Impact of *Saccharomyces cerevisiae* metabolites produced during fermentation on bread quality parameters: a review

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Abstract

Although bread making with the use of Baker's yeast has a long tradition in human history, little attention has been paid to the connection between yeast addition and the final bread quality. Nowadays, bakers mainly use different flour additives such as enzymes (amylases, hemicellulases, and proteases) to change and improve dough properties and/or bread quality. Another strategy is the use of modified industrial Baker's yeast. To date, there is no yeast strain used in the baking industry, which is genetically modified, despite some studies demonstrating that the application of recombinant DNA technology is a possibility for improved strains suitable for baking. However, due to the fact that the majority of consumers in Europe highly reject the use of genetically modified microorganisms in the production of food, other strategies to improve bread quality must be investigated. Such a strategy would be a reconsideration of the selection of yeast strains used for the baking process. Next to the common criteria, the requirement for adequate gas production, more attention should be paid on how yeast impacts flavour, shelf life, colour and the nutritional value of baked products, in a similar way to which yeast strains are selected in the wine and brewing industries.

Keywords

Yeast, Metabolism, Baked products, Yeast selection

Abbreviations

(GDL) Glucono-delta-lactone

(ATP) Adenosine triphosphate

(I) Invertase

(G) Glucosidase

(GPD) Glycerol-3-phosphate dehydrogenase

(GP) Glycerol-3-phosphatase

(AD) Alcohol dehydrogenase

(AcD) Acetaldehyde dehydrogenase

(PD) Pyruvate dehydrogenase

(PDc) Pyruvate decarboxylase

(Ac-CoA-S) Acetyl-CoA synthase

(TCA) Tricaboxylic acid

(CS) Citrate synthase

(A) Aconitase

(ID) Isocitrat dehydrogenase

(α-KD) Alpha-Ketoglutarate dehydrogenase

(S-CoA-S) Succinyl-CoA synthase

(SD) Succinate dehydrogenase

(F) Fumarase

(MD) Malat dehydrogenase

(IL) Isocitrate lyase

(MS) Malate synthase

(GS) Glutamate synthase

(QPS) Qualified Presumption of Safety

(GRAS) Generally Regarded as Safe

(GABA) γ-aminobutyric acid

(GAD) Glutamic acid decarboxylase

(S.) *Saccharomyces*

(P.) *Penicillium*

(M.) *Meyerozyma*

(vit.) Vitamin

1. Introduction

Bread making is one of the oldest biochemistry processes in the whole world. *Saccharomyces cerevisiae* also known as Baker's yeast is one of the main ingredients for bread making. The term "cerevisiae" (meaning beer) signifies closely linked relationship between beer and bread making, originating centuries ago in Egypt and the Middle East. Historically, the same strain of yeast was used for both processes. In the nineteenth century, yeasts' left over from the brewing industry were shared with the bakers for bread production. Today, thousands of different genetically improved microbial cultures are used for different applications, like baking, brewing and wine making. Although bread making has a long tradition throughout human history, little attention has been focused on the connection between yeast addition and the final bread product quality (Dequin, 2001; Mondal and Datta, 2008). To date, bakers mainly use different flour additives, such as enzymes (amylases, hemicellulases, and proteases) to change and improve dough properties and/or bread quality. Another strategy is the use of modified industrial Baker's yeast. During fermentation yeast produces mainly carbon dioxide, but the role of yeast goes much deeper than just gas production (Randez-Gil et al., 1999), concerning the production of ethanol and other secondary metabolites, which have an impact on the final product quality. Yeast affects the volume, structure, flavour, colour and shelf life of each fermented product (Fleet, 2007). The characteristic volume and aerated cell structure of bread are mainly influenced by the addition of yeast its metabolism and carbon dioxide production during fermentation. Due to the production of secondary metabolites through different metabolic pathways, yeast influences the flavour (by producing precursors such as esters, aldehydes and ketones), colour

(carbohydrates, amino acids) and shelf-life (acids, glycerol) of baked products. All these metabolic products demonstrate the important role of yeast in bread making. Nevertheless, the most important characteristic, which is usually considered during strain selection is the ability to ferment sugars anaerobically with adequate gas production (Reed and Nagodawithana, 1991). In our opinion, the production of other metabolites by the yeast is underestimated when considering the selection of yeast strains. The purpose of this study is therefore to describe the impact of yeast in view of final bread quality parameters. This article reviews critically published literature on studies related to yeast and bread quality and identifies potential future investigations for applied yeast research with particular reference to the production of wheat bread. The main intention of this study is to better understand the complex dough fermentation reactions performed by yeast and their impact on product quality. This may enable the adaption of new yeast strains including those currently used in other applications, such as the brewing and wine industries, which can specifically enhance bread properties and so the final bread quality. The present review further examines the metabolites produced by yeast during dough fermentation and their impact on bread quality parameters. This knowledge could help to create new procedures and criteria for yeast strain selection for application in bread making.

2. Yeast in bread making

Yeast is an ubiquitous, unicellular, asexual eukaryote belonging to the kingdom Fungi, which is able to ferment sugars (added or produced by enzymatic hydrolysis) into alcohol and carbon dioxide (Cauvain and Young, 2007) and therefore is known as the leavening agent in baked goods. Their shape is typically spherical, oval or cylindrical with an average diameter of around 8 µm. The cells contain a double layered cell wall through which the cell is able to absorb

nutrients and release metabolites. The main yeast strains related to bread making are from the species *S. cerevisiae* (Cauvain and Young, 2007; Fleet, 2007). Fresh Baker's yeast comprises of 30-33 % of dry materials, 40.6-58.0 % of proteins, 35.0-45.0 % of carbohydrates, 5.0-7.5 % of minerals, 4.0-6.0 % of lipids and several vitamins (vit.) (Bekatorou et al., 2006). The European yeast industry produces 1 million tonnes of yeast annually of which around 30 % is exported globally (http://www.cofalec.com/business-and-economy/). The annual growth rate of the global market is expected to be 8.8 % from 2013 to 2018 (http://www.marketsandmarkets.com/Market-Reports/yeast-industry-268.html). Typically, an aerobic fed-batch process with molasses as a nutrient source is used for the commercial production of yeast (Attfield, 1997). The process consist of growing, separating, washing and processing to remove extracellular and intracellular water by filtration or pressing (Randez-Gil et al., 1999). To decrease damage to the yeast cells additives like emulsifiers and/or antioxidants are added during production. Growth conditions including temperature (25-30 °C), moisture, and nutrients (starch, sugar) must be optimised. When yeast is grown outside these optimal parameters, a complex stress response occurs (Attfield, 1997). Stresses can cause direct and/or indirect cell damage influencing the membrane permeability, inhibiting enzymes activity and result in the formation of reactive oxygen species. Cell responses include a decrease in intracellular pH through the production of glycerol, formation of several antioxidant defences such as glutathione and increased membrane permeability for intracellular components. Stress response is an important factor for survival and growth in industrial applications (Attfield, 1997). Intensive biochemical, microbiological and technical knowledge has led to commercial Baker's yeast preparations which contain one or more strains from the species *S. cerevisiae.* Through the addition of sourdough, other species can

be incorporated in the bread making process like *Pichia* and *Candida* (De Vuyst and Neysens, 2005). In general, a yeast used for the bakery industry should fulfil specific requirements with respect to the application and processing characteristics, such as adequate gas production to ensure a uniform dough leavening, tolerance to a wide range of pH, temperature and salt/sugar concentrations, as well as formation of desirable aroma compounds (Linko et al., 1997). Specialised brewers and/or distillers yeast could be incorporated in the bread making process, but because they are not adapted for the bread making process, it is common knowledge that they are unsuitable due to their different metabolism and tolerances (Cauvain and Young, 2007). Nevertheless, from the safety point of view European Union regulations allow these yeasts for use in dough fermentation and bread production. In fact, the safety of food is a major concern of consumers. Therefore, regulations and safety assessment guidelines are available in the European Union. The Qualified Presumption of Safety (QPS) list summarises a wide variety of biological agents including bacteria, yeasts, fungi and viruses that may be used in the food and feed chain (EFSA, 2012). In the United States, food and substances used in food are regulated by the U.S. Food and Drug Administration and are summarised in the Generally Regarded as Safe (GRAS) status.

Interesting yeast species that could be used as an alternative to *Saccharomyces* include *Debaromyces*, *Kluyveromyces* and *Schizosaccharomyces*. Heitmann et al., (2015) recently studied the impact of different beer yeasts in comparison to Baker's yeast on wheat bread quality. This study showed that various beer yeasts are suitable for bread making and the resulting wheat bread showed both superior and inferior characteristics in comparison to the Baker's yeast control bread. Nowadays, yeast is produced in a huge variety of different forms

throughout the world. However, these "domestic" yeasts are different from "wild strains" due to genetic modification and adaption, which allows them to grow in inappropriate situations (Ali et al., 2012). The main formats in which yeast is available include fresh, compressed, active dry and instant active dry yeast. The difference between these formats is related to their physical appearance due to differences in moisture content. Reduction in moisture content is used to prolong the shelf life of the strain but such preservation methods have an impact on yeast performance factors such as metabolic activity, acid- and osmo-tolerance as well as temperature stability (Cauvain and Young, 2007). Product shelf life ranges from 3 weeks (fresh and compressed yeast) to 1 (dry yeast) or 2 (instant dry yeast) years (Hui, 2006). Fresh and compressed yeasts are most commonly used in industry, since they are considered to be the most reliable. The format of the yeast also has an influence on the fermentation intensity. Fresh yeast produces the most carbon dioxide during fermentation resulting in superior dough-rising capacity. Considering the fermentation speed, the yeast acts in the following order: compressed yeast > instant active dry yeast > active dry yeast (Hui, 2006). Although fresh yeast is slightly dehydrated it doesn't need hydration time like dry yeast. The biggest problem is the shorter shelf life of fresh yeast in comparison to processed yeast. Instant yeast is available since the 1960s and is characterised by its very low moisture content and its fine particle size. In comparison to dried yeast, instant yeast can be directly added to the flour and its main use is for bread and pizza premixes (Cauvain and Young, 2007). Some studies have already investigated the impact of these different formats on product quality parameters. Codina and Voica, (2010) studied the impact of different yeast (*S. cerevisiae*) forms on carbon dioxide retention using a rheofermentometer. They found that active dry yeast had the highest fermentation rate followed

by compressed yeast and active instant dry yeast (Codina and Voica, 2010). Rollini et al., (2007) analysed four commercial compressed Baker's yeast (*S. cerevisiae*) strains which were originally used in different applications (pastries, bread, frozen doughs and Panettone) and tested them in complex dough formulations. They found that the different strains were indeed suitable for different applications in contrast to what was indicated by the producer. However, all their Baker's yeasts belonged to the species *S. cerevisiae* and they showed variations regarding their growth efficiency and gassing power.

To the authors' knowledge, there is no yeast strain used in the baking industry which is genetically modified. However Randez-Gil et al., (1999) showed that recombinant DNA technology is a possibility of constructing new strains with improved suitability for the baking industry.

3. Yeast vs. chemical leavening agents

Besides yeast, it is a common practice to produce leavened products using chemical leavening systems which produce carbon dioxide either through chemical decomposition using heat or through an acid-base reaction. For bakery products, particularly pastries, the two major gas producing chemicals used are sodium bicarbonate (baking soda) and ammonium bicarbonate (Amendola and Rees, 2003). Baking soda is a powerful leavening agent which starts as soon as it comes into contact with an acidic environment like batter or dough (Amendola and Rees, 2003). The disadvantages of these chemical leavening agents are the creation of off-flavours as well as an over browning. An advantage is the short production time; no fermentation step has to be included in the production, since some gas is already released at room temperature with the majority released during baking. In comparison to yeast the release of gas is much faster and the

gas cells are therefore much bigger. A few products naturally containing acids can be used for leavening like lemon juice or sour milk. Other chemical leavening agents include salts of phosphoric acid such as aluminium phosphate, mono-calcium phosphate, sodium acid pyrophosphate and di-calcium phosphate. Mono-potassium tartrate (cream of tartar) and glucono-delta-lactone (GDL) can be also used. The common baking powder consists of a mixture of different acids, mostly in combination with baking soda and starch as a carrier to separate the acids and bases to prevent premature reactions (Hui, 2006). Due to the neutralising effect of the different ingredients, no off-flavour is left and the pH is not influenced (Amendola and Rees, 2003). Similar to yeast, chemical leavening agents affect the structure, colour, flavour and pH of the final product. Each leavening agent creates a slightly different texture, so when choosing the appropriate leavening agent, the reaction rate and desired effects in the finished products must be known (Hui, 2006). Plessas et al., (2005) produced leavened bread by using kefir grains instead of yeast or chemical leavening. The produced bread showed a smaller specific volume but better ability to retain moisture after production, with a firmer texture. Another advantage was the lower acidity when using kefir grains with a positive effect on the mould-free shelf life. This study highlights that other substrates should be considered as leavening agents for baked goods beside Baker's yeast and chemical leavening agents.

4. Main Metabolic pathways

Yeasts are facultative anaerobes which means that they can grow with or without oxygen. In general, yeasts convert sugars into carbon dioxide, energy and biomass in the presence of oxygen. In the absence of oxygen they use alcoholic fermentation to convert sugar into ethanol, carbon dioxide and glycerol. The dominant fermentation products, which have the greatest

impact on bread quality are carbon dioxide and ethanol (Pronk et al., 1996; Trevelyan and Harrison, 1952). They are formed as soon as the yeast has been added to the dough/batter. *S. cerevisiae* also produces a range of other secondary metabolites as glycerol, organic acids, flavour compounds and precursors. The production of these compounds is linked to several different metabolic pathways, like glycolysis, alcoholic fermentation, the tricarboxylic acid cycle (TCA) and the glyoxylate cycle, which are summarised in Figure 1. The primary carbon metabolism is performed by glycolysis. During glycolysis the yeast produces energy by consuming low molecular sugars available in the dough (sucrose, maltose, glucose and fructose). Hexoses such as glucose and fructose, are the preferentially utilised sugars which enter the glycolytic metabolic pathway. However, glucose is preferred over fructose, since they are transported with the same carrier into the cell which has a greater binding specificity for glucose (Verstrepen et al., 2004). When glucose and fructose are consumed, the yeast starts to deplete maltose but without hydrolysing it to glucose, as Baker's yeast lacks the necessary enzyme. In beer production the most fermentable sugars are maltose, maltotriose and glucose. Again, glucose is the preferred sugar, but to obtain appropriate substantial alcohol content, the complete fermentation of maltose and maltotriose is also required. Consequently, the majority of brewing yeasts are able to ferment maltose and maltotriose after glucose. However, some yeast cells are not able to take up maltotriose for their metabolism which can lead to difficulties in beer brewing leading to lower ethanol yields or atypical beer flavours (Alves-Jr et al., 2007). To utilise maltose the yeast requires an active transport system across the plasma membrane. Subsequently, the maltose is hydrolysed by glucosidase enzymes (G) into two glucose molecules (Alves-Jr et al., 2007). The repression of the synthesis of glucosidase enzymes is a major concern in limiting the

dough fermentation rate (Dequin, 2001) which is also the reason for a lag phase in the carbon dioxide production. Osinga et al., (1988) suggested a means of avoiding this lag phase by replacing the promoters of the maltose permease and maltase with constitutive promoters to increase the metabolic conversion of maltose. Other higher sugars like sucrose need to be degraded by invertase (I) before the yeast can use them for metabolism. Therefore, the yeast harbours two different invertase enzymes. One invertase is located in the cytoplasm of the yeast cell and therefore it requires sucrose uptake. The second invertase is located between the plasma membrane and cell wall. The hexoses formed by this enzyme are taken up by hexose transport systems, and made available for yeast metabolism (Pronk et al., 1996). Codina and Voica, (2010) showed that after mixing no sucrose was left in the dough samples due to the presence the yeast invertase, which degraded the sucrose to glucose and fructose for yeast fermentation. Maltose concentration increases during dough fermentation due to activity of amylases found in wheat flour. A common pathway which is involved in all sugar-metabolising microorganisms is the lower part of the Embden-Meyerhof pathway and the formation of pyruvate (Koshland and Westheimer, 1950; Pronk et al., 1996). Pyruvate has a central position in many metabolic pathways as it can be seen in Figure 1. The production of pyruvate and, therefore glycolysis, plays a key role in the fermentation metabolism of yeast. The definition of glycolysis is well known as a sequence of ten enzyme-catalysed reactions, which converts sugars like glucose to pyruvate coupled with the production of ATP as an energy source. Di-hydroxy acetone phosphate as an intermediate in glycolysis and a precursor of glycerol, a compound which plays an important role in the cytosolic redox balance during anaerobic growth (Ansell et al., 1997; Bakker et al., 2001; Nevoigt et al., 2002; Nevoigt and Stahl, 1997; van Dijken and Scheffers,

1986). Di-hydroxy acetone phosphate is reduced to glycerol-3-phosphate by glycerol-3-phosphate dehydrogenase (GPD) and finally dephosphorylated to glycerol by glycerol-3-phosphatase (GP) (Nevoigt et al., 2002; Sigler and Hofer, 1991). In addition, during growth of yeast, pyruvate is transformed into many different compounds, such as carbon dioxide, ethanol and other organic metabolites, which have an influence on bread quality (Pronk et al., 1996). Since yeast favours an alcoholic fermentation metabolism over respiration *("Crabtree effect")* (De Deken, 1966), in the presence of high sugar concentrations the main metabolic pathway which must be considered is the alcoholic fermentation, starting from pyruvate (Fiaux et al., 2003; Gancedo, 1998). This "*Crabtree effect"* can cause several problems, such as an incomplete fermentation, production of off-flavours, undesirable by-products and loss of biomass yield (Verstrepen et al., 2004). During alcoholic fermentation ethanol is via pyruvate decarboxylase (PDc) conversion of pyruvate into acetaldehyde and carbon dioxide. Further, alcohol dehydrogenase (AD) reduces acetaldehyde to ethanol, by oxidation of NADH.

Another important metabolite is acetyl-CoA, which can be formed in two different pathways; either from pyruvate (glycolysis) or acetaldehyde (alcoholic fermentation). In the latter pathway, acetaldehyde is oxidised to acetate by acetaldehyde dehydrogenase (AcD). Acetate is converted to acetyl-CoA by acetyl-CoA synthase (Ac-CoA-S). With lowering sugar concentrations the yeast switches their metabolism from alcoholic fermentation to respiration which utilises the tricarboxylic acid cycle (TCA), known as "diauxic shift" (DeRisi et al., 1997; Foulkes, 1951; Galdieri et al., 2010; Gasch and Werner-Washburne, 2002). The production of acetyl-CoA from pyruvate is performed by pyruvate dehydrogenase (PD). Acetyl-CoA can be used for the production of fatty acids and fat. Thurston et al., (1982) showed that fatty acids are mainly

produced during the first four hours of fermentation in beer with a four-fold increase over this time. Another fate of acetyl-CoA is its funnelling into the TCA cycle within the mitochondria, with the ultimate production of secondary metabolites and additional carbon dioxide. By definition, the TCA cycle is known as a series of chemical reactions used for carbon dioxide and ATP generation through oxidation of acetate. In this cycle, pyruvate is oxidised to carbon dioxide and water with the concomitant production of ATP. Most of the carbon dioxide involved in dough fermentation comes from alcoholic fermentation due to the "*Crabtree effect*" of yeast. The primary role of the TCA cycle is production of additional ATP. The expression of genes involved in the TCA cycle is down regulated during the first 30 min of dough fermentation, however, because of the presence of glucose and oxygen, these enzymes still have a low level activity which explains the production and excretion of organic acids such as citrate, malate and succinate. Several research groups showed that the such organic acids are produced in the TCA cycle (Arikawa et al., 1999a, 1999b; Whiting, 1976). Another enzyme in the TCA cycle is aconitase (A), which converts citrate into isocitrate (Gangloff et al., 1990). Aconitase is located in the mitochondria but also in the cytosol as part of the glyoxylate cycle (Duntze et al., 1969; Regev-Rudzki et al., 2005). The enzyme isocitrate dehydrogenase (ID) oxidases isocitrate to α-ketoglutarate, with the production of carbon dioxide, which also represents the starting point of glutamate metabolism. Via the reductive pathway of the TCA cycle, beginning from oxaloacetate, malate and fumarate can be produced (Arikawa et al., 1999a). Further oxidation to succinyl-coenzyme A is catalysed by α-ketoglutarate dehydrogenase (αKD) with the production of carbon dioxide. Beside the TCA cycle, the formation of succinate and malate by the enzymes isocitrate lyase (IL) and malate synthase (MS) can take place in the glyoxylate cycle which

occurs in the cytosol (Arikawa et al., 1999b; Fernandez et al., 1992). In addition to the production of glycerol, ethanol and organic acids, the yeast is able to produce free amino acids using the Ehrlich Neubauer-Fromherz pathway, which is linked to the shikimate pathway (Herrmann and Weaver, 1999; Maga and Pomeranz, 1974). Amino acid biosynthesis is controlled by about 30 enzymes involving different pathways (Pronk et al., 1996). Coming from the amino acids flavour formation takes place. It can start with a deamination of free amino acids like valine, leucine, phenylalanine or tryptophan followed by a decarboxylation, which can produce aldehydes. These aldehydes can be reduced to higher alcohols (isobutyl alcohol, isoamyl alcohol, phenylethanol) or transformed into acids by oxidation (Maga and Pomeranz, 1974). In general, the biosynthesis of higher alcohols commences with a transamination reaction of amino acid such as valine, leucine and phenylalanine and is catalysed by aminotransferases. The produced α-keto acid is further converted by decarboxylation into fusel alcohols, and finally reduced to higher alcohols via the Ehrlich pathway (Hazelwood et al., 2008; Procopio et al., 2011). In addition, the corresponding organic acids can be produced, like phenylacetate, hydroxyphenylacetate, or isobutyrate (Hazelwood et al., 2008).

5. Loaf volume/Cell structure

Achieving a desired loaf volume by yeast fermentation is only possible by providing a favourable environment for yeast growth and for formation of gluten matrix that enables maximum gas retention (Sahlström et al., 2004). The gas bubbles, which are incorporated in the dough after mixing, grow during fermentation until they are saturated with carbon dioxide. This growth leads to expanding of the dough and thinning of the dough matrix between the gas cells. If over-fermentation occurs the dough is not capable of retaining the additional gas produced by

the yeast and the gas bubbles fracture, which leads to a lower bread volume. The gas holding capacity is an important characteristic for determining the bread quality and suitability of yeast for baking. The more gas that is entrapped in the dough, the smaller the gas cells and the higher their distribution is after proofing. These gas cells can resist more strength before they rupture, which leads to lower extensibility and a higher specific volume (Dobraszczyk, 2003; Sroan et al., 2009; Verheyen et al., 2014). During the baking process, the ethanol produced evaporates with some of the water, which helps to develop the aerated structure of the cell crumb. It is well known that dough mixing time can be reduced by adding instant active dry yeast, due to an effect on the gluten network development (Pyler and Gorton, 2008a). In dried yeast some non-viable cells are present which release glutathione as a stress response (Penninckx, 2002; Reed and Nagodawithana, 1991; Verheyen et al., 2015). Rheological dough properties are influenced by oxidising and reducing agents, which have an effect on the glutenin subunits that are linked by disulphide bonds and can affect their degree of polymerization (Delcour and Hoseney, 2010). The release of glutathione has a strong reducing effect and therefore increases the rate of thiol-disulphide interchange reactions which leads to a modification of the viscoelastic gluten network (Verheyen et al., 2015). As a result, gluten proteins with reduced size and lower molecular weight are present (Delcour and Hoseney, 2010). For the reason, that rheological dough properties are strongly influenced by thiol-disulphide exchange reactions; by removing thiol groups the dough gets stronger Frater & Hird, (1963). Strong and weak flours differ in their amount of protein-bond glutathione. Li et al., (2004) measured 10 different flours varying in their amount of protein-bond glutathione; Only 5 flours resulted in bread doughs showing a strong performance. They reported that flours with a significantly higher amount of protein-bond

glutathione result in a strengthening effect on the dough and therefore a stronger gluten-network development and better bread characteristics. Moreover, yeast is able to produce glycerol and pyruvic acid in the early stage of fermentation (Whiting, 1976). Glycerol has a positive effect on the texture of bread, especially during freezing. (Corsetti et al., 2000) reported that the addition of glycerol reduces the firming of baked products during storage.

6. Flavour and aroma

Aroma and flavour are important quality parameters for bread. These are mainly affected by ingredients and secondary fermentation products produced by yeast and generated under baking conditions (Birch et al., 2013b; Frasse et al., 1993; Gassenmeier and Schieberle, 1995; Maeda et al., 2009; Schieberle and Grosch, 1991). The most influential compounds are volatile compounds like alcohols, aldehydes and ketones and non-volatile compounds like acids, esters, sugars, phenolic compounds free fatty acids and lipids (Hui, 2006). Non-volatile compounds act mainly as precursors for reactions that form new flavour compounds (Hui, 2006). Sugars remaining from the fermentation have an effect on aroma due to their high reactivity in Maillard reactions (Nilsson et al., 1987). The Maillard reaction is a complex mechanism between reducing sugars like maltose, glucose and fructose and amino acids like leucine and phenylalanine, peptides and/or proteins during baking, influencing the colour, flavour and nutritional properties of baked products (O'Brien et al., 1989). Dough fermentation with yeast results in a decrease of the concentration in free amino acid content. An increased amount could influence the aroma through Maillard reactions and the Ehrlich pathway. Some volatile compounds are lost during baking, while others form complexes with other dough constituents, thus affecting the flavour profile of the final product. Not all components which contribute to the overall flavour and

aroma of yeast leavened breads have been identified thus far. The total number of contributing components is enormous and their specific interactions in flavour and aroma formation are still not fully understood (Reed and Nagodawithana, 1991). A few authors have reviewed flavour formation in bread (Cho and Peterson, 2010; Maga and Pomeranz, 1974; Pyler and Gorton, 2008b; Rothe, 1988). Most of the compounds responsible for aroma formation in bread crumb made from yeast fermented dough result from yeast metabolism (Frasse et al., 1993; Schieberle and Grosch, 1991), whereas the aroma compounds of the crust are products of Maillard reactions (Purlis, 2010). The most significant compounds reported in the literature are alcohols and aldehydes such as 2,3-butanedione and 3-hydroxy-2-butanone and esters which are produced by yeast cells using the Ehrlich Pathway to degrade amino acids (Hazelwood et al., 2008). Nowadays in the baking industry the trend is to use a short bread making process in terms of fermentation, whereby the development of aroma and flavour is very limited (Cauvain and Young, 2007; Maeda et al., 2009). The application of different bacterial starter cultures, such as wine or beer yeast could compensate for these short fermentation process and produce flavour and aroma during such short fermentations (McKinnon et al., 1996; Suomalainen and Lehtonen, 1978). Research on alcoholic beverage fermentation and production reveals that the choice of starter cultures is an important factor, related to the formation of aroma and flavour in the final product (Procopio et al., 2011; Suárez-Lepe and Morata, 2012). Several studies have dealt with the effects of yeast on aroma development during the production of wine and beer (Molina et al., 2007; Saerens et al., 2008). In these industries, yeast identification and strain characterisation is essential, due to the wide variety of different flavour and aroma profiles yeast can impart (Dashko et al., 2015; Huangl et al., 2010; Katarína et al., 2014; Pires et al., 2014; Vararu et al.,

2016). In the recent years the aroma of bread gain more focus and recognition as an important bread quality parameter (Birch et al., 2014, 2013a, 2013b).

Birch et al., (2013a) studied the influence of seven commercial compressed Baker's yeasts on the formation of bread aroma using dynamic headspace extraction. They found significant differences in the aroma profile of the bread crumb with fermentation time, between the breads. Furthermore, they stated that the choice of Baker's yeast is a very important decision for the bakers with respect to fermentation activity and aroma formation potential. Another study by the same group showed that with increasing yeast concentration, the main flavour components like 2-methyl-1-propanol, 2-phenylethanol, phenylacetaldehyde, 2,3-butanedione, ethyl acetate, ethyl 3- methylbutanoate, ethyl hexanoate, ethyl octanoate and phenyl-ethyl acetate increase concomitantly (Birch et al., 2013b). On the other hand, an increase in fermentation temperature caused an increase in lipid oxidation products, which are often described as off-flavours. However, their formation is independent of yeast concentration. It was suggested that short fermentation time at low temperatures and high yeast concentrations could be used to develop a bread with a high concentration of aroma compounds and less off-flavour. Thurston et al., (1982) suggested a relationship between yeast's fatty acids and the aromatic profile of fermented foods. Such fatty acids have been shown to contribute to the production of fatty acid ethyl esters especially in beer. They are connected to the yeast cell wall and can be released when yeast cells dies. Fatty acid esters are secondary metabolites produced by yeast and many bacteria, which play a key role in the flavour of alcoholic beverages. Ethyl esters of short and medium fatty acids are important flavour compounds characterised by their strong fruity flavour. Beside their

application in food and beverage production, they are also used by the cosmetic and pharmaceutical industries.

7. Colour

Another important attribute for consumer's acceptability is colour. Surface colour is of considerable importance in the baking industry (Pathare et al., 2013; Purlis, 2010; Zanoni et al., 1995) as it is the first parameter assessed by consumers. Colour formation depends on physico-chemical characteristics such as moisture, pH, sugar concentration, amino acid content and the process conditions used during production, like baking temperature, fermentation time and temperature and starter culture (Zanoni et al., 1995). Colour formation results chemical, biochemical, microbial and physical changes, which arise during production (Pathare et al., 2013). Colour formation on the crust develops mainly throughout bread baking due to chemical changes via the Maillard reactions (Purlis, 2010). Maillard reaction occurs between proteins and carbohydrates at temperatures higher than 50 °C at a pH range of 4-7. Another important reaction is caramelisation (Kroh, 1994; Zanoni et al., 1995), which is the direct degradation of sugars and starch occurring in high-sugar foods at higher temperatures, >120 °C or 9<pH<3 (Kroh, 1994; Zanoni et al., 1995). Both reactions appear concurrent and depend on the type of sugar and amino acids present as well as the pH and water activity of the product (Zanoni et al., 1995). The residual reducing sugars remaining after fermentation strongly influence the crust and crumb colour (Finot, 1990; O'Brien et al., 1989). Due to increased mobility of reactants, the reaction rate increases exponentially with higher moisture content, up to a maximum at 30% moisture (Wolfrom et al., 1948; Wolfrom and Rooney, 1953). Both the initial pH of the product and the buffering capacity of the system influence the rate and direction of the reaction. The rate of

browning is low at acidic pH values and intensifies with increasing pH to a maximum at a pH of ~10 (Ashoor and Zent, 1984; Wolfrom et al., 1946). In general, the rate of Maillard reaction is if excess reducing sugars are present rather than excess amino compounds (O'Brien et al., 1989). Crust colour can be also controlled by using different starter cultures. Alpha amylase activity is the main reaction to be considered in relation to crust colour formation, due to the production of increasing amounts of maltose and dextrins, which participate both in the Maillard and caramelisation reactions. Use of different starter cultures can have an influence on colour formation due to differences in sugar metabolism (Goesaert et al., 2005; Heitmann et al., 2015; Ormrod et al., 1991).

8. Shelf life

Shelf life is a parameter relating to the loss of perceived freshness. This can be correlated to several different factors which are summarised in two different categories, staling and microbial spoilage. These parameters will be discussed further in the next two paragraphs.

a. Staling/Hardness/Firmness

Modifications in crumb structure due to changes other than spoilage organisms, such as chemical and physical changes of the crust (soft, leathery) and crumb (hard, dry, and crumbly) is referred to as staling (Kulp and Ponte, 1981). Bread staling is mainly associated with the firming of the crumb, which is an important factor in terms of consumer acceptability (Pateras, 2007). Although bread staling is not yet completely understood, the baking industry uses different anti-staling agents to inhibit staling. These include enzymes, alcohol, lipids, emulsifiers and sweeteners (Hui, 2006; Pateras, 2007). In particular, *alpha*-amylase is well known to retard crumb firming (Giménez et al., 2007; Hui, 2006; Pateras, 2007). Lipases, lipoxygenases, endoxylanase,

arabinosidase and protease are also known to prevent bread staling due to a crumb softening effect. Heitmann et al., (2015) examined the effect of different yeast strains on bread hardness during storage. By using different starter cultures they were able to produce a significant change in crumb hardness, explained by the negative correlation of $r = -0.90$ ($p < 0.05$) between crumb hardness and specific volume. It is known that breads produced with a bulk fermentation step have a longer shelf life, due to larger amounts of alcohol produced during fermentation. Some studies examining the effect of ethanol on bread staling, showed that the crumb modulus of bread, treated with ethanol, increases during storage at a slower rate than the control bread using a differential scanning calorimeter and crumb compressibility measurement (Fearn and Russell, 1982; Russell and Chorleywood, 1983). Russell and Chorleywood, (1983) showed, that bread treated with ethanol firms at a slower rate than control bread. Increasing sugar and salt levels are also known to slow the staling of baked products (Cairns et al., 1991; Taylor et al., 2009). (I'Anson et al., 1990) reported a decreasing effect of ribose> sucrose> glucose on the retrogradation of wheat starch, but the full mechanism of action is not fully understand. It is suggested that sugars are able to increase the glass transition temperature and concurrently decrease the diffusion of polymers to a crystal nucleus (I'Anson et al., 1990). On the other hand (Levine and Slade, 1990) stated that sugars increase the glass transition temperature of the amylose matrix and therefore the re-crystallization of amylopectin is repressed. Glycerol has been reported to influence moisture distribution and staling of bread during storage. Yeast leavened breads show a higher water content than unleavened breads which results in more carbon dioxide and therefore a coarser bread crumb (Mondal and Datta, 2008).

b. Microbial spoilage

Microbial spoilage is another important factor when considering bread shelf life due to post-processing contamination (Pateras, 2007). Microbial spoilage is commonly caused by microorganisms belonging to the species *Aspergillus*, *Penicillium*, *Fusarium*, *Rhizopus*, *Mucor*, *Endomyces* and *Cladosporium* (Legan, 1993). Aside from the economic losses caused by these microorganisms, consumers are concerned about the potential mycotoxins produced by these microorganisms. Mycotoxins can cause severe health problems in humans (Legan, 1993; Pateras, 2007). The parameters determining the microbial shelf life are water activity, pH and storage conditions. The most common method for preventing mould growth is the application of chemical preservatives such as propionic acid and its salts or potassium sorbate. However, the current trend is towards production without the use of additives. One solution is the incorporation of sourdough as a natural bio-preservative to increase the mould-free shelf life of baked products. Lactobacilli produce weak organic acids, other low molecular weight compounds, peptides, cyclic dipeptides and proteins, which are known for their antifungal activity (Axel et al., 2015, 2014; Magnusson and Schnürer, 2001; Niku-Paavola et al., 1999; Okkers et al., 1999; Röcken and Vorsey, 1995; Stiles, 1996). Physical methods of prolonging the shelf life are modified atmosphere packaging, pasteurisation or irradiation of packed bread (Legan, 1993; Pateras, 2007). Some spoilage organisms such as spoilage yeast cause off-odours. Post-processing contamination is likely due to physical contact with contaminated equipment. The two main types of yeast associated in spoilage are filamentous yeast (“chalky moulds”) and fermentative yeast (Berni and Scaramuzza, 2013; Pateras, 2007). *S. cerevisiae* is the most common fermentative yeast spoilage organism, characterised by an alcoholic or estery off-odour. Filamentous yeast like *Pichia burtonii* form white colonies on the surface of bread. This growth

can be easily referred to as mould (Legan, 1993; Pateras, 2007). Berthels et al., (2004) identified yeast strains with a discrepancy in their consumption preference for glucose and fructose, and found the ability of such strains to reduce residual fructose levels and increase ethanol yield to be helpful in partially solving the spoilage problem. They suggested use of such strains as a criteria for selection of new yeast strains for wine production. Heitmann et al., (2015) demonstrated the effect of different *S. cerevisiae* strains, originating from the brewing industry, on the shelf life of white wheat bread. They showed both inferior and superior behaviour in terms of mold-free shelf life of the breads, which ranged between 3 and 5 days. They also demonstrated differences ability to propagate mould on breads baked with the different *S. cerevisiae* strains.

It is well known that some fungi and bacteria are able to produce secondary metabolites with antifungal properties. Nowadays most of the attention has been given to antifungal lactic acid bacteria present in sourdough bread and little attention has been given to yeast as possible producers of antifungal compounds. Yeasts, however, are promising candidates as fungicides. Coda et al., (2013) screened 146 different yeast strains (genera including *Candida*, *Metschnikovia*, *Debaromyces*, *Pichia* and *Kazachstania*) focusing on antifungal activity against *Penicillium roqueforti*. They found six *Meyerozyma guilliermondii* with noticeable *in vitro* activity. Their work showed the possibility of extending shelf-life of baked goods using *M. guilliermondii* LCF1353 as a mixed starter while maintaining optimal taste and structure at the same time. In another study the same group demonstrated, similarly, the potential of *Wickerhamomyces anomalus* as a mixed starter to extend the shelf-life of baked goods (Coda et al., 2011). Mo & Sung, (2014) investigated *Pichia anomala* SKM-T, which is known for its antagonistic properties against some spoilage moulds like *Penicilium paneum* KACC44834, and

found it to be suitable as a leavening agent for the production of white pan bread. The bread containing this strain exhibited less *P. paneum* spoilage colonies on the surface than bread baked with *S. cerevisiae*, due to a production of the flavour compounds 2-phenylethyl acetate, 2-phenylethyl alcohol, 2-decenal and nonanal, which enabled a shelf life extension. The production of antifungal compounds is considered in the selection of yeast strains for wine production. However, it is not a characteristic considered when choosing Baker's yeast.

9. Nutrition

Since ancient times, cereals have been a staple in the human diet. They are considered as an important source of energy and supply macronutrients including complex carbohydrates, fibre, protein as well as micronutrients such as calcium, phosphorus, iron, sodium, magnesium and potassium. Cereal grains can be considered a source of vitamins, especially B vitamins like thiamine (vit. B1), riboflavin (vit. B2) and niacin (vit. B3) (Cauvain and Young, 2007). Yeast represent a nutritional source of carbohydrates, fats, vitamins, especially B vitamins, minerals and amino acids, in particular, lysine (Rincón and Benítez, 2001). Studies on the effects of cereal fermentation on nutritional quality are scarce. Due to bread being a staple food it represents an important means to supplementing human nutrition. During fermentation yeast can have an effect on the levels vitamins, phenolic compounds, phytates and folates, which is discussed more detail below.

During the production of yeasted bread, a 48% loss of thiamine (vit. B1) and pyridoxine (vit. B6) were observed (Batifoulier et al., 2005). However, a longer fermentation increased the levels again. Compared to thiamine (vit. B1) and pyridoxine (vit. B6), folate (vit. B9) showed good stability during bread making and an increased amount could be found in comparison to the flour

(Osseyi et al., 2001). The content of thiamine (vit. B1) has also been reported to decrease in the wheat and rye baking process, (Martinez-Villaluenga et al., 2009) but to increase with a longer fermentation time (Batifoulier et al., 2005). The fermentation step can therefore have an effect on the overall formation or retention of vitamins during baking. A short baking process was also presented to reduce the content of thiamine (vit. B1) in whole-wheat, but a prolonged yeast or sourdough fermentation maintained its levels (Batifoulier et al., 2005). Batifoulier et al., (2005) also found that the thiamine content was increased when fermentation time was prolonged and that the increase was significantly higher in white bread with yeast compared to sourdough, despite comparable vitamin production by the microorganisms (0.25 mg/g dry matter). Long fermentations could support a net synthesis of thiamine by yeast, while fermentation with lactic acid production in sourdough bread could origin in a decrease of thiamine (Khetarpaul and Chauhan, 1989). In contrast to these findings, (Rucker et al., 2006) reported a 35% loss of thiamine during bread making. A small amount of the riboflavin (B2) in bread derives from yeast. As a result, bread often contains more riboflavin than the original flour. Sourdough fermentation does not lead to any enrichment of riboflavin (Batifoulier et al., 2005). Whole-wheat bread making with yeast (from kneading to final bread) undergoing a long fermentation process, resulted in a 30 % enrichment in riboflavin. The use of yeast and sourdough during fermentation did not show a synergistic effect on B vitamin levels (Batifoulier et al., 2005), but a longer fermentation time could increase the level of pyridoxine (Batifoulier et al., 2005). Yeast fermentation has been shown to result in an increase of folate in the baking process of wheat and rye breads (Kariluoto et al., 2006). Kariluoto et al., (2006) investigated the ability of yeasts and lactic acid bacteria to have an influence on the folate content in a rye sourdough and showed that

the effects of sourdough bacteria are negligible. Proofing does not influence the total folate content but changes in vitamin distribution were observed. Folate losses during baking were about 25 % (Kariluoto et al., 2004). However, the synthesis of folate by yeast results in an increase of the content over three-fold in bread. Another important advantage of yeast fermentation is the reduction of phytates (phytic acid) by phytase activity which results in an increase of the bioavailability of magnesium and phosphorus. However, phytase activity depends on the substrate flour, proofing temperature and time as well as dough pH and the amount of yeast (Pozrl et al., 2009). Commercial Baker's yeast has been shown to express phytase activity (Tu et al., 2000). A wide variation in phytase activity was identified in sourdough starters containing both yeast and lactic acid bacteria (Chaoui et al., 2003; Reale et al., 2004). Another potential suggestion was the use of high-phytase yeast strains to act as phytase carriers in the gastrointestinal tract. The reduction of phytic acid has repeatedly been reported in yeast and sourdough processes. Although yeast fermentation reduces the unfavourable effects of phytic acid, sourdough bread seems to be a better source of available minerals, especially magnesium, iron and zinc (De Angelis et al., 2003; Turk et al., 1999). Therefore, it should be possible to control the phytase activity by modifying the process conditions or by selecting specific microbial starters. Losses have been observed for tocopherol (vit. E) during sourdough preparation and dough making (Wennermark and Jägerstad, 1992). Katina et al., (2007) observed reduction in tocopherol (vit. E) and tocotrienol (vit. E) content. This may have been due to oxygen sensitivity. Fermentation has been shown to increase the antioxidant activity in the methanol extracted fraction of rye sourdough, concurrent with increased levels of easily extractable phenolic compounds (Katina et al., 2007). A reduction in kneading time combined

with a longer fermentation time could be able to retain carotenoids and vitamin E contents. Fermentation of rye bran with yeast was also shown to increase the level of free ferulic acid (Katina et al., 2007). The antioxidant capacity of rye breads baked with sourdough showed an increase than that of white wheat bread. The highest values were reported for breads using wholemeal flour (Martinez-Villaluenga et al., 2009; Michalska et al., 2007). Recently, it was shown that a yeast fermentation using wheat bran together with cell wall hydrolytic enzymes increased the bioaccessibility of phenolic compounds in breads as well as the metabolite 3-phenylpropionic (Anson et al., 2009). (Poutanen et al., 2009) An increase in free ferulic acid was observed as a result of dough mixing and proofing. However, the amount of released ferulic acid was about 1 % of the total amount of ferulic acid originate from wholemeal rye. An increase of the levels of total phenolic compounds and free phenolic acids could be found by sourdough and yeast fermentation of wholemeal rye (Katina et al., 2007). In contrast, Boskov Hansen et al., (2002) did not observe a significant change in the content of phenolic acids during dough proofing. Baking showed a slightly increase of the concentration of phenolic compounds in the crust, probably through Maillard reaction (Gélinas and McKinnon, 2006). However, this effect was not detected in wholemeal bread (Boskov Hansen et al., 2002; Dewettinck et al., 2008; Gélinas and McKinnon, 2006). One other study used different yeast strains for the production of selenium enriched baked products. Stabnikova et al., (2008) used a yeast, which biomass was enriched with organic forms of selenium, to increase the amount of selenium in bread. The non-protein monocarboxylic acid, γ–aminobutyric acid (GABA), plays an important role in the animal and human nervous system as a neurotransmitter. An increased intake of GABA can be related to different health benefits, such as lowering of blood pressure, prevention of diabetes,

inhibition of leukaemia cell proliferation and cancer cell apoptosis. Collar et al., (1992) and Benedito De Barber et al., (1989) suggested, however, that GABA is rapidly consumed by yeast at the beginning of a fermentation, due to the high demand of nitrogen for cell growth, or takes part in the Maillard reaction. More recently Lamberts et al., (2012) showed the important role of yeast in the GABA dynamics during bread making. During dough mixing the level of GABA is increasing, but during fermentation yeast consumes it as a nitrogen source. However, the authors were able to produce GABA enriched bread through the addition of exogenous glutamic acid decarboxylase (GAD) in the recipe. Hudec et al., (2015) screened different microorganisms from 10 different food applications as well as seven pure bacterial strains for GABA. They showed a small production of GABA from *S. cerevisiae* Baker's yeast and wine yeast of 0.8 and 1.3%, respectively. The highest selectivity of GABA production could be detected using *Lactobacillus delbrueckii* subsp. *bulgaricus* of 90.0 %. Using strains from the genera *Lactobacillus,* via sourdough production, could be a good alternative to increase the GABA content in bread. Rizzello et al., (2008) previously reported a GABA concentration of 258.7 mg/kg in a wholemeal wheat sourdough by the addition of an adjunct culture using lactic acid bacteria.

10. Conclusion

The baking industry is currently selecting their yeast strains based on their ability to ferment sugars anaerobically with adequate gas production. However, other important quality parameters for consumer acceptance of bread including colour, texture and flavour, are not considered when selecting yeast strains. At the moment the production of additional metabolites by yeast plays an underestimated role in the selection of strains. Wine yeasts have been traditionally selected by their fermentative power, suitable fermentation kinetics, in additional to their low acetic acid

production and resistance to sulphur dioxide (Suárez-Lepe and Morata, 2012). Recently, new selection criteria have been sought to improve the technological properties and sensorial features of wines, since the metabolic uniqueness and physiological properties of yeast could, through the production of metabolites, improve the sensorial properties of wine. Included in these criteria are the ability to enhance wine colour, the absence of β-glucosidase activity, the facilitation of colloidal stabilisation in red wines, the appropriate enhancement of aroma via the production of volatile compounds and the provision of structure and body (Suárez-Lepe and Morata, 2012). Similarly detailed selection criteria are commonplace in the production of beer. The brewing industry, in general, separates yeast strains into ale and lager yeasts. In addition, they also use more specific selection criteria, such as the fermentation behaviour (top or bottom fermentation), fermentation performance (fermentation rate and degree of attenuation), the ability to ferment meliobiose, temperature tolerance, ability to flocculate (powdery or flocculant yeast), oxygen requirements and the ability to form or remove fermentation metabolites (aroma compound formation) (Bokulich and Bamforth, 2013; Kunze, 2014). Therefore, specific selection of Baker's yeast should be as carefully considered as it is done for wine and beer yeasts, particularly in terms of flavour, colour and shelf life. The wine industry has also recognised the potential of non-*Saccharomyces* yeast strains, which haven't yet been studied in the process of bread making (Suárez-Lepe and Morata, 2012). Randez-Gil et al., (1999) previously suggested to use recombinant DNA technology for the creation of new yeast strains expressing enzymes to allow elimination of the extensive use of baking additives. Choosing the perfect starter culture for bread/baked product manufacturing should not solely be determined by the gas production capacity during fermentation. Other characteristics like enzyme activity are an important

parameters to predict the final bread quality, due to their impact on shelf life (microbial and staling) as well as colour and flavour formation. Consumer acceptance will not allow use of genetically engineered yeasts. More targeted yeast selection, based on broader criteria, offers a good way to obtain yeast strains from the species *S. cerevisiae* (even other genera and species) with novel technological properties, within the limitation of current Food Legislation. Such strains should enable improvements in the technological and/or sensorial qualities of baked products.

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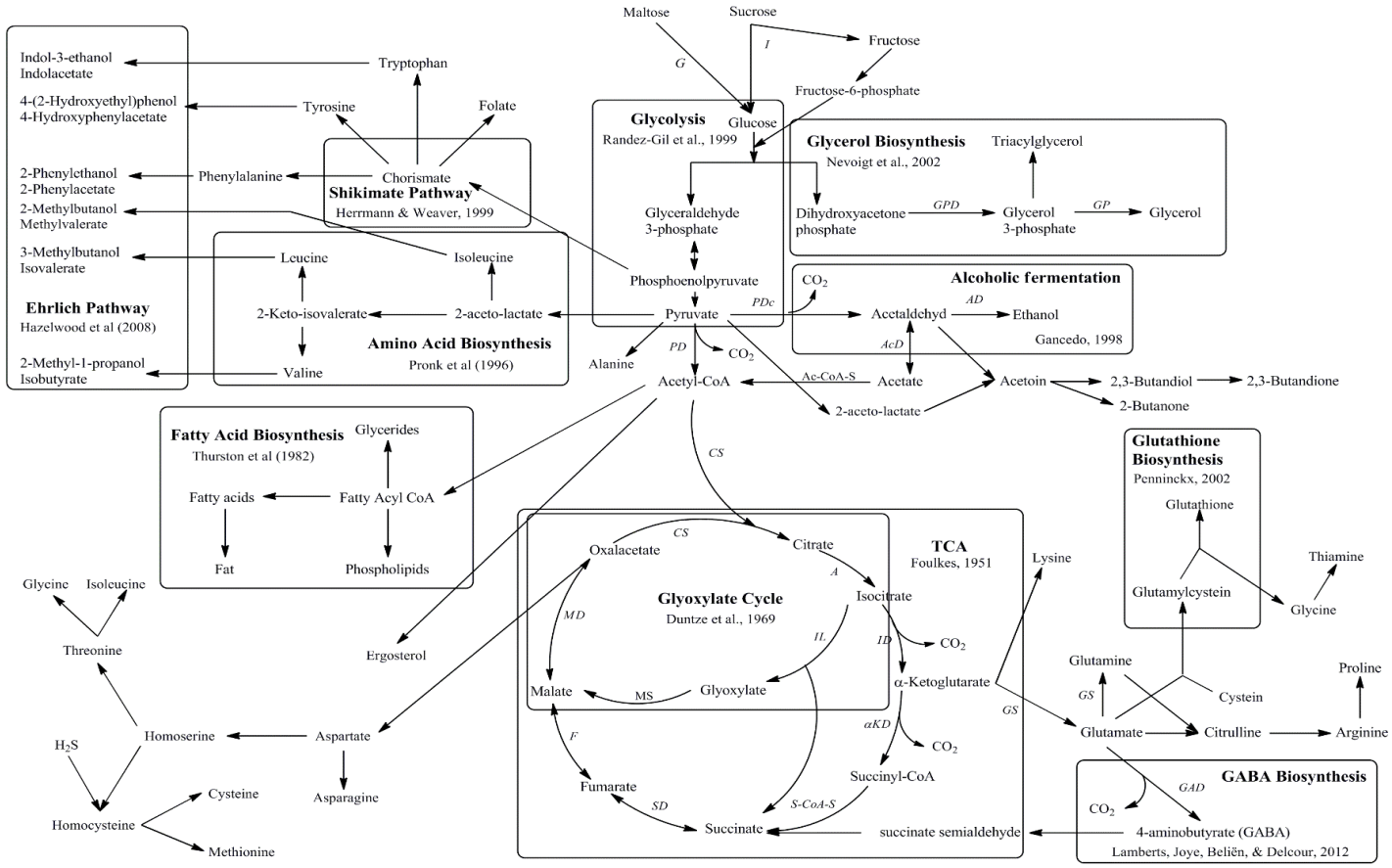

Figure 1. Schematic representation of the most important metabolic pathways, following the carbohydrate dissimilation, their enzymes (Abbreviation) and references in *Saccharomyces cerevisiae* influencing bread quality parameters.