MODELING YEAST SPREAD IN BREAD DOUGH

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ABSTRACT. Yeast undergoes complex interactions with the other ingredients in bread dough. We sought to determine if we could use an understanding of the chemical reactions yeast undergoes to build accurate models of sugar consumption, yeast growth, and byproduct production. Similarly, we examined the results of each model to see how well they qualitatively fit our expectations. In this paper we build four models that estimate the lifecycle of yeast in bread. We compare the results to data from other papers and observe that our models performed surprisingly well.

1. BACKGROUND/MOTIVATION

The primary question this paper seeks to answer is determining the sorts of models that accurately match the chemical reactions that yeast undergo within bread. Yeast interacts in complicated ways with the other ingredients in bread, and even with its own byproducts. We also want to verify if existing SIR and other pandemic models can accurately mimic the spread of yeast, and if not, what factors make these models no longer accurate. Determining the optimal initial conditions (quantities of yeast, water, etc.) and how these affect the growth is a secondary focus of this paper.

Every breadmaker has noticed that small changes in initial dough conditions can lead to wide variations in the quality of the baked bread. By having a good model for how yeast interacts with the other ingredients in bread, we will be able to better understand the breadmaking process and how to optimize initial conditions.

The Chemistry of Bread.

There are four primary ingredients in bread dough: flour, water, salt, and yeast. Flour provides not only the gluten that gives bread its structure, but also contains sugars that the yeast consumes. Salt strengthens the bread dough, making it more elastic.

Once water is mixed with flour, enzymes from the flour activate, including alpha-amylase and beta-amylase. These enzymes break up the long starch chains in the flour, quickly converting these into glucose and maltose. These sugars, unlike starch itself, are edible by yeast. [Bru]

Yeast is a type of single-celled fungus that produces the CO_2 that forms bubbles in bread. This process is called fermentation, and yeast undergoes

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two primary phases within bread. The first is aerobic respiration, where yeast consumes oxygen and sugar and produces carbon dioxide and ATP, which is a molecule that stores energy for cells.

$$6\,O_2 + C_6H_{12}O_6 \rightarrow 6\,CO_2 + 6\,H_2O + ATP.$$
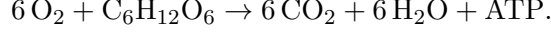
In the second phase, called anaerobic respiration, occurs once the oxygen in the bread is exhausted. Yeast consumes glucose and begins producing ethanol instead of water as a biproduct. The amount of ethanol produces is very minimal compared to alcohol fermentation, and evaporates during the baking process. The yeast still produces CO_2 as a byproduct, but it produces it at a slower rate.

$$C_6H_{12}O_6 \rightarrow 2\,CO_2 + 2\,C_2H_5OH + ATP.[Sci]$$
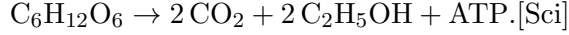
[Sci]

Some of the more advanced models in this paper sought to incorporate this two-phase structure.

We reviewed some existing models for modeling yeast fermentation in the literature. The KM mechastic model was one model created to describe the dynamics of alcoholic fermentation of yeast. It is given by

$$\dot{x} = \frac{\rho_1 xy}{\rho_2 + y} - \rho_3 xz - \rho_4 x$$
$$\dot{y} = -\rho_5 xy - \rho_6 yz - \rho_7 y$$
$$\dot{z} = \rho_8 xz + \rho_9 yz - \rho_{10} z,$$

where $x(t)$, $y(t)$, and $z(t)$ describe yeast biomass concentration, glucose consumption, and ethanol production respectively. [ea] Each rho_k value depicts a specific constant related to a specific part of the fermentation process. The plotted solution for this model is given in 2

2. Modeling

In this section we go over the four models we built in detail.

Simple Compartmental Model. This was the simplest of the models we implement. The goal was to get a baseline for future models and to see if we can fit real-world data with a simple compartmental model. If this did not fit data well, we at least hoped that the model would be qualitatively accurate, in that the amount of yeast and byproducts increase over time while the amount of sugar decreases. We used sugar, yeast, and byproducts as our three compartments. The model's differential equation is given by

$$\dot{S} = -\alpha SY$$
$$\dot{Y} = \beta SY - \gamma Y$$
$$\dot{B} = \delta SY,$$

where α, β, γ and δ are constants. In particular, α controls the quantity of sugar eaten by yeast in each interaction, β controls the reproduction rate of

yeast as it consumes sugar, γ controls the death rate of yeast, and δ controls the rate at which byproducts are produced as yeast consumes sugar.

Compartmental Model with Monod Equation. We now seek to incorporate the Monod equation into a compartmental model. The Monod equation models the growth of a microorganism based on the concentration of a limiting substance. [Mon49] The standard form of the Monod equation is given by

$$\mu = \mu_{\max}\frac{S}{K_s + S},$$

where μ is the growth rate of a microorganism, $\mu_{\max}$ is the maximum growth rate of the microorganism, S is the concentration of the limiting substance for growth, and K_s is the "half-velocity" constant (the value of S when $\mu/\mu_{\max} = 0.5$). [oESM]

Some modifications to a traditional SIR model were required in order to fit the Monod equation into a compartmental model. SIR models typically assume a closed population, but for modeling yeast fermentation, compartments don't simply flow into one another as some mass escapes the system. Similarly, the yeast growth and fermentation are based on growth rates and yield coefficients, not just population flow. Let Y depict the quantity of yeast, S denote the quantity of sugar, and P denote the byproducts produced (e.g. ethanol and CO_2). The monod categorical model is given by

$$\dot{Y} = \mu_{\max}\frac{S}{K_s + S}Y$$

$$\dot{S} = -\frac{1}{Y_{X/S}}\dot{Y}$$

$$\dot{P} = Y_{P/S}(-\dot{S}),$$

where $Y_{X/S}$ denotes the grams of biomass of yeast per gram of sugar, and $Y_{P/S}$ denotes the product yield of yeast per gram of sugar. Plotting for $t \in [0, 10]$, the plot of the solution is given by We use the initial conditions $(Y_0, S_0, P_0) = (0.1, 10, 0)$ (each with units g/L). We also suppose that $K_s = 0.6$, $Y_{X/S} = 0.1$, and $Y_{P/S} = 1$.

KM Mechanistic. We plot the solution for the KM Mechanistic model ([ea]) for $t \in [0, 5]$. Values of ρ_k as given in the paper and we use initial conditions $(x_0, y_0, z_0) = (5, 200, 0.5)$ (measured in g/L).

MacArthur Consumer-Resource. The previous models make the following simplifying assumptions: 1) That all sugar is initially available to be consumed by yeast and only decreases over time, 2) that the rate and efficacy of yeast's consumption of sugar depends only on the respective amounts of yeast and sugar, and 3) that oxygen is not a resource on which yeast feeds.

In this section, we attempt to incorporate more realistic assumptions into our model and better approximate the real dynamics of a rising loaf of dough. A more appropriate family of models to use would be Consumer-Resource
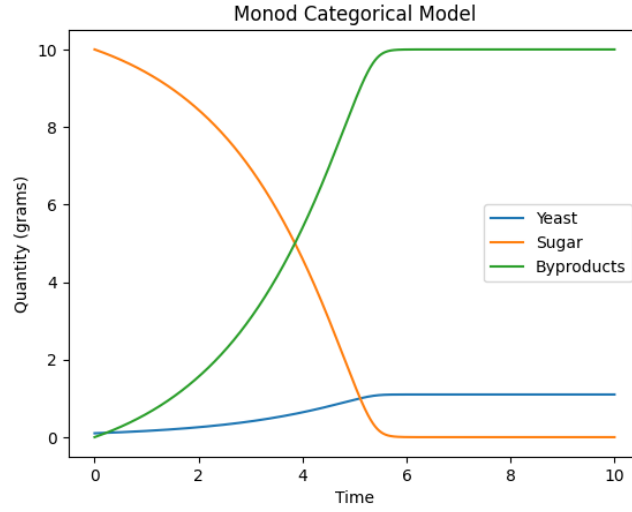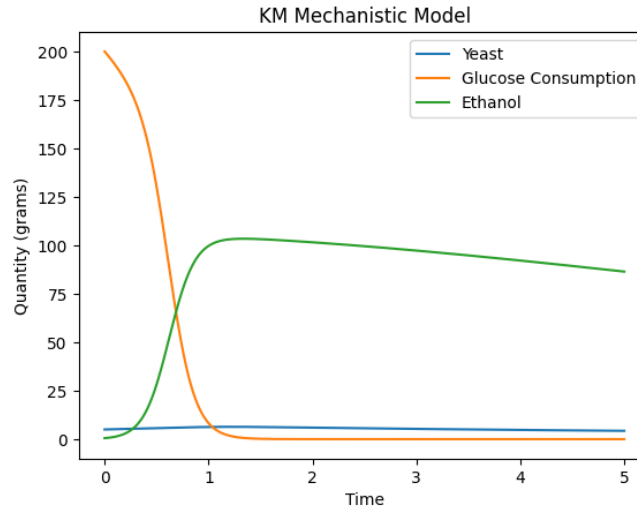
FIGURE 1. The monod categorical model.

FIGURE 2. A KM mechanistic model plot.

models, which are designed to factor in multiple consumers and multiple replenishing resources. This family of models considers the replenishment of resources, predators' affinity for different resources (called uptake in this paper), and the yield in biomass for the consumer per unit of resource consumed. In the case considered by this paper, there is a single consumer (yeast), and two resources (sugar and oxygen). Additionally, both the uptake and yield of sugar vary with the amount of oxygen, as we will discuss.

The general form of the MacArthur consumer-resource model for S species of consumers with concentrations N_i for $i \in 1, 2, ..., S$, and M resources with concentrations R_α for $\alpha \in 1, 2, ..., M$ is

$$\text{(1)} \qquad \frac{dN_i}{dt} = N_i \sum_\alpha (u_{i\alpha}(R_\alpha)w_{i\alpha}) - m_i$$

$$\text{(2)} \qquad \frac{dR_\alpha}{dt} = F_\alpha(R_\alpha) - \sum_i (N_i u_{i\alpha}(R_\alpha))$$

$u_{i\alpha}$ controls the uptake of the resource by the consumer, or how quickly consumer i consumes resource α per unit biomass. This can vary with the concentration of the resource, as it can saturate [PMGSM20]. $w_{i\alpha}$ is the biomass *yield* that resource α provides consumer i, and controls the proportion between resource α consumed and biomass added to consumer i. m_i is the natural mortality rate of consumer i. F_α is the function that controls the replenishment of resource α in the absence of consumers.

The zoo of parameters and associated dimensions can be disorienting. We will provide a sort of index here of the parameters we will use in our model, and then we will detail the way each fits into our model.

Parameter	Units	Notes
Y	g_Y/L	Dry Yeast concentration
O	$mmol/L$	O_2 concentration
S	GGE/L	Sugar concentration
C	mol/L	Count of CO_2 per liter of dough
K_O	$mmol/L$	Half saturation for Oxygen
K_S	GGE/L	Half saturation for Sugar
P_S	g_S/L	Carrying capacity for sugar
r_S	$1/h$	Sugar logistic growth rate
$f(O)$	$dimensionless$	Oxygen availibility switch
w_S^{aer}	g_Y/g_S	aerobic ATP yield, very efficient
w_S^{ana}	g_Y/g_S	anaerobic ATP yield, inefficient
w_O	$g_Y/mmol$	Oxygen yield
c_S	$L/g_Y h$	Maximum Sugar uptake
u_S	$dimensionless$	Instantaneous uptake of sugar
c_O	$L/g_Y h$	Oxygen uptake

TABLE 1. Parameter Index

Uptake. Uptake describes the rate at which the consumer metabolizes each resource, and is a function of the available amount of the resource. It is often modeled with a Monod equation, as previously discussed. We modeled the sugar uptake as a function of S using the Monod equation.

$$u_S(S) = c_S \frac{S}{K_S \cdot S}$$

See Table 1 for an explanation of each term. Thus the sugar uptake climbs quickly when below half saturation, and then grows more slowly past that point.

Because the amount of Oxygen starts low and thus its uptake varies little, we chose to control it with just a constant.

$$u_O(O) = c_O O$$

Decrease and Replenishment of Resources. As no sugar is ordinarily added to the loaf, the sugar present is tied up in the flour. As discussed in a previous section, the sugar becomes available as more complex molecules are broken down–it replenishes logistically. Therefore the change in sugar equation becomes

$$\frac{dS}{dt} = r_S S(1 - \frac{S}{P_S}) - c_S Y S$$

See Table 1 for an explanation of each term.

Since oxygen is not replenished, its change equation has only a consumption term.

$$\frac{dO}{dt} = -c_O O Y$$

Yield. Additionally, the biomass yield sugar provides yeast varies with the amount of oxygen available. Our model should reflect both aerobic and anaerobic metabolism of sugar. We want to model a smooth switch between aerobic and anaerobic metabolism. We accomplish this via a switching function, which we name f in our model.

$$f(O) = \frac{O}{K_O + O}$$

See Table 1 for details about the terms. The full effective yield term, which controls the yield that sugar provides the yeast for a given amount of oxygen, is the following.

$$w_S^{eff} = [w_S^{ana} + (w_S^{aer} - w_S^{ana})f(O)]$$

Thus, when $O \gg K_O$, $f(O) \approx 1$, and $w_S^{eff} \approx w_S^{aer}$ indicating fully aerobic yield. Likewise, when $O \ll K_O$, $f(O) \approx 0$, and $w_S^{eff} \approx w_S^a na$, indicating fully anaerobic yield.

Byproduct. The CO_2 created during this process exists outside the consumer resource relationship, and is simply stoichiometrically related to the rate of anaerobic sugar consumption. By straightforward rearrangement of the $f(O)$ equation given above, and since in the anaerobic reaction one gram of sugar becomes 0.0111 mols of CO_2, the instantaneous rate of production of CO_2 in mols per liter is given by

$$(1 - f(O))u_S(S)Y \cdot 0.0111$$

Final Form. By assembling these pieces into the general MacArthur consumer resource model found above, we have the following ODE.

$$\frac{dY}{dt} = Y\left[w_O c_O O + [w_S^{ana} + (w_S^{aer} - w_S^{ana})f(O)]u_S(S) - m\right]$$

$$\frac{dO}{dt} = -c_O OY$$

$$\frac{dS}{dt} = r_S S(1 - \frac{S}{P_S}) - c_S YS$$

$$\frac{dC}{dt} = (1 - f(O))u_S(S)Y \cdot 0.0111$$
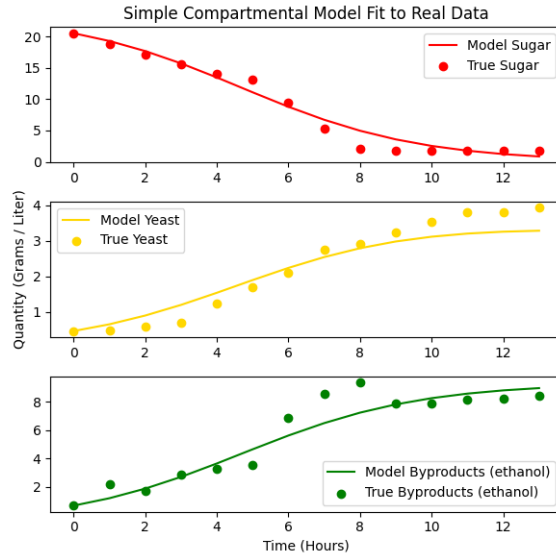
3. Results

FIGURE 3. This figure shows the results of the categorical model after having the constants trained on real data. The three graphs show the three categories in the model; sugar, yeast, and byproducts - in this case, just ethanol is tracked. [ea]

Simple Compartmental Model. The simple model fit the real-world data [ea] surprisingly well. 3

This model, which was by far the simplest of the models we implemented, performed surprisingly well quantitatively. It sadly does not incorporate the two-phase structure that some of the other models do, but each category's graph looks similar to the data it trained on.

The constants of this model, which were computed using SciPy, were estimated to equal

$$\alpha = 0.1128, \beta = 0.0178, \gamma = 0.010, \delta = 0.0475.$$

The constant γ controls the death rate of yeasts, and is therefore not possible to estimate with stoichiometry. Similarly, the rate at which sugar is eaten is hard to estimate. However, the ratio of sugar eating to byproducts (namely, ethanol) produced is something we can estimate. We know that yeast consumes 1 molecule of glucose to produce 2 molecules of ethanol during its anaerobic phase. Since glucose weighs 180.156 grams / mol, and ethanol weighs 46.069, [Pro] we see that the ratio $\frac{\alpha}{\delta}$, which represents sugar consumption by yeast divided by ethanol production, should roughly equal $\frac{180.156}{2 \cdot 46.069}$. We see that we have:

$$\frac{\alpha}{\delta} = 2.375, \quad \frac{180.156}{2 \cdot 46.069} = 1.955,$$

yielding a 21% error compared to the true value. For being such a simple model, getting a result that is this near to matching the underlying chemistry is incredible.

Compartmental Model with Monod Equation.

KM Mechanistic Model.

MacArthur Consumer-Resource. Unfortunately we were unable to find real-world data which we could use to evaluate this model quantitatively. Instead we will pick reasonable parameter values and evaluate the results qualitatively. Using parameters in the ranges in Table 2, we obtain Figure 4.

Parameter	Value	units	Sources
Y_0	5.3	g_L/L	calculated
O_0	0.25	$mmol/L$	[DJDV$^+$16]
S_0	3-5	GGE/L	[BAK]
C_0	0	mol/L	
K_O	0.01 - 0.03	$mmol/L$	[VdCBRG18] [VdCBRG19]
K_S	0.1 - 0.5	GGE/L	[PSvD89]
P_S	10 - 20	g_S/L	[CMVM13]
r_S	0.4	h^{-1}	[SVC16] [SVC15]
w_S^{aer}	0.45 - 0.55	g_Y/g_S	[Els25] [VSSvD91]
w_S^{ana}	0.1	g_Y/g_S	[Ltd25] [WASvD93]
w_O	0.016	$g_Y/mmol$	[WVLM$^+$24]
c_S	0.15	$L/(g_Y h)$	[PSvD89]
c_O	0.1	$L/g_Y h$	[AOT$^+$12]

TABLE 2. Reasonable Parameter Values

Using these parameter values and these initial values, we can visually inspect the resulting prediction made by this model. There is a clear aerobic
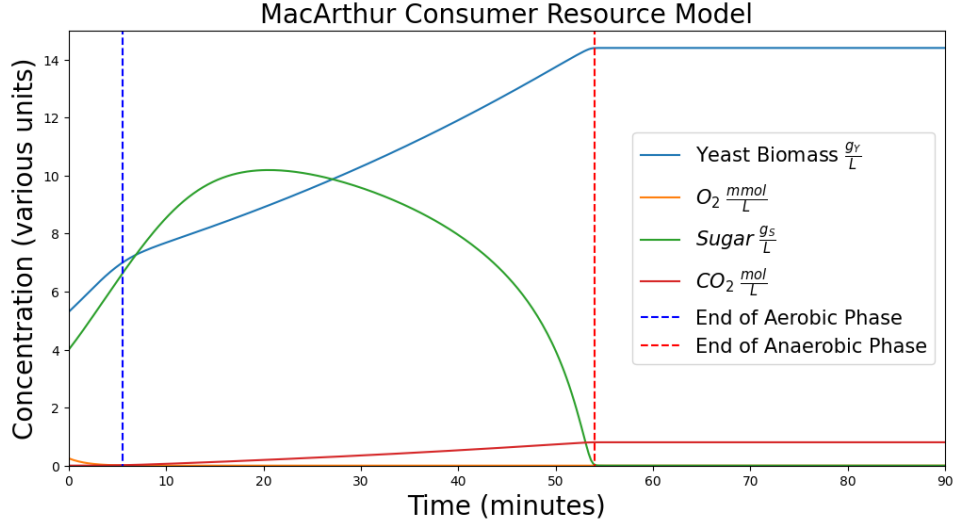
FIGURE 4. MacArthur Consumer-Resource Model Results

phase where yeast concentration encreases very quickly, before switching to anaerobic when oxygen is depleted. CO_2 concentration also rises until sugar is depleted and the anaerobic phase finishes. However, the model reaches equilibrium in about 55 minutes, while in reality yeast continues to grow for much longer.

4. Analysis/Conclusions

We attempted to model the dynamics present in a rising loaf of bread dough using four models: A simple compartmental model, a compartmental model with a Monod Equation, a KM Mechanistic Model, and a MacArthur Consumer-Resource model, ordered in terms of complexity.

Appropriateness of models. The two compartmental models captured the changing concentrations of their assumed dynamics with surprising accuracy, considering their simplicity. The fitted simple compartmental model yielded a mere 21% error for the glucose consumed to ethanol produced ratio. However, the assumed dynamics are quite a far cry from the dynamics of a rising loaf of bread dough. The most egregious simplifiying assumption was that all sugar is initially available and does not replenish. Fortunately experimental data that matched the assumptions validated these models nicely.

The most complex model we attempted to use, the MacArthur Consumer-Resource model, corrected the previous simplifications by including terms to describe 1) a replenishing supply of available sugar, 2) a variable rate of sugar consumption and yield depending on the oxygen supply, and 3) metabolism of oxygen when available. Although we were unable to find or

produce experimental data to validate this model, we found it satisfactory qualitatively. The phases of aerobic metabolism, anaerobic metabolism, and equilibrium are each amenable to visual inspections of the figures the model produces.

4.1. **Potential improvements.** Our model which most closely approximates the dynamics of fermentation in a loaf of bread dough, the MacArthur Consumer-Resource model, has several shortcomings. The most glaring is that it is not fit to experimental data, and its parameters' true values are not verified to the desired degree of accuracy. Furthermore, the model does not capture enviornmental factors such as temperature, humidity, or pressure, which are known to affect the rate of fermentation. Parameters and functions that describe uptake, yield, resource replenishment, and maintenance each in reality depend on such enviornmental factors as these. Similarly, we do not consider the effects of key added ingredients such as salt (which is known to inhibit yeast growth), or of elective added ingredients such as jalapeño and cheddar.

Another shortcoming is the limitation of bread making practices represented in even our broadest assumptions. We do not consider a double-rising period or the effect of several intermediate "stretch and folds". Bread makers report that small changes in the mixing, kneading, and intermediate checkpoints lead to large changes in the results of the loaf. Nonetheless, these effects are not captured in our model.

What we learned. Our main takeaway was the effectiveness of relatively simple models to decently approximate complicated dynamics. We also enjoyed reasoning mathematically with chemistry, basic stoichimetry, and reasoning through relationships between compartments/consumers and resources.

Impact. The impact of an accurate bread-rising model would be profound and far-reaching. Bread is a worldwide staple, and is much beloved by nearly all cultures. An accurate model would create tremendous accessibility consistently higher quality bread, exactly as desired by its bakers, despite the complexity.

Such a day is yet beyond us. Using the models we produced, by fiddling with initial values, a user can easily see the effects of changing the initial concentrations of yeast, sugar, and oxygen, and use these initial concentrations to create the desired effect while baking bread.

Much work remains to be done.

REFERENCES

[AOT⁺12] Felipe F. Aceituno, Marcelo Orellana, Jorge Torres, Sebastián Mendoza, Alex W. Slater, Francisco Melo, and Eduardo Agosin. Oxygen response of the wine yeast *saccharomyces cerevisiae* ec1118 grown under carbon-sufficient, nitrogen-limited enological conditions. *Applied and Environmental Microbiology*, 78(23):8344, 2012.

[BAK] BAKERpedia. Yeast nutrients. `https://www.bakerpedia.com/processes/yeast-nutrients/`. Accessed on 2025-12-02.

[Bru] Andy Brunning. Baking bread: The chemistry of bread-making. https://www.compoundchem.com/2016/01/13/bread/.

[CMVM13] Georgiana Gabriela Codină, Silvia Mironeasa, Daniela V. Voica, and Costel Mironeasa. Multivariate analysis of wheat flour dough sugars, gas production, and dough development at different fermentation times. *Czech Journal of Food Sciences*, 31(3):222–229, 2013.

[DJDV⁺16] Karolien Decamps, Iris J. Joye, Dirk E. De Vos, Christophe M. Courtin, and Jan A. Delcour. Molecular oxygen and reactive oxygen species in bread-making processes: Scarce, but nevertheless important. *Critical Reviews in Food Science and Nutrition*, 56(5):722–736, 2016.

[ea] Salazar et al. `https://www.mdpi.com/1099-4300/25/3/497`.

[Els25] Elsevier. Biomass yield, 2025. Accessed: 2025-11-15.

[Ltd25] Triyambak Life Sciences Pvt. Ltd. Practice questions & video solutions for gate biotechnology, 2025. Accessed: 2025-11-15.

[Mon49] Jacques Monod. The growth of bacterial cultures. *Annual Review of Microbiology*, 3:371–394, 1949.

[oESM] UCSB Bren School of Environmental Science and Management. `https://web.archive.org/web/20091229043435/http://www.bren.ucsb.edu/academics/courses/219/Lectures/Lecture_4_ESM219_06.ppt.pdf`.

[PMGSM20] Leonardo Pacciani-Mori, Andrea Giometto, Samir Suweis, and Amos Maritan. Adaptive metabolic strategies in consumer-resource models. *PLOS Computational Biology*, 16(6):e1007896, 2020. Originally published as bioRxiv preprint 385724, doi:10.1101/385724.

[Pro] Powder Process. `https://powderprocess.net/Tools_html/Data_Diagrams/Chemical_Compound_Molecular_Weight.html`.

[PSvD89] E Postma, W.A. Scheffers, and J.P. van Dijken. Kinetics of growth and glucose transport in glucose-limited chemostat cultures of *saccharomyces cerevisiae* cbs 8066. *Applied and Environmental Microbiology*, 55(12):3214–3220, 1989.

[Sci] UCSB Scienceline. http://scienceline.ucsb.edu/getkey.php?key=692.

[SVC15] Nore Struyf, Joran Verspreet, and Christophe M. Courtin. The effect of amylolytic activity and substrate availability on sugar release in non-yeasted dough (preprint / conference or repository version). KU Leuven repository / J-GLOBAL entry, 2015. Preprint of the 2016 Journal of Cereal Science article.

[SVC16] Nore Struyf, Joran Verspreet, and Christophe M. Courtin. The effect of amylolytic activity and substrate availability on sugar release in non-yeasted dough. *Journal of Cereal Science*, 69:111–118, 2016.

[VdCBRG18] Bruno Labate Vale da Costa, Thiago Olitta Basso, Vijayendran Raghavendran, and Andreas Karoly Gombert. Anaerobiosis revisited: growth of *saccharomyces cerevisiae* under extremely low oxygen availability. *Applied Microbiology and Biotechnology*, 102(5):2101–2116, 2018.

[VdCBRG19] Bruno Labate Vale da Costa, Thiago Olitta Basso, Vijayendran Raghavendran, and Andreas Karoly Gombert. Forever panting and forever growing:

physiology of *saccharomyces cerevisiae* at extremely low oxygen availability in the absence of ergosterol and unsaturated fatty acids. *FEMS Yeast Research*, 19(6):foz054, 2019.

[VSSvD91] Cornelis Verduyn, Adriaan H. Stouthamer, W. Alexander Scheffers, and Johannes P. van Dijken. A theoretical evaluation of growth yields of yeasts. *Antonie van Leeuwenhoek*, 59(1):53, 1991.

[WASvD93] Ruud A. Weusthuis, Hendrik Adams, W. Alexander Scheffers, and Johannes P. van Dijken. Energetics and kinetics of maltose transport in Saccharomyces cerevisiae: a continuous culture study. *Applied and Environmental Microbiology*, 59(9):3104, 1993. Accessed: 2025-11-15.

[WVLM+24] Marieke Warmerdam, Marcel A. Vieira-Lara, Robert Mans, Jean Marc Daran, and Jack T. Pronk. Specific growth rates and growth stoichiometries of saccharomycotina yeasts on ethanol as sole carbon and energy substrate. *FEMS Yeast Research*, 24, 2024.