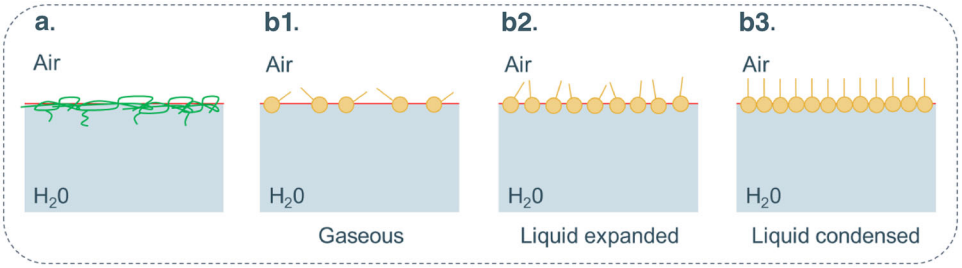

FIGURE 5 Schematic representation of possible structures of air–water interfaces stabilized by proteins and lipids. (a) Proteins adsorbed at the air–water interface unfold and engage in intermolecular interactions leading to a strongly viscoelastic film. (b) Lipids adsorbed are not involved in intermolecular interactions but occur as a weak viscoelastic fluid monolayer. Depending on their orientation at the air–water interface, the monolayers are gaseous (b1), liquid expanded (b2), or liquid condensed (b3)

are insoluble in water can weaken the gradient by diffusing to regions of lower surface concentration and thus higher σ. When the lipids are soluble, the strength of the gradient relies on the rate at which they exchange between the bulk phase and the A–W interface (Manikantan & Squires, 2020). As DL contains lipids with varying polarities (see section "Identification of DL/BL (foam) lipid classes"), both mechanisms may be in play.

Of further note is that the mechanisms whereby proteins and lipids stabilize A–W interfaces are mostly incompatible. Indeed, proteins hinder lipids from moving along the A–W interface, whereas lipids prevent the formation of a coherent viscoelastic protein layer (Wilde, 2000). Mixed protein–lipid interfaces are therefore unstable.

DL/BL foaming properties

A first approach to assess the potential of DL/BL constituents to stabilize gas cell A–W interfaces is to study their foaming properties by stirring or whipping a DL solution and monitoring foam volume over time. Such measurements are typically carried out with either fresh or freeze-dried and redissolved DL samples at concentrations generally much lower than those in DL itself (Table 1). It should be mentioned that freeze-drying of DL removes the carbon dioxide and ethanol produced by yeast and that, as noted above (see Section 2.1.2), ethanol may alter the surface activity of DL proteins. Table 1 provides an overview of various DL/BL isolation procedures including whether DLs were freeze-dried or not prior to assessing their functional properties. Evidently, the outcome of foaming experiments depends on the setup used. Care must therefore be taken when comparing results from different research groups. For instance, the mixing conditions (e.g., type of mixer, time, and speed) co-determine the outcome of whipping or stirring tests. In addition, foams may also be produced by sparging gas or shaking (Phillips et al., 1990). The interested reader is referred to Wilde and Clarke (1996) for some easy methods for assessing the foaming characteristics of proteins.

MacRitchie (1976) compared the foaming properties of DL isolated from yeast-leavened doughs prepared from either defatted wheat flour or defatted wheat flour to which its extracted lipids were added again in progressively increasing levels. Reconstituting the flour pronouncedly reduced the stability of foam from the isolated DL, which led to the suggestion that lipids act as "antifoaming" agents (MacRitchie, 1976). Dubreil et al. (1998) reported that foam could only be produced from wheat DL either when enriched with puroindoline-a, highlighting its possible significance in bread making, or when isolated from doughs prepared from defatted flour. Pauly et al. (2014) noted that yeast-leavened doughs (containing added sugar and salt) yielded DLs that resulted in far less-stable foams than did those of similar nonyeast-leavened doughs. These observations were ascribed to

(i) fermentation increasing the DL lipid level, and
(ii) yeast cells themselves containing a substantial amount of lipids (see section "Yeast lipids") (Pauly et al., 2014).

Evidence for the first interpretation is that foam from DL from yeast-leavened and fermented dough prepared from partially defatted wheat flour has higher stability than when prepared from control flour (Pauly et al., 2014). That superior DL foaming properties are observed when using defatted flour was also reported by MacRitchie (1976). Also, Turbin-Orger, Della Valle, et al. (2015) observed that when the recipe of yeast-leavened wheat flour dough contained not only salt but also rapeseed oil, DL foams had much lower stability than when such oil was not used.

Based on the above, it seems that flour endogenous and added lipids have a negative effect on the foaming properties of wheat DL.

Turbin-Orger, Della Valle, et al. (2015) noted that DL foams are more stable when recovered from sugar containing dough. This can possibly be ascribed to an increased η_{bulk} of the DL that slows down drainage of liquid from between gas cells.

Janssen, Wouters, Pauly, et al. (2018) observed that rye DL constituents form much more foam and thus gas cell A–W interface than wheat DL or oat BL constituents. At the same time, wheat and rye DL foams seemed to be less stable than oat BL foam (Janssen, Wouters, Meeus, et al., 2020). Enzymatic hydrolysis of wheat or rye DL AX has an overall negative impact on their foaming capacity (Janssen, Wouters, Meeus, et al., 2020). A similar but less pronounced effect was observed for foam from oat BLs when its β-D-glucan population was enzymatically hydrolyzed (Janssen, Wouters, Meeus, et al., 2020). Thus, NSPs contribute to the foaming properties of DL and BL, most likely by increasing η_{bulk}. Indeed, high-viscosity liquids drain slower than low-viscosity liquids, leaving more material confined in the foam, leading to greater foam stability.

DL/BL A–W interfacial properties

A second approach to investigate the potential of DL/BL constituents to stabilize A–W interfaces is to study their surface activity as well as their intrinsic ability to form stress-carrying interfacial films. The former is typically done by monitoring the decrease of σ of DL-stabilized A–W interfaces over time. The latter can be studied by deforming the A–W interfacial area either under shear or under dilation. As is the case for DL/BL foaming properties, these analyses are mostly carried out either with fresh or with freeze-dried and redissolved DL/BL samples, both at concentrations generally much lower than those occurring in DL/BL (Table 1). Sahi (1994, 2003) reported σ values in a 28 to 49 mN/m range for DLs isolated from nonyeast-leavened doughs prepared with flour from four different wheat cultivars. They observed that wheat DL constituents over time develop A–W interfacial films with considerable shear moduli. Furthermore, a strong correlation between both σ and interfacial shear moduli and DL lipid content was noted. Indeed, DL samples with a higher lipid content seemingly produced A–W interfaces with substantially lower σ and shear moduli than those stabilized by constituents in DL with a lower lipid content (Sahi, 1994). This was in line with the observation that defatting wheat DL (via organic solvent extraction) led to pronounced increases in both σ and the interfacial shear moduli (Sahi, 1994). Furthermore, the incorporation of more water in the dough resulted in DL-stabilized A–W interfaces with lower σ, presumably because lipid recoveries were higher (Sahi, 2003). Based on the above observations, Sahi (1994, 2003) suggested that competition of proteins and lipids for adsorption at wheat DL-stabilized A–W interfaces leads to unstable interfacial films. Evidence for this hypothesis was later provided by Primo-Martín et al. (2006), Salt et al. (2006), and Janssen, Wouters, Linclau, et al. (2020). In the former study, σ and E values of A–W interfaces stabilized by constituents in "lipid-poor" and "lipid-rich" wheat DLs were compared. Lipid removal led to DL constituent-stabilized A–W interfacial films with higher σ and E values (Primo-Martín et al., 2006). Salt et al. (2006) observed that DLs from doughs prepared from partially defatted wheat flour have pronouncedly higher σ values and surface dilatational moduli (E values) than DLs from regular doughs. In line with the above observations, Janssen, Wouters, Linclau, et al. (2020) reported that defatting wheat DL (via organic solvent extraction) pronouncedly increases its σ as well as the interfacial shear moduli. Even though wheat DL proteins and lipids compete for adsorption at A–W interfaces, 126 min after adsorption (i.e., a typical fermentation time in straight dough bread making) wheat DL-stabilized A–W interfaces possess considerable resistance to shear deformations (Janssen, Wouters, Linclau, et al., 2020).

Mills et al. (2003) observed that increasing the concentration of wheat DL solutions markedly decreased σ and shear elastic moduli of the obtained A–W interfacial films. Similarly, Salt et al. (2006, 2018) reported higher σ (Figure 6a) and interfacial shear elasticity (Figure 6b) at lower than at higher and even native DL protein concentrations. These findings are somewhat unexpected as higher bulk concentrations would be expected to result in higher interfacial concentrations and therefore lower σ values (see section "Surface activity") and greater resistance to deformation (see section "Surface rheology"). Indeed, the stability of A–W interfacial films depends on their composition in general and on their ratio of lipid to protein molecules in particular. It has been hypothesized that increasing bulk concentrations, which of course result in proportionate increases in the bulk protein and lipid concentrations, can still result in different ratios of lipid to protein at the A–W interface (Salt et al., 2006). When present at sufficiently high bulk concentrations, lipids adsorb faster at A–W interfaces than proteins (Bos & van Vliet, 2001). Thus, lipids in a more concentrated system (i.e., at higher bulk concentrations) may occupy a relatively larger interfacial area than in a more dilute system (i.e., at lower bulk concentrations). Proteins have higher MWs than lipids and therefore occupy a relatively larger interfacial area in a more dilute system than in a more concentrated system (i.e., at lower and higher bulk concentrations, respectively). As proteins and lipids interfere with each other's interfacial stabilization mechanism (see section "Surface rheology"), the abovementioned concentration-dependent surface activity may explain why higher σ and E values are observed at lower bulk concentrations (i.e., a more dilute system), leading to protein-dominated A–W interfacial films, than at higher bulk concentrations (i.e., a more concentrated system), leading to mixed protein–lipid A–W interfacial films.

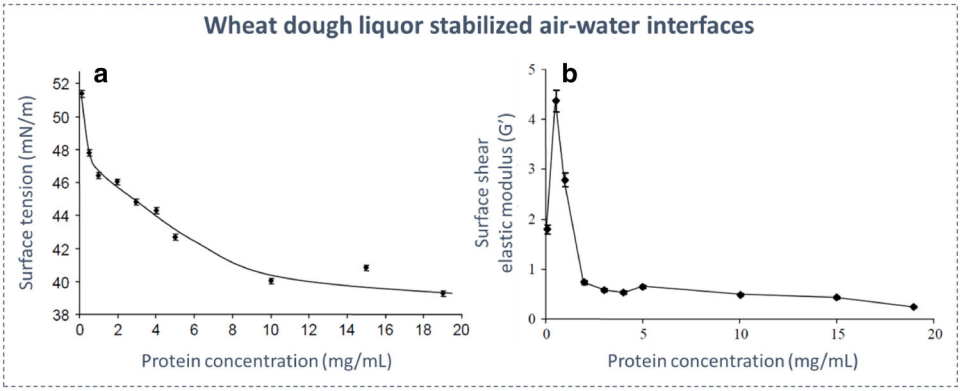

FIGURE 6 Surface tension 900 s after adsorption (a) and surface elastic modulus 300 s after adsorption (B) as a function of bulk protein concentration of wheat dough liquor (DL)-stabilized air–water (A–W) interfaces, as measured with pendant drop tensiometry and interfacial shear rheometry, respectively. Reproduced with permission from Salt et al. (2006)

Salt et al. (2006) reported that inclusion of salt in nonyeast-leavened wheat flour–water doughs pronouncedly lowered σ and E values of DL-stabilized A–W interfaces. They also observed that freezing and subsequent thawing of fresh DL from nonyeast-leavened wheat flour–water dough lead to a considerably lower E value of the A–W interfacial film. Given that partial prior defatting of wheat flour did not generate such decrease upon freezing and subsequent thawing of fresh DL, it was argued that freezing induced the formation of lipid aggregates that withstood thawing and when thawed may have exerted antifoaming properties (Salt et al., 2006).

Several authors have attempted to alter the A–W interfacial properties of wheat DLs by impacting the dough lipid population. For example, use of a lipase acting on both PLs and NPLs in either nonyeast-leavened (Primo-Martín et al., 2006) or yeast-leavened (Melis, 2019) doughs lowers the σ and E values of DL-stabilized A–W interfaces. This indicates that the obtained lipid hydrolysis products were recovered in DL and were more surface active than the lipids in control DL (Melis, 2019; Primo-Martín et al., 2006). In contrast, no significant change in σ of a DL-stabilized A–W interface was observed when doughs were prepared with and without inclusion in the recipe of a lipase acting primarily on TAGs (Primo-Martín et al., 2006). Rather surprising is that including fat or diacyl tartaric esters of MAGs in nonyeast-leavened wheat flour–water doughs resulted in DLs with higher σ values (Sahi, 2003). This shows both that these added lipids were not recovered in DL, which could be expected from their poor solubility in water, and that their use resulted in lower recovery of flour endogenous lipids in DL. Finally, Min et al. (2020) observed that DL produced from nonyeast-leavened doughs prepared from regular wheats or wheats typified by high MGDG and DGDG levels has similar A–W interfacial properties in terms of σ and E values.

In conclusion, it seems that at the DL bulk concentrations tested proteins and lipids compete for adsorption at wheat DL-stabilized A–W interfaces (Figure 7), leading to weakly viscoelastic and thus unstable A–W interfacial films. This most likely also explains the overall poor wheat DL foaming characteristics when tested at similar concentrations (see above).

Janssen, Wouters, Linclau, et al. (2020) demonstrated that rye DL constituents adsorb more rapidly at

A–W interfaces than their wheat DL counterparts. In addition, rye DL-stabilized A–W interfaces have pronouncedly lower σ values than wheat DL-stabilized ones (Janssen, Wouters, Linclau, et al., 2020). As low σ implies that little energy is needed to create A–W interfacial area and thus to incorporate gas cells in rye DL foams, this may at least to an extent explain the high foaming capacity of rye DL constituents mentioned in section "DL/BL foaming properties." Adsorbed rye DL proteins develop a strong predominantly viscous A–W interfacial film almost immediately after adsorption (Figure 7), implying that strong intermolecular interactions between adsorbed proteins take place (Janssen, Wouters, Meeus, et al., 2020). That in contrast lipids dominate oat BL-stabilized A–W interfaces (Figure 7) was deduced from two observations. First, oat BL constituents adsorb extremely fast at A–W interfaces and reduce their σ at equilibrium to 32 mN/m. Second, adsorbed oat BL constituents do not develop viscoelastic A–W interfacial films over time indicating that they do not engage in intermolecular interactions (Janssen, Wouters, Linclau, et al., 2020).

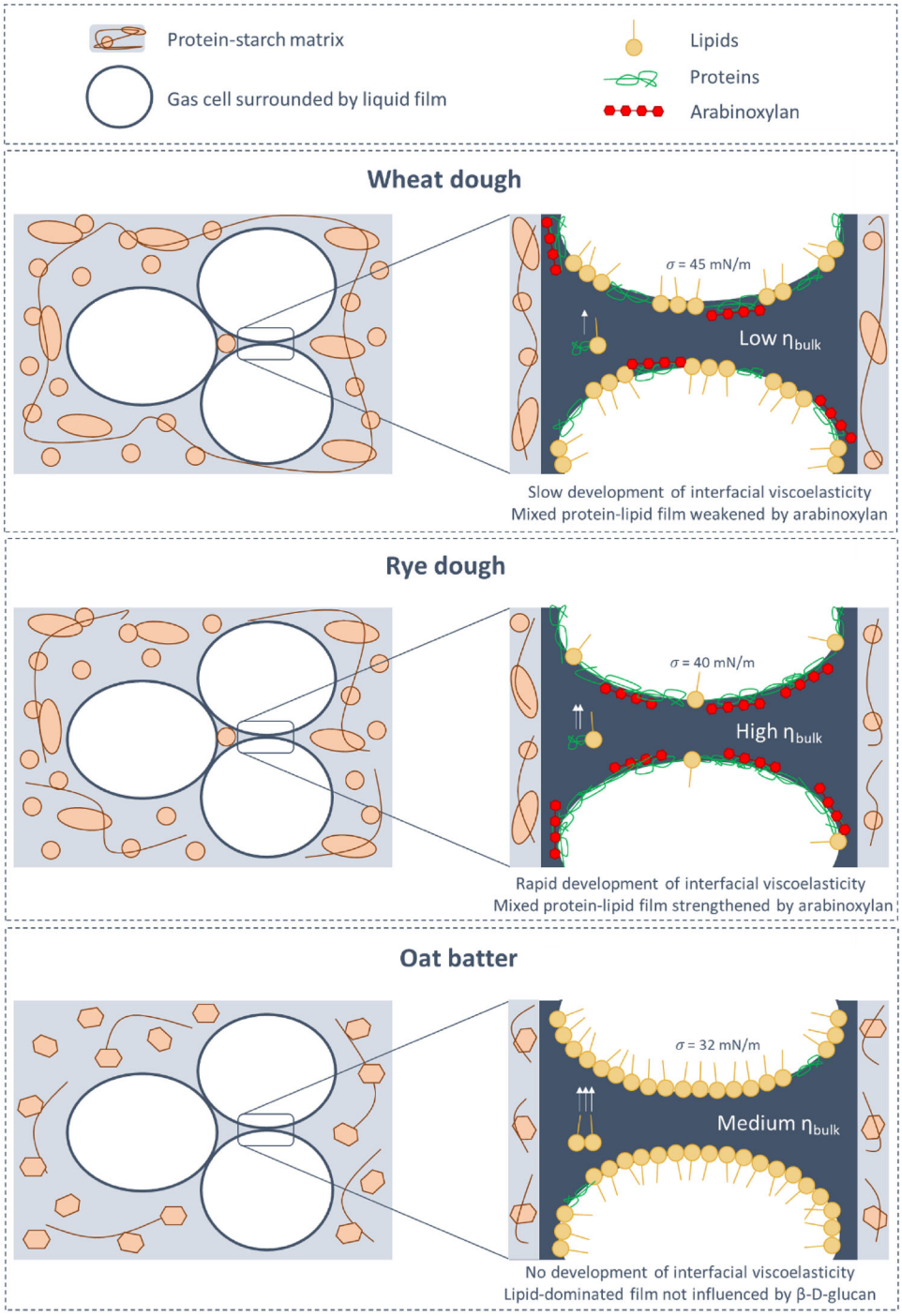

FIGURE 7 Schematic representation of the liquid films in wheat dough, rye dough, and oat batter with indication of their surface tension (σ) and bulk viscosity (η_{bulk})

3.4.2 | Non-surface-active constituents: Nonstarch polysaccharides

In contrast to proteins and lipids, AX and β-D-glucan are not surface active and thus do not adsorb at A–W interfaces. However, they may indirectly stabilize gas cell A–W interfaces in dough (Janssen, Wouters, Meeus, et al., 2020; Sarker et al., 1998; Primo-Martín et al., 2006).

DL/BL bulk viscosity

First, NSPs bind large amounts of water and confer high η_{bulk} to the dough aqueous phase. WE-AX to a large extent accounts for the η_{bulk} of aqueous wheat dough extracts (Baker et al., 1943, 1946; Perlin, 1951). A similar observation was made by Courtin et al. (2001), who reported a pronounced decrease of the η_{bulk} of extracts of freshly mixed and fermented doughs when *Aspergillus aculeatus*

or *Bacillus subtilis* xylanase was included in the recipe. Later, Liu et al. (2020) noted a considerable decrease in the η_{bulk} of wheat DL when *Aspergillus oryzae* xylanase was included in a dough recipe containing wheat flour, water, and wheat bran. That this is the case implies that the used *A. oryzae* xylanase (also) hydrolyzed the WE fraction of the present AX population. Janssen, Wouters, Meeus, et al. (2020) by enzymatically treating DL/BL demonstrated that WE-AX accounts for the high η_{bulk} of wheat and rye DLs, whereas the η_{bulk} of oat BL mostly originates from the presence of β-D-glucan. Indeed, in all cases the η_{bulk} of the enzyme-treated DLs/BLs was comparable to that of water (Janssen, Wouters, Meeus, et al., 2020), implying that neither monosaccharides (either endogenously present in flour or released by enzymes) nor possibly present oligosaccharides (released by enzymes from AX [xylo-oligosaccharides], β-D-glucan [cellotriose and/or cellotetraose], and damaged starch [dextrins]) have a strong impact on the η_{bulk} of DL/BL. One could reason that increasing the η_{bulk} of the dough/batter aqueous phase may slow down the rate of fluid drainage from the liquid films that supposedly separate adjacent gas cells during the proofing and oven rise. However, gas cells that are regionally separated by such liquid films are likely still surrounded by protein–starch matrix in the Plateau border region (Figure 7). Therefore, the liquid drainage rate from such films in dough or batter can be expected to be substantially lower than in freely draining foams (Wilde, 2012).

DL/BL A–W interfacial properties

NSPs can interact with constituents adsorbed at A–W interfaces and thereby increase its stability (Janssen, Wouters, Meeus, et al., 2020; Primo-Martín et al., 2006; Sarker et al., 1998). Sarker et al. (1998) observed an increase in the foam stability of a mixed bovine serum albumin–Tween 20 solution when wheat flour AX was added at concentrations lower than 0.30 mg/mL. This improved foam stability was ascribed to

(i) an increased η_{bulk}, as reflected from reduced liquid film drainage rates,
(ii) to interactions occurring between AX and adsorbed proteins, as deduced from a higher A–W interfacial film thickness at equilibrium,
(iii) to slower lateral diffusion of a fluorescently labeled surface-active probe in the adsorbed layer, and
(iv) to an increased E value (Sarker et al., 1998).

Also, Primo-Martín et al. (2006) reported a small increase in the E value of wheat DL-stabilized A–W interfaces when the dough recipe contained a xylanase of unspecified origin that specifically hydrolyzes WU-AX. Later, Turbin-Orger, Della Valle, et al. (2015) found a relatively strong negative relation ($R^2 = 0.83$) between the DL arabinogalactan peptide content and the "rate of rearrangement" (i.e., a parameter extracted from surface tension kinetics) of adsorbed constituents, which led them to speculate that it contributes to gas cell stability in bread making by reducing the mobility of proteins and lipids at DL-stabilized A–W interfaces. Because no direct experimental evidence was brought forward to support this hypothesis, it remains to be investigated whether arabinogalactan peptide contributes to the stability of bread dough gas cell A–W interfaces. Recently, Janssen, Wouters, Meeus, et al. (2020) demonstrated that AX strengthens rye but weakens wheat DL-stabilized A–W interfacial films. Indeed, enzymatic hydrolysis of DL AX by *A. aculeatus* xylanase leads to a considerable decrease and increase in the interfacial shear moduli of rye and wheat DL interfacial films, respectively (Janssen, Wouters, Meeus, et al., 2020). It was argued that AX forms a secondary layer at the A–W interface by participating in hydrogen bonding with the primarily adsorbed protein layer (Janssen, Wouters, Meeus, et al., 2020). It thus appears that interaction between AX and proteins at A–W interfaces in some but not all cases improves their resistance to shear deformations. Oat BL β-D-glucan neither weakens nor strengthens the primary adsorbed lipid film (Janssen, Wouters, Meeus, et al., 2020). As oat BL A–W interfaces are likely dominated by lipids (see section "DL/BL A–W interfacial properties"), it seems that the presence of proteins at the A–W interface is a prerequisite for (non-surface-active) NSPs to engage in intermolecular interactions with the adsorbed constituents.

From the above, it is clear that DL constituents either stabilize or destabilize A–W interfaces. In what follows, the extent to which dough aqueous-phase constituents contribute to the loaf volume and crumb structure of bread will be addressed. In addition, the relation between DL functionality and bread properties is discussed.

4 | RELATING DL FUNCTIONAL PROPERTIES TO BREAD LOAF VOLUME AND CRUMB STRUCTURE

Baker et al. (1946) reported a bread volume increase when a wheat bread recipe was supplemented with dough aqueous-phase constituents up to double their level present in the control bread recipe. Hoseney et al. (1969) fractionated wheat flour into gluten, starch, and a water-soluble fraction and observed that gluten–starch-based bread loaves had volumes almost 40% lower than those of breads prepared from the fully reconstituted flour.

However, no further increase in volume was observed when the total amount of water solubles was increased to levels exceeding those originally present in the flour (Hoseney et al., 1969). Delcour et al. (1989) supplemented blends of wheat gluten and wheat starch with 0.0% to 4.0% (w/w) ethanol-precipitated water solubles from wheat or rye flour and noted relative bread volume increases of almost 30% in both cases. Pauly et al. (2014) did not observe a bread volume increase when a wheat dough formula was supplemented with 2.0% dm wheat DL (expressed as % w/w of flour). However, a significantly ($P < 0.05$) lower mean crumb gas cell area was observed in the bread made from the DL-supplemented formula (Pauly et al., 2014). More recently, Pauly and Delcour (2018) reported that substituting 5.0% dm oat flour by an aqueous extract from wheat, rye, or oat flour leads to relative oat bread volume increases of 13%, 28%, or 5%, respectively.

Only five studies of those dealing with the properties of DL have discussed the possible relation between the functional properties of DL and bread quality. In Section 3, it was illustrated that wheat DL constituents display poor foaming and A–W interfacial properties. However, wheat bread still has a high specific volume and finely grained crumb. This is of course mostly due to the viscoelastic gluten network that by displaying strain hardening acts as the primary gas cell stabilizing force (see section "Strain hardening by the viscoelastic gluten network"). In contrast, although rye DL and oat BL constituents have more potential for stabilizing A–W interfaces than wheat DL constituents (see section "DL/BL A–W interfacial properties"), the specific volumes of rye and oat bread loaves are lower than that of wheat bread (see Section 2). Thus, even if rye and oat dough aqueous-phase constituents contribute to gas cell stability in rye and oat bread making, they cannot match the efficacy of the combined contributions of the gluten network and dough aqueous-phase constituents in terms of stabilizing gas cells in wheat bread making. However, that less gas cells per surface unit were observed in oat than in rye and wheat bread crumb (Janssen, Wouters, Pauly, et al., 2018) indicates lower resistance against coalescence in the former, presumably because lipids dominate their A–W interfaces. As mentioned, lipids form a much weaker viscoelastic network at interfaces than proteins (see section "Surface rheology"). Therefore, the presence of a strong viscoelastic interfacial protein film during fermentation may be essential for withstanding the increase in interfacial area caused by gas cell expansion in systems lacking the wheat viscoelastic gluten network.

Of further importance is that bread-making experiments with an *A. aculeatus* xylanase revealed that AX contributes substantially to the fine-grained crumb of rye bread (Figure 8) (Janssen, 2020). Indeed, AX enzymatic hydrolysis resulted in rye bread crumbs with considerably larger mean gas cell areas and lower numbers of cells per surface unit than was the case for control rye bread. This implies that rye flour AX delays gas cell coalescence during rye bread making presumably because of its contribution to the η_{bulk} of the dough aqueous phase.

5 | CRITICAL CONSIDERATIONS

Overall, some dough aqueous-phase constituents have a positive impact on the incorporation and/or stabilization of gas cells in bread making. However, it remains challenging to directly relate the composition of DL/BL and its A–W interfacial properties on the one hand to bread loaf volume or crumb characteristics on the other hand. This lack of a meaningful relationship between DL/BL and bread properties raises several questions. In this regard, a few critical remarks need to be made.

First and foremost, foaming tests (see section "DL/BL foaming properties") and A–W interfacial measurements (see section "DL/BL A–W interfacial properties") have been conducted at much lower dm concentrations, and thus at lower surface-active constituent concentrations than those in freshly isolated DLs. This is mainly due to the considerably lower accuracy and sensitivity of such measurements at higher η_{bulk}. Nonetheless, it is well-known that the behavior of proteins (Damodaran, 2005; Murray, 2007) and lipids (Bos & van Vliet, 2001; Lucassen-Reynders, 1993) at A–W interfaces, and their interplay with lipids, strongly depends on the bulk concentrations of both proteins and lipids. Hence, future research efforts should focus on accurately assessing the foaming and A–W interfacial properties of highly viscous systems such as DLs/BLs at their native concentration (i.e., as they would occur in the dough aqueous phase).

Second, the stability of gas cells in bread making not only depends on the characteristics of the A–W interfaces surrounding them, but most likely also on the rate at which fluid drains from the liquid films separating them. Very recently, the drainage dynamics of free-standing liquid films prepared from DL/BL solutions at native and lowered bulk concentrations were compared (Janssen et al., 2021) with a pressure-controlled dynamic thin film balance (Chatzigiannakis et al., 2020, 2021). It was observed that free-standing wheat DL and oat BL thin films at their native bulk concentration have much greater stability than such films at lowered bulk concentration (Janssen et al., 2021). This lends support to our above statement that wheat DL and oat BL constituents at their native concentration may contribute substantially to gas cell

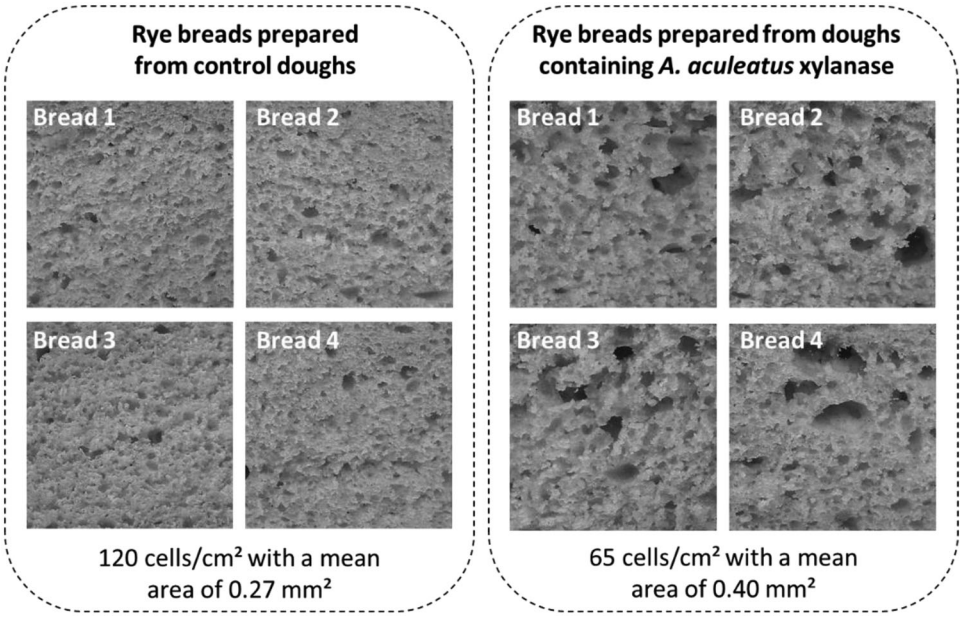

FIGURE 8 Digital images of the crumb of four typical rye breads prepared from control doughs (left) and from doughs containing *Aspergillus aculeatus* xylanase (right)

stabilization in bread making. This supports our previous statement that studying the foaming and A–W interfacial properties of DL/BL at their native concentration may be very rewarding.

Third, although a fraction of the dough aqueous phase is recovered as DL/BL (see Section 3.2) and given that the insights gathered here strongly indicate that DL/BL is—at least to an extent—a representative model system for the aqueous phase of dough/batter, it remains unclear whether all soluble constituents that play a role in bread dough gas cell stabilization end up in the supernatant obtained by UF. Indeed, that flour constituent recoveries in DL/BL are often rather low (see Section 3.3) suggests that not all constituents taking part in gas cell stabilization are recovered in it. At the same time, it is equally plausible that (part of) these constituents associate with the dough matrix (e.g., lipid binding; see Section 2.1.1) and that they are in fact not available for gas cell stabilization in dough/batter. This merits further investigation including the development of innovative strategies for extracting aqueous-phase constituents from bread dough/batter. At the same time, DL/BL evidently does not comprise water-unextractable nonwheat flour constituents (e.g., most wheat flour gliadins, rye flour secalins). Their role in gas incorporation and gas cell stabilization in bread making, to the best of our knowledge, also remains to be investigated.

Fourth, there is still no direct experimental proof that gas cells in bread doughs are enclosed by liquid films. Although super-resolution confocal scanning laser microscopy allows investigating biological phenomena at nanometer scales, such technique has to the best of our knowledge not been applied to study the stability of gas cells in dough. Another approach to (dis)proving that liquid films surround gas cells in bread doughs would be to develop mass spectrometry imaging methodologies for localizing lipids in situ. A major challenge associated with each of these techniques will be to preserve the fragile structure of fermented dough during the measurements.

6 | CONCLUSIONS

The incorporation and stabilization of gas cells in bread making depend on several interrelated phenomena. In wheat bread making, gas cells are surrounded and physically stabilized by a viscoelastic gluten network that displays strain hardening under extension and ensures uniform gas cell expansion. When the gluten network supposedly locally ruptures, gas cells are stabilized by a liquid film only. The protein networks in rye doughs and oat batters do not strain harden when extended. Hence, it can be argued that the mechanism of gas cell stabilization by liquid films is of greater relevance in nonwheat than in wheat bread making.

Even though there is still no direct experimental evidence that gas cells in dough are enclosed by such liquid films, observations from various studies lend support to the hypothesis that dough aqueous-phase-soluble constituents contribute to gas cell stability in bread making. The gas cell stabilizing potential of wheat dough aqueous-phase constituents has been studied for several

decades, whereas that of nonwheat dough/batter constituents has only been investigated recently. The most common approach to assess the potential role of these constituents is to investigate the composition and functional properties (i.e., foaming behavior, A–W interfacial properties, and η_{bulk}) of DL/BL, which contains a complex mixture of inter alia proteins, lipids, and NSPs, each representing a population with great structural heterogeneity. Evidently, the composition of DL and the functionality at the A–W interface of its constituents strongly depend on the dough/batter recipe and DL/BL isolation conditions. Another notable conclusion is that rye DL and oat BL constituents have more potential for stabilizing A–W interfaces than wheat DL constituents.

Despite all this, it has been challenging to establish a direct link between DL functionality on the one hand and bread properties on the other hand. As thoroughly discussed in Section 5, in our view this mostly relates to

(i) foaming tests and A–W interfacial measurements often being carried out at bulk concentrations much lower than those in freshly isolated DLs/BLs,
(ii) a lack of studies focusing on the drainage dynamics of DL/BL thin films,
(iii) the uncertainty over whether all soluble constituents involved in bread dough gas cell stabilization are recovered as DL/BL, and
(iv) a lack of experimental evidence for proving or disproving that gas cells in bread doughs are enclosed by liquid films.

The above encourage researchers to optimize methods for accurately assessing the functionality of DLs/BLs at their native concentration, to explore alternative strategies for extracting aqueous-phase constituents from dough/batter, and to develop imaging techniques for in situ localizing and quantifying surface-active constituents at gas cell A–W interfaces in dough.

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AUTHOR CONTRIBUTIONS

Frederik Janssen organized the manuscript and wrote the first draft of most sections. Arno Wouters co-wrote sections; provided critical comments, corrections, and suggestions; and proofread the entire manuscript. Jan Delcour provided critical comments, corrections, and suggestions and proofread the entire manuscript.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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