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Mathematical Model of Sugar Uptake in Fermenting Yeasted Dough

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Fermentation prior to freezing significantly reduces the shelf life of frozen dough, measured as a decline in proofing power. Changes during fermentation caused by yeast metabolism have previously been described empirically on a dough weight basis and have not been mathematically modeled. In this work, yeast metabolites were quantified in fermenting dough and their concentrations were estimated in the aqueous environment around yeast cells. The osmotic pressure in the aqueous phase increases by 23% during 3 h of fermentation, which depresses the freezing point by 1 °C. The rise in osmotic pressure and the accumulation of ethanol may affect phase equilibria in the dough, baking properties, and the shelf life of frozen dough. Predictive modeling equations fitted sugar concentration data accurately. It was found that the preference of baker's yeast for glucose over fructose was stronger in fermenting dough than in liquid fermentations. The usefulness of the model in industrial bakery formulation work was demonstrated.

KEYWORDS: Bakery; dough; frozen dough; fermentation; yeast; *Saccharomyces cerevisiae*; mathematical model; glucose; fructose; ethanol; osmotic pressure

INTRODUCTION

The shelf life of frozen unproofed dough is determined mainly by the rate of carbon dioxide production by yeast following thawing (*1*). However, the reasons for the decline in carbon dioxide production following a period of frozen storage are complex and remain elusive. There is clear evidence that fermentation of dough prior to freezing results in a significant reduction in frozen shelf life (*2*, *3*). It is difficult to directly examine yeast cells and their surrounding environment in situ in fermenting dough, but mathematical modeling can mimic the basic elements of the environment and describe the events occurring during fermentation that may result in shortened frozen dough shelf life.

Saccharomyces cerevisiae cells metabolize endogenous or added sugars to pyruvate via glycolysis. In the absence of oxygen, pyruvate is decarboxylated to carbon dioxide and acetaldehyde, which is then reduced to ethanol to regenerate NAD^+ (*4*). During mixing of dough, water-soluble proteins, pentosans, and low molecular weight solutes dissolve to form a mixed protein−polysaccharide aqueous phase incompatible with the hydrated gluten gel (*5*−*7*). Yeast cells are suspended in the aqueous phase, from which they take up sugars and into which they excrete metabolic byproducts.

Sugar consumption has been modeled in other yeast-fermented foods such as wine (*8*) and beer (*9*, *10*), in addition to numerous models of fermentation in synthetic medium (*11*−*13*). Several workers have quantified changes in sugar content during dough fermentation (*14*−*18*), but these data were reported on a dough basis (% w/w or g per 100 g etc.), which gives little information about the environment experienced by yeast cells. No workers have applied models to the data. Thus, this paper is the first time where yeast metabolite dynamics in fermenting dough have been considered on a molar basis and mathematically modeled.

A significant proportion of the water in dough does not behave like pure water because of interactions with other dough constituents, especially polymers such as glutenin and soluble polysaccharides. This "nonsolvent water" has a lower mobility (*19*) and depressed freezing point (*20*), cannot be centrifugally separated from the dough (*21*), and has an isoteric heat of adsorption higher than the latent heat of condensation (*22*). Nonsolvent water is not part of the aqueous phase and must therefore be excluded from calculations of aqueous phase solute concentrations.

In simple flour−water doughs, the transition between nonsolvent and solvent water occurs at 0.3 g of water per g of flour dry matter (*19*, *22*−*25*). In this work, the water content of the aqueous phase was calculated based on the assumption that nonsolvent water did not form part of it. The aqueous phase of dough is similar to the liquid medium in broth culture or brewing

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fermentations, and on that basis, an analogous mathematical model is elaborated here.

MATERIALS AND METHODS

Dough Manufacture. One kilogram batches of dough were made with 600 g of wheat flour (Champion High grade white, Goodman Fielder, Auckland, New Zealand, 11.5% protein and 12.0% moisture), 330 mL of reverse-osmosis filtered water, 20 g of compressed yeast (Pinnacle brand, New Zealand Food Industries, Auckland, New Zealand, 67% moisture), 20 g of canola oil, 10 g of iodized salt, and 20 g of either added glucose (BDH, England), fructose (Sigma, United States), or sucrose (M&B, England). Ingredients were combined in the pan of a domestic breadmaker (Breville Breadmaster, Breville Holdings Ltd.) and mixed for 18 min according to the breadmaker's mixing cycle.

Batches of dough were divided by hand into 50 g pieces, which were shaped into slabs approximately 1 cm thick and sealed in plastic bags. Dough pieces were fermented at 30 °C in a temperature-controlled room for 0−180 min.

Sugar Extraction and Analysis. Sugars were extracted from dough as described earlier (*26*). Approximately 30 g of dough was torn into small pieces and dropped into liquid nitrogen in an aluminum dish. The quench-frozen dough was shattered with liquid nitrogen in a precooled laboratory Waring blender, producing a fine powder. The dough powder was stored in plastic bags at −80 °C until extraction.

A 2.5 g sample of frozen dough powder was added to 25 mL of water at room temperature in a centrifuge tube, and the slurry was homogenized with an ultra turrax (Heidolph Diax 600) at 13500 rpm for 30 s. An aliquot of each homogenate was filtered through a syringe-driven 0.8 μm Minisart disposable filter (26 mm diameter, Sartorius AG, Goettingen, Germany) into a 1.5 mL plastic tube (Eppendorf AG, Germany).

Extracts were held at 85 °C for 1 h in a water bath to inactivate enzymes, cooled on ice for 10 min, and then centrifuged at 13200 rpm for 5 min (Centra MP4R, IEC). The supernatant was pipetted into a fresh tube and stored at −20 °C.

Sugars in dough extract supernatants were quantified with enzymatic assays (BioAnalysis kits, Roche Diagnostics, Mannheim, Germany) using a Cobas Fara II robotic transfer analyzer (Roche Diagnostics). Results are expressed as mmol per 100 g dough (fresh weight). Duplicate analyses were performed on three independent doughs.

Data Analysis. Sugar uptake rates were expressed as differential equations and solved numerically with Matlab version 6.5 release 13 (The Mathworks Inc.). Statistical analyses were performed with Minitab release 14 (Minitab, Inc.).

RESULTS AND DISCUSSION

The only quantitatively important yeast substrates in dough are glucose, fructose, sucrose, and maltose. The content of each sugar in the unyeasted dough held at 30 °C for 180 min is shown in **Figure 1**. The sugar content of dough ingredients is plotted to the left of zero fermentation time; that is, fermentation time begins immediately after mixing. Error bars are larger for maltose than for other sugars because the calculation used in the enzyme assay involved subtraction of glucose and sucrose results (*27*), thus increasing total uncertainty.

In unyeasted dough, maltose and sucrose increased during mixing but did not change significantly thereafter (**Figure 1**). There was a significant increase in glucose and fructose throughout, probably due to the action of endogenous amylases, but the increase was negligible as compared with the changes in yeasted doughs.

In yeasted doughs, sucrose was almost completely hydrolyzed into glucose and fructose during mixing (**Figure 2**) as reported by other workers (*15*, *17*, *28*). The maltose concentration did not change during 3 h of fermentation. The conversion of sucrose during mixing to glucose and fructose was not stoichiometric and presumably reflects the preferred consumption of glucose by yeast during that period (*4*, *17*, *29*).

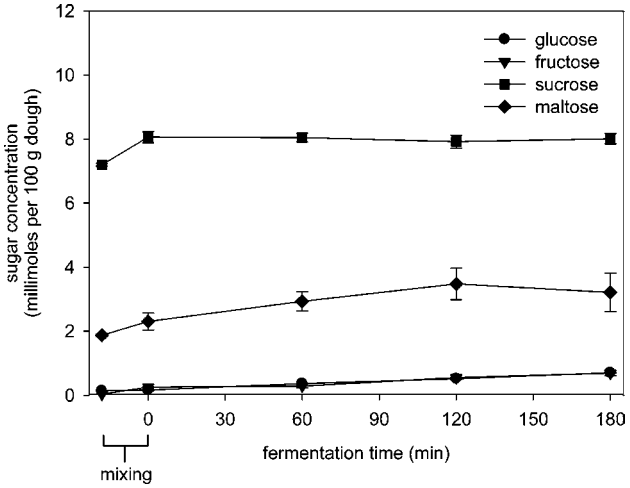

Figure 1. Sugars in unyeasted doughs made with 2% added sucrose held at 30 °C. Vertical bars are one standard error. Fermentation time is defined as the time elapsed after mixing is completed.

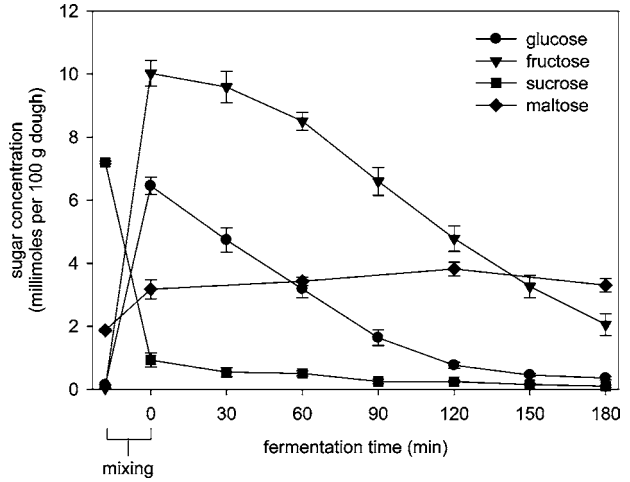

Figure 2. Sugars in yeasted doughs made with 2% sucrose fermenting at 30 °C. Vertical bars are one standard error. Fermentation time is defined as the time elapsed after mixing is completed.

The total moisture present in doughs, calculated from the moisture content of ingredients, was 41.55 g per 100 g dough. According to the literature, nonsolvent water (0.3 g per 100 g flour) was associated with flour solids, which represented 60% (wet weight) of the dough. The flour used contained 12.0% moisture. Thus, the nonsolvent water in the dough was calculated as $60 \times (1 - 0.12) \times 0.3 = 15.84$ g per 100 g dough. Therefore, the amount of solvent water in the dough was $41.55 - 14.04 = 25.71$ g per 100 g dough. Low molecular weight solutes dominate the osmotic properties of the dough aqueous phase. Yeast metabolism during fermentation dramatically alters the concentrations of glucose, fructose, and ethanol (**Table 1**), and osmotic properties change correspondingly. The initial concentration of added solutes (**Table 1**) was 56.22 mmol per 100 g dough. This equates to $56.22/25.71 = 2.19$ mol solute per kg water in the dough.

Dough fermented for 180 min contained 69.35 mmol solutes per 100 g dough (**Table 1**) or 2.70 mol kg^{-1} in the aqueous phase, an increase of 23% from unfermented dough. In dilute aqueous solutions, solutes depress initial freezing point by 1.86 °C mol^{-1} kg^{-1} (*30*). Using this principle, unfermented dough will freeze at −4 °C, and following 180 min of fermentation,

Table 1. Concentration of Low Molecular Weight Solutes in the Aqueous Phase of Dough

fermentation time at 30 °C[a]	concentration[b]	
solute	0 min	180 min
glucose	6.46	0.36
fructose	10.02	2.06
sucrose	0.93	0.10
maltose	3.18	3.30
ethanol	1.44	29.34
Na^+ and Cl^- ions[c]	34.19	34.19
total	56.22	69.35

[a] Time elapsed after the completion of mixing. [b] mmol (100 g dough)$^{-1}$. [c] From 1% salt in dough formulation, assumed to completely dissociate into Na^+ and Cl^- ions.

dough will freeze at −5 °C (**Table 1**). Accurate determination of the freezing point of dough required equipment to which the authors did not have access. However, these predictions were corroborated using similar doughs with differing osmolality measured in another laboratory (personal communication from D. Lonergan, The Pillsbury Corp., 2003).

Following fermentation, a greater proportion of water will remain unfrozen in the fermented dough. Reactions detrimental to shelf life are likely to proceed faster in the fermented dough because of increased molecular mobility (*31*). Baking properties would also be affected by the osmotic pressure change resulting from fermentation (*32*). The changes in osmotic properties of dough during fermentation affect water distribution between the aqueous phase, the solutes, and the macromolecules. Two-carbon ethanol molecules with one −OH group will replace six-carbon sugars with five −OH groups as the predominant low molecular weight solute. Surprisingly, osmotic changes during dough fermentation have received almost no attention in the literature.

Using the data generated in this paper, a mathematical model was devised to predict the concentration of glucose, fructose, and ethanol in the aqueous phase during fermentation. The consumption of glucose by yeast cultures is often well-fitted by a Michaelis−Menten type hyperbolic equation:

$$V_G = V_{maxG} X \frac{G}{G + K_G} \quad (1)$$

where V_G is the rate of glucose uptake (mmol L^{-1} h^{-1}), V_{maxG} is the maximum specific rate of glucose uptake (mmol g biomass^{-1} h^{-1}), X is the yeast biomass concentration (g biomass L^{-1}), G is the concentration of glucose (mmol L^{-1}), and K_G is the affinity constant (mmol L^{-1}).

This type of equation is mechanistic in nature and derives from consideration of sugar uptake as a series of equilibrium reactions involving sugar molecules and sugar carriers traversing the cell membrane. Detailed derivations can be found in enzyme kinetic textbooks, for example, ref *33*.

S. cerevisiae cells consume glucose in preference to fructose when both are available (*4*, *17*, *29*). In broth cultures fed with a mixture of glucose and fructose, the influence of glucose on fructose uptake is well-fitted by eq 2 (*13*), which is derived from mechanistic competitive enzyme inhibition equations (*33*).

$$V_F = V_{maxF} X \frac{F}{F + K_F\left(1 + \frac{G}{K_{FG}}\right)} \quad (2)$$

K_{FG} is a constant describing competitive inhibition of fructose uptake by glucose (units mmol L^{-1}), while F, V_F, V_{maxF}, and K_F are analogous to G, V_G, V_{maxG}, and K_G in eq 1. Initial values of G and F (designated G_i and F_i) were calculated from glucose and fructose concentrations immediately after mixing in doughs made with 2% added sucrose (**Table 2**).

Table 2. Summary of Mathematical Model Parameters

symbol	description	unit	value
G_i	initial glucose concentration	mol L^{-1}	0.250
F_i	initial fructose concentration	mol L^{-1}	0.389
X	biomass concentration	g L^{-1}	25.4
V_{maxG}	maximal glucose uptake rate	mol (g biomass)$^{-1}$ h^{-1}	0.00653
V_{maxF}	maximal fructose uptake rate	mol (g biomass)$^{-1}$ h^{-1}	0.00626
Y_{EG}	yield of ethanol from glucose		1.82
Y_{EF}	yield of ethanol from fructose		1.87

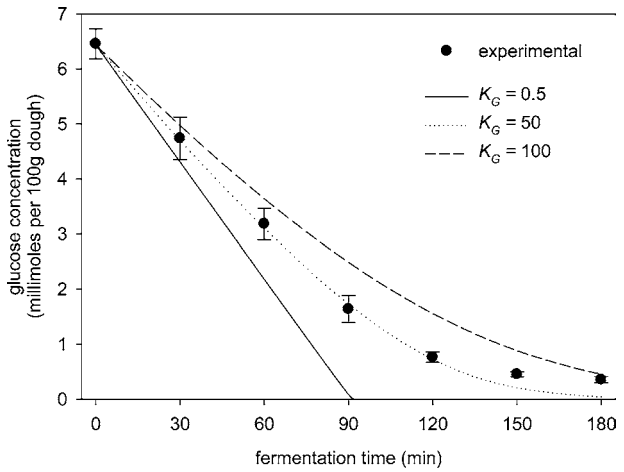

Figure 3. Glucose concentration in fermenting dough, measured or simulated with eq 1. Vertical bars are one standard error. Fermentation time is defined as the time elapsed after mixing is completed.

In yeasted doughs made with added glucose or fructose only, sugar was consumed at a constant rate and ethanol accumulated at a constant rate during fermentation at 30 °C. V_{maxG} and V_{maxF} were calculated from the rate of decline of each sugar during 90 min of fermentation at 30 °C. Yields of ethanol from glucose and fructose (Y_{EG} and Y_{EF}, respectively) were calculated from the ratio of ethanol accumulation rate to sugar consumption rate. Ethanol concentration (E, units mol L^{-1}) was modeled with eq 3.

$$E = Y_{EG}(G_i - G) + Y_{EF}(F_i - F) \quad (3)$$

Yeast biomass, X, was calculated from the solids content of compressed yeast and the amount of solvent water present. Cell numbers were assumed to remain constant throughout fermentation, which is in agreement with the low biomass yield from anaerobic fermentation (*34*). Experimental parameters are summarized in **Table 2**. K_G, K_F, and K_{FG} were initially set at the values reported by Barford et al. (*7*) and then modified to improve the fit to experimental results.

Glucose uptake was described extremely well by eq 1 (**Figure 3**). The best fit was achieved with K_G = 50 mmol L^{-1}, which is two orders of magnitude higher than the value used by Barford et al. (*7*) but within the range reported by others (*35*). The magnitude of K_G is consistent with high-affinity uptake, which occurs in broth culture at sugar concentrations >10−20 mmol L^{-1} (*35*−*37*). Dough contained 1−10 mmol 100 g^{-1} glucose during fermentation or 39−390 mmol L^{-1} in the aqueous phase. The observation of high-affinity kinetics is confirmation that the concentration of sugar immediately adjacent to yeast cells

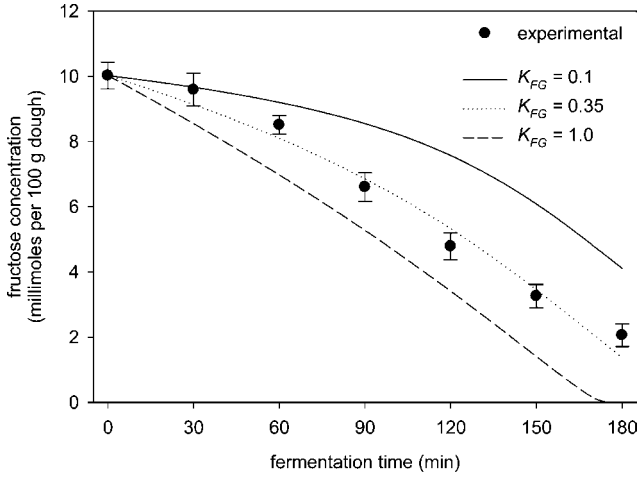

Figure 4. Fructose concentration in fermenting dough, measured or simulated with eq 2 with $K_F = 1$ mmol L^{-1}. Vertical bars are one standard error. Fermentation time is defined as the time elapsed after mixing is completed.

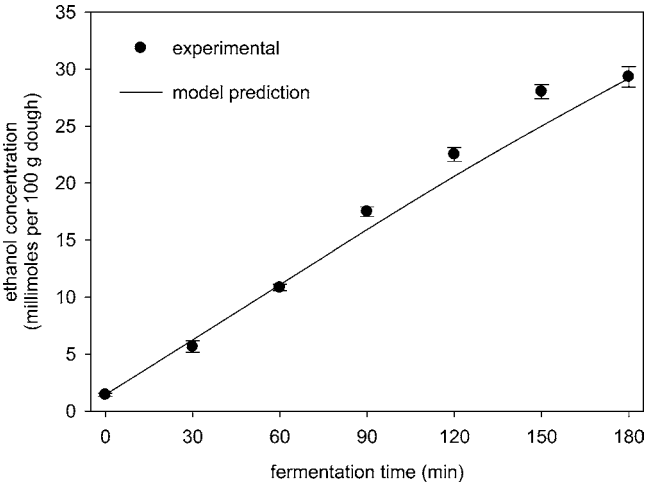

Figure 5. Ethanol concentration in fermenting dough, measured or simulated with eq 3. Vertical bars are one standard error. Fermentation time is defined as the time elapsed after mixing is completed.

is of similar magnitude to the assumed bulk aqueous phase concentration.

Equation 2 described fructose concentration well with $K_F = 1$ mmol 100 g^{-1}, as reported by Barford et al., and $K_{FG} = 0.35$ mmol 100 g^{-1} (**Figure 4**). K_{FG} is smaller than the value used by Barford et al., indicating that glucose has a stronger influence on fructose uptake in dough than in liquid broth.

Ethanol accumulation was described well by eq 3 during the early and late stages of fermentation (**Figure 5**). At 90−150 min, ethanol was slightly underpredicted due to discrepancies between predicted and experimental results in the sugar models.

To illustrate the utility of the model, a simulation was run with the parameters determined above and levels of yeast ranging from 1 to 3% of dough (**Figure 6**). The 1 and 3% results were not experimentally verified, but they suggest that in dough containing 3% yeast, sugar would be nearly exhausted after 2 h of fermentation. Gas production is likely to dip as yeast cells adapt to metabolizing maltose (*16*, *18*). In the food industry, such information saves time and money during formulation and process development.

This work has shown that mathematical models derived in liquid fermentations can be successfully applied to a semisolid system, provided suitable consideration is given to the phase

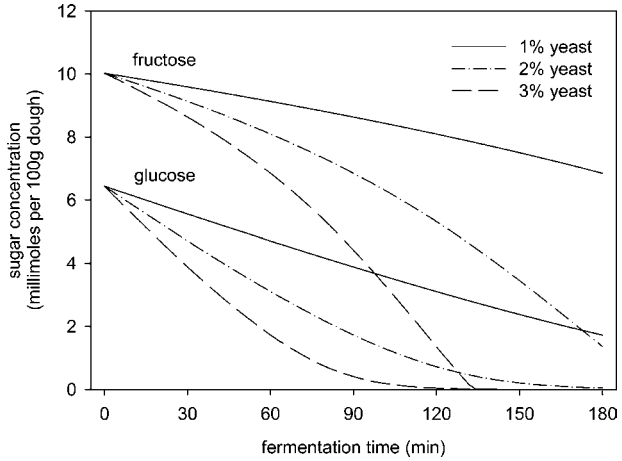

Figure 6. Model predictions for the consumption of glucose and fructose in doughs containing 2% added sucrose and from 1 to 3% yeast (percentages are on a dough basis).

distribution of water in the system. It has shown that *S. cerevisiae* has a stronger preference for glucose over fructose in dough than in liquid fermentation medium.

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