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Review

Endogenous redox agents and enzymes that affect protein network formation during breadmaking – A review

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A B S T R A C T

During breadmaking, wheat gluten proteins form a continuous network which is stabilized by disulfide bonds and modified by thiol/disulfide interchange reactions. This gluten network results in visco-elastic dough that holds together the other dough components and assists in retaining carbon dioxide. Wheat flour contains several components, enzyme co-factors and enzymes which can affect the formation and properties of the gluten network and, hence, the dough and bread characteristics. We present a brief overview of our current knowledge of the fate of gluten proteins during breadmaking, and how they are affected by endogenous wheat components (e.g. glutathione, cysteine and NAD(P)(H)) and enzyme systems (e.g. tyrosinase, peroxidase, the NADP-dependent thioredoxin and glutathione enzyme systems, protein disulfide isomerase, lipoxygenase, catalase and dehydrogenases).

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Abbreviations: AH_2, ascorbic acid; CAT, catalase; CSH, cysteine; CSSC, cystine; FAD, flavin adenine dinucleotide; GR, glutathione reductase; GRAS, generally recognized as safe; GS, glutenin subunit; GSH, glutathione; GSSG, oxidized glutathione; HMW-GS, high molecular weight glutenin subunit; LMW-GS, low molecular weight glutenin subunit; LOX, lipoxygenase; MW, molecular weight; NAD, nicotinamide adenine dinucleotide; NADP, nicotinamide adenine dinucleotide phosphate; NGS, NADP glutathione system; NTR, NADP dependent thioredoxin reductase; PDI, protein disulfide isomerase; POX, peroxidase; PSSG, protein bound glutathione; SH, thiol; SS, disulfide; TYR, tyrosinase.

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1. Introduction

Hexaploid wheat (*Triticum aestivum*) is one of the most widely grown and important cereal crops in the world (FAOSTAT, 2007). It is used for the production of numerous food and non-food products. During breadmaking wheat flour, water, salt and yeast are mixed into visco-elastic dough, which is subsequently fermented and baked. Wheat flour is an ideal raw material for the preparation of leavened bread mainly because of the unique properties of its protein fraction, although starch and non-starch polysaccharides also affect the quality of the final product.

The present review focuses on gluten proteins and endogenous wheat components, enzymes and co-factors that affect the protein network during breadmaking. The effects of exogenous components on breadmaking are reviewed by Joye et al. (2009), and Goesaert et al. (2005).

2. Gluten and non-gluten proteins

Gluten comprises the major storage proteins of wheat that make up 80 to 85% of the total wheat proteins. Gluten proteins contain high proportions of glutamine and proline, while amino acids with charged side chains only rarely occur (Wieser, 2007). The quantity as well as the quality (composition) of the gluten proteins affect the dough and breadmaking quality of wheat flour and the characteristics of the resulting loaf such as its volume, crumb structure and crispness of the crust (Every et al., 1998; Finney and Barmore, 1948; Primo-Martin et al., 2006; Scanlon et al., 1997; Zghal et al., 2001).

Based on their solubility in 70% aqueous ethanol (Belitz et al., 2004), gluten proteins can be divided into two functionally distinct groups, the monomeric gliadins and polymeric glutenins. Both groups are important for dough rheology, imparting different properties to dough.

Gliadins mainly contribute to dough viscosity and extensibility. They have molecular weights ranging from about 30,000 to 80,000 (MacRitchie et al., 1990). Four groups (α, β, γ and ω) have been identified based on their mobility in gel electrophoresis at low pH. However, based on amino acid sequences, α- and β-gliadins have been grouped together (α/β) (Wieser, 2007). The C-terminal domains of α/β-, and γ-gliadins contain six or eight cysteine (CSH) residues, respectively, which form intramolecular disulfide (SS) bonds. Hence, the gliadins do not participate in the polymeric structure of glutenin (Shewry and Tatham, 1997; Wieser, 2007) (Fig. 1). In contrast to the α/β- and γ-gliadin, ω-gliadins do not contain CSH residues.

Glutenins form a heterogeneous group of polymers and principally provide cohesiveness and elasticity to dough. The glutenin polymers have molecular weights ranging from about 80,000 to several millions and are thus much larger molecules than gliadins (Kasarda, 1989). They cannot be solubilised completely without reduction or partial shearing to reduce their molecular weights. Intermolecular SS bonds can be reduced by addition of reducing agents, releasing the component glutenin subunits (GS) which have similar solubility to gliadins. GS are biochemically related to gliadins and can be divided into four distinct groups: high molecular weight GS (HMW-GS, MW 65,000–90,000) and B-, C- and D-type low molecular weight GS (LMW-GS, MW 30,000–60,000) (D'Ovidio and Masci, 2004). The LMW-GS contain six C-terminal CSH residues in similar positions to these in gliadins and at least one additional CSH residue (Fig. 2), which can form intrachain SS bonds with other gluten proteins and thereby contribute to network formation (Wieser, 2007). HMW-GS are classified based on the coding genome (A, B or D), the type [*x* (MW 83,000–88,000) and *y* (67,000–74,000)] and the mobility on SDS–PAGE (1–12) (Payne et al., 1980, 1981, 1982; Wieser, 2007). HMW-GS have high proline (10 mol%), glycine (20 mol%), and glutamine (35 mol%) contents (Belton, 1999; Gianibelli et al., 2001b). The CSH residues are nearly all located near the terminal ends of the subunits (Veraverbeke and Delcour, 2002). For a more detailed review of gluten protein structure and SS bonds, we refer to Veraverbeke and Delcour (2002) and Wieser (2007).

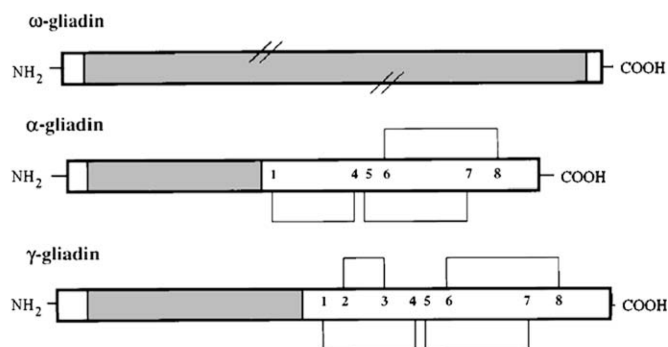

Fig. 1. Modular structures of ω-, α- and γ-gliadins. The repetitive and non-repetitive domains are shown in gray and white, respectively (adapted from Gianibelli et al., 2001a and reprinted with permission of AACC International). ω-Gliadin does not contain cysteine (CSH) residues, while α- and γ-gliadin contain six and eight CSH residues at the C-terminal end forming intramolecular SS bonds.

Non-gluten proteins include albumins (water extractable) and globulins (dilute salt medium extractable) (Osborne, 1907) which comprise metabolic proteins (enzymes or inhibitors) and minor storage proteins. Their importance in breadmaking is largely unknown, although some endogenous enzymes such as peptidases (EC 3.4) (Caballero et al., 2007), amylases (EC 3.2.1.1) (Lagrain et al., 2008) and xylanases (EC 3.2.1.8) (Courtin and Delcour, 2002; Courtin et al., 1999; Dornez et al., 2007), and some inhibitors [xylanase inhibitors (Debyser et al., 1997, 1999; Gebruers et al., 2001) and amylase inhibitors (Klockiewiczkaminska et al., 1995; Sorensen et al., 2004; Zawistowska et al., 1988)] have the potential to influence final bread quality.

3. Gluten network formation during breadmaking

During breadmaking, a number of chemical and physical transformations occur that determine final bread quality. Some of these can be influenced by the presence or deliberate addition of substances that alter structural and physicochemical characteristics of flour constituents and optimise their functionality in breadmaking. During mixing, a gluten network is formed by depolymerisation and (re-)polymerisation processes (Weegels et al., 1997), eventually resulting in a buildup rather than a breakdown of the polymeric structure (Belton, 2005). The gluten matrix assists in retaining the carbon dioxide produced by yeast during fermentation and early baking stages (oven rise). As such, gas retention determines loaf volume and crumb structure. As mentioned above, glutenins provide dough strength and elasticity as they form a continuous network (Shewry et al., 2002; Singh et al., 1990). Glutenin quality depends on glutenin structure, size distribution and subunit composition. As such, a high proportion of HMW-GS increases dough strength and improves dough stability against overmixing (Veraverbeke et al., 1998), while LMW-GS influence dough extensibility and resistance (Ciaffi et al., 1996; D'Ovidio and Masci, 2004). Gliadins probably act as 'plasticizer' for the glutenins and provide plasticity and viscosity (Wieser, 2007; Wieser and Kieffer, 2001). Weegels and Hamer (1992) suggested that the gliadin fraction prevents the detrimental overaggregation of

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