Math 337 - Elementary Differential Equations

Lecture Notes – Systems of Two First Order Equations: Applications

Joseph M. Mahaffy,
⟨jmahaffy@sdsu.edu⟩

Department of Mathematics and Statistics
Dynamical Systems Group
Computational Sciences Research Center
San Diego State University
San Diego, CA 92182-7720

http://jmahaffy.sdsu.edu

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Outline

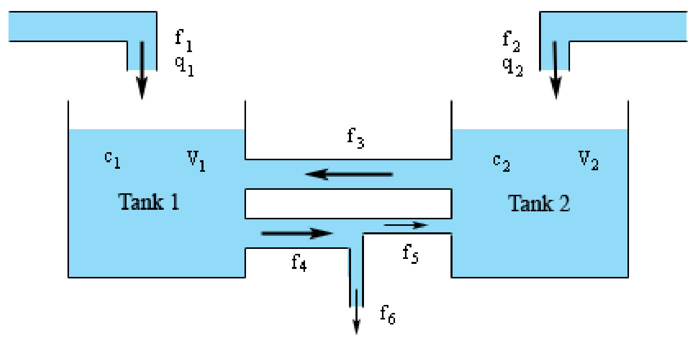
Introduction

Introduction

- Applications of **Systems of Two 1^{st} Order Differential Equations**
  - Basic Mixing Problem - Water and Inert Salts
  - Pharmokinetic Problem
- Extensions of techniques to **Nonlinear Systems in Two Dimensions**
  - Glucose and Insulin Dynamics
  - Competition of Species

Basic Mixing Problem 1

Basic Mixing Problem



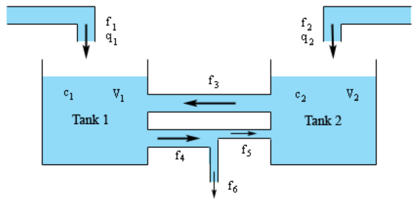
This problem examines the mixing of an **inert salt** in **two tanks**

The flows are balanced to constant volume in each tank, and **linear differential equations** are developed to analyze this system

The DEs describe concentrations of the state variables $c_1(t)$ and $c_2(t)$

Basic Mixing Problem

Conditions of the Model



Assume **constant volumes**, V_1 and V_2, so the following conditions hold:

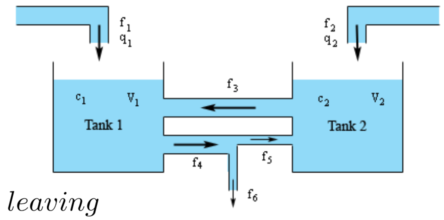
$$f_1 + f_2 = f_6 \qquad f_1 + f_3 = f_4$$
$$f_2 + f_5 = f_3 \qquad f_5 + f_6 = f_4$$

Assume inflowing concentrations of **inert salt**, q_1 and q_2, into **Tank 1** and **Tank 2**

Assume **initial concentrations**, $c_1(0) = c_{10}$ and $c_2(0) = c_{20}$

Basic Mixing Problem

Conservation of Amounts



Assume **amounts**, $A_1(t)$ and $A_2(t)$, then conservation demands:

$$\frac{dA_i}{dt} = amount\ entering - amount\ leaving$$

This results in the DEs describing the **amounts**

$$\begin{aligned}\frac{dA_1}{dt} &= f_1q_1 + f_3c_2 - f_4c_1 \\ \frac{dA_2}{dt} &= f_2q_2 + f_5c_1 - f_3c_2\end{aligned}$$

These are transformed into concentration equations by dividing by V_1 and V_2

Basic Mixing Problem

Concentration Equations

$$\begin{aligned}\frac{dc_1}{dt} &= \frac{f_1q_1 + f_3c_2}{V_1} - \frac{f_4}{V_1}c_1 \\ \frac{dc_2}{dt} &= \frac{f_2q_2 + f_5c_1}{V_2} - \frac{f_3}{V_2}c_2\end{aligned}$$

This can be written as a **system of 1^{st} order linear DEs**

$$\begin{pmatrix} \dot{c}_1 \\ \dot{c}_2 \end{pmatrix} = \begin{pmatrix} -\frac{f_4}{V_1} & \frac{f_3}{V_1} \\ \frac{f_5}{V_2} & -\frac{f_3}{V_2} \end{pmatrix} \begin{pmatrix} c_1 \\ c_2 \end{pmatrix} + \begin{pmatrix} \frac{f_1q_1}{V_1} \\ \frac{f_2q_2}{V_2} \end{pmatrix}$$

with $c_1(0) = c_{10}$ and $c_2(0) = c_{20}$, which in shorthand is

$$\dot{\mathbf{c}} = \mathbf{A}\mathbf{c} + \mathbf{Q}$$

Basic Mixing Problem

Equilibrium: We find the equilibrium by solving

$$\mathbf{A}\mathbf{c}_e = -\mathbf{Q}$$

or

$$\begin{pmatrix} -\frac{f_4}{V_1} & \frac{f_3}{V_1} \\ \frac{f_5}{V_2} & -\frac{f_3}{V_2} \end{pmatrix} \begin{pmatrix} c_{1e} \\ c_{2e} \end{pmatrix} = \begin{pmatrix} -\frac{f_1q_1}{V_1} \\ -\frac{f_2q_2}{V_2} \end{pmatrix}$$

This has the general solution

$$\begin{pmatrix} c_{1e} \\ c_{2e} \end{pmatrix} = \begin{pmatrix} \frac{f_1q_1+f_2q_2}{f_4-f_5} \\ \frac{f_1f_5q_1+f_2f_4q_2}{f_3(f_4-f_5)} \end{pmatrix}$$

Basic Mixing Problem 5

Eigenvalues: We find the eigenvalues by solving

$$\det|\mathbf{A}-\lambda\mathbf{I}| = 0$$

or

$$\det\begin{vmatrix} -\frac{f_4}{V_1}-\lambda & \frac{f_3}{V_1} \\ \frac{f_5}{V_2} & -\frac{f_3}{V_2}-\lambda \end{vmatrix} = 0$$

This has the **characteristic equation**

$$\lambda^2 + \left(\frac{f_4}{V_1}+\frac{f_3}{V_2}\right)\lambda + \frac{f_3(f_4-f_5)}{V_1V_2} = 0$$

Since $\det|\mathbf{A}| > 0$, discriminant $D > 0$, and $tr(\mathbf{A}) < 0$, the **Stability Diagram** from before shows this system has a **Stable node** or **sink**, as we would expect

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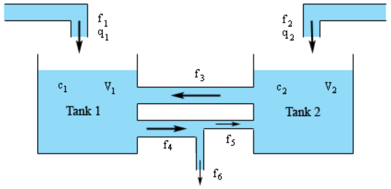
Mixing Problem Example 1

Mixing Problem Example

Assume the following parameters:



$V_1 = 100$ l,	$V_2 = 60$ l,
$q_1 = 7$ g/l,	$q_2 = 12$ g/l,
$f_1 = 0.2$ l/min,	$f_2 = 0.15$ l/min,
$f_3 = 0.25$ l/min,	$f_4 = 0.45$ l/min,
$f_5 = 0.1$ l/min,	$f_6 = 0.35$ l/min

This can be written as a **system of 1^{st} order linear DEs**

$$\begin{pmatrix} \dot{c}_1 \\ \dot{c}_2 \end{pmatrix} = \begin{pmatrix} -0.0045 & 0.0025 \\ 0.00167 & -0.004167 \end{pmatrix}\begin{pmatrix} c_1 \\ c_2 \end{pmatrix} + \begin{pmatrix} 0.014 \\ 0.03 \end{pmatrix}$$

with $c_1(0) = 2$ g/l and $c_2(0) = 1$ g/l

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Mixing Problem Example 2

Mixing Problem Example satisfies the model equation

$$\begin{pmatrix} \dot{c}_1 \\ \dot{c}_2 \end{pmatrix} = \begin{pmatrix} -0.0045 & 0.0025 \\ 0.00167 & -0.004167 \end{pmatrix}\begin{pmatrix} c_1 \\ c_2 \end{pmatrix} + \begin{pmatrix} 0.014 \\ 0.03 \end{pmatrix}$$

From our analysis of the general case, the **equilibrium** satisfies:

$$\begin{pmatrix} c_{1e} \\ c_{2e} \end{pmatrix} = \begin{pmatrix} 9.14286 \\ 10.85714 \end{pmatrix}$$

The eigenvalues satisfy $\lambda_1 = -0.006381$ and $\lambda_2 = -0.002285$ with corresponding eigenvectors

$$\xi_1 = \begin{pmatrix} 1 \\ -0.7525 \end{pmatrix} \quad \text{and} \quad \xi_2 = \begin{pmatrix} 1 \\ 0.8859 \end{pmatrix}$$

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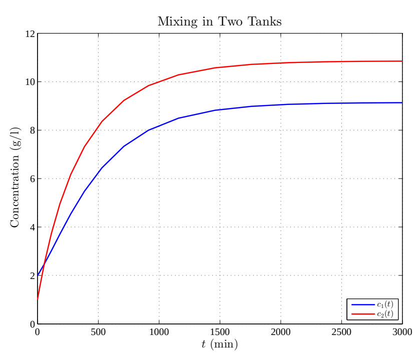
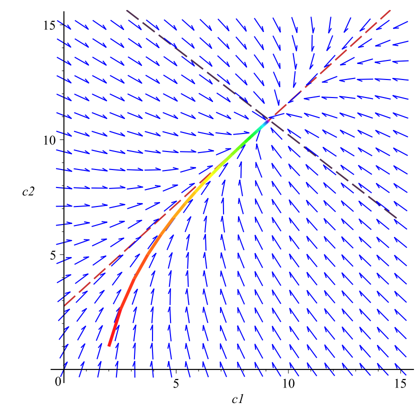
Mixing Problem Example 3

Mixing Problem Example: The system is solved with ODE23 in MatLab, and Maple is used to create a direction field with the solution trajectory and eigenvectors at equilibrium



Time series for c_1 and c_2



Phase Portrait

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Pharmokinetic Problem 1

Pharmokinetic Problem: Consider some drug (legal or illegal) acting on the brain

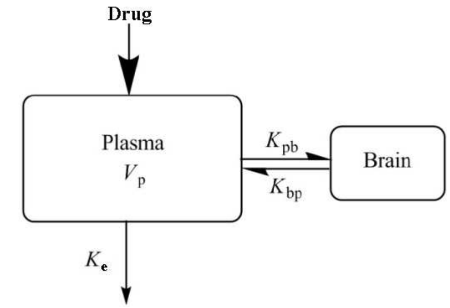
- This application examines a **drug** injected into the bloodstream
- The simplified model divides the body into a **Plasma compartment** and a **Brain compartment**
  - Track fraction of **drug** in each compartment, $d_1(t)$, in plasma and $d_2(t)$, in brain
  - Assume **linear transfer** between compartments
  - Common assumption if gradient transfer between compartments
  - Can assume preferential uptake by certain tissues
- Assume **drug** eliminated only from **Plasma compartment**
  - Elimination can be from **metabolism** or **kidney filtration**
  - Neglect uptake in other tissues

Pharmokinetic Problem 2

Pharmokinetic Problem: Diagram and Kinetic Equations

d_1 and d_2 are fractions of **drug** in Plasma and Brain compartments

Kinetic constants of transfer are K_{pb}, K_{bp}, and K_e



Pharmokinetic Model

$$\begin{pmatrix} \dot{d}_1 \\ \dot{d}_2 \end{pmatrix} = \begin{pmatrix} -(K_{pb}+K_e) & K_{bp} \\ K_{pb} & -K_{bp} \end{pmatrix} \begin{pmatrix} d_1 \\ d_2 \end{pmatrix}$$

Assume initial conditions $d_1(0) = 1$ and $d_2(0) = 0$

Pharmokinetic Problem 3

Pharmokinetic Model satisfies

$$\dot{\mathbf{d}} = \begin{pmatrix} \dot{d}_1 \\ \dot{d}_2 \end{pmatrix} = \begin{pmatrix} -(K_{pb}+K_e) & K_{bp} \\ K_{pb} & -K_{bp} \end{pmatrix} \begin{pmatrix} d_1 \\ d_2 \end{pmatrix} = \mathbf{Ad}$$

- Use $\mathbf{A}$ to compute elements of the **stability diagram**
  - The **trace** satisfies $tr(\mathbf{A}) = -(K_{pb}+K_{bp}+K_e) < 0$
  - The **determinant** is $\det|\mathbf{A}| = K_{bp}K_e > 0$
  - The **discriminant** is
  $$D = (K_{pb}+K_{bp}+K_e)^2 - 4K_{bp}K_e > 0$$
- These facts prove the **eigenvalues** are negative and real
- Since $\lambda_1 < \lambda_2 < 0$, this model has a **stable node** at the origin

Pharmokinetic Problem 4

Eigenvalues satisfy

$$\det\begin{vmatrix} -(K_{pb}+K_e)-\lambda & K_{bp} \\ K_{pb} & -K_{bp}-\lambda \end{vmatrix} = 0,$$

which gives the **characteristic equation**

$$\lambda^2 + (K_{pb}+K_{bp}+K_e)\lambda + K_{bp}K_e = 0$$

so

$$\lambda = 0.5\left(-(K_{pb}+K_{bp}+K_e) \pm \sqrt{(K_{pb}+K_{bp}+K_e)^2 - 4K_{bp}K_e}\right)$$

- This produces the negative, real **eigenvalues**
- This model has a **stable node** at the origin
- Want to find parameters to fit data
- Data often only from the **Plasma compartment**

LSD Example 1

LSD Example: In the early 1960's 5 healthy male subjects were given LSD (lysergic acid diethylamide) in an experiment to determine its effect on brain function [1]

Below is a table averaging the data over the 5 subjects

Time (hr)	0.0833	0.25	0.5	1	2	4	8
Plasma (ng/ml)	9.54	7.24	6.44	5.38	4.18	2.825	1
Score (%)	68.6	44.6	29	33.2	38.4	58.8	79.4

Want to fit our **Drug Model** to these data

Have information on **Plasma compartment**, but must infer levels in **Brain compartment**

Examine correlation between **LSD levels** and **Test performance**

[1] Aghajanian, G. K. and O. H. L. Bing. 1964. *Persistence of lysergic acid diethylamide in the plasma of human subjects.* Clinical Pharmacology and Therapeutics. **5**: 611-614.

LSD Example 2

LSD Model: From before we have the model

$$\begin{pmatrix} \dot{d}_1 \\ \dot{d}_2 \end{pmatrix} = \begin{pmatrix} -(K_{pb}+K_e) & K_{bp} \\ K_{pb} & -K_{bp} \end{pmatrix} \begin{pmatrix} d_1 \\ d_2 \end{pmatrix}$$

- Can only directly fit solution $d_1(t)$ to the **plasma data**
- Modify interpretation of model so d_1 and d_2 are masses in their respective compartments
- Perform a **nonlinear least squares fit** of $d_1(0)$ and the kinetic parameters, K_{pb}, K_e, and K_{bp} to the **LSD plasma data**
- Graph solution and compare to the data for the test scores

LSD Example 3

MatLab Code for finding best parameters

Though this linear model could be solved, we'll fit the numerical solution to the data

```
function Lp = LSD(t,L,Kpb,Kbp,Ke)
% Model for LSD - rhs of Linear Drug Model
 L1t = -(Kpb + Ke)*L(1) + Kbp*L(2);
 L2t = Kpb*L(1)-Kbp*L(2);
 Lp = [L1t;L2t];
end
```

Use a nonlinear least squares fit for finding best parameters

LSD Example 4

MatLab Code for finding best parameters (Nonlinear least squares)

```
function J = leastLSD(p,tdata,xdata)
% Create the least squares error function
  n1 = length(tdata);
  [t,L] = ...
      ode45(@LSD,tdata,[p(1),0],[],p(2),p(3),p(4));
  errL1 = L(:,1)-xdata(1:n1);
  J = errL1'*errL1;
end
```

Make an initial guess $p_0 = [12, 5, 4, 0.4]$, then use the MatLab command `[p,J,flag] = fminsearch(@leastLSD,p0,[],td,L1);` where *td* and *L1* are the data

This produces the best parameter values for our model

LSD Example 5

MatLab Code finds the best parameters with previous programs

Make an initial guess $p_0 = [12, 5, 4, 0.4]$, then use the MatLab command

```
[p,J,flag] = fminsearch(@leastLSD,p0,[],td,L1);
```

where td and $L1$ are the data

This produces the best initial condition and parameter values for our model

$$d_1(0) = 9.5330 \qquad K_{pb} = 2.0580 \qquad K_{bp} = 5.6030 \qquad K_e = 0.32904$$

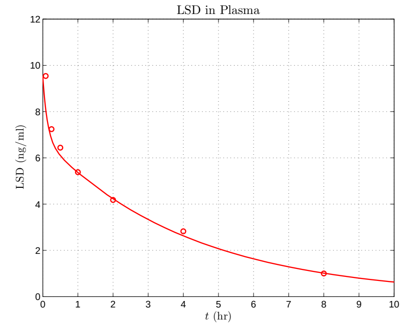
The sum of square errors is $J = 0.079948$

The following MatLab commands produce the graph of the **plasma compartment**

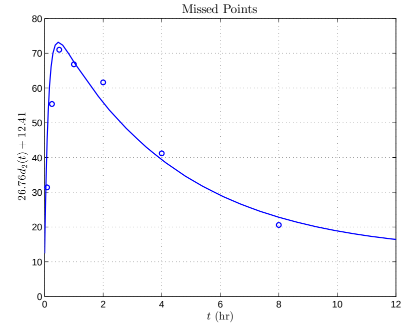
```
[t,L] = ode23(@LSD,[0,15],[9.5330;0],[],2.0580,5.6030,0.32904);
plot(t,L(:,1),'r-',td,L1,'ro');grid;
```


LSD Example 6

Model Graphs



$d_1(t)$ with Data



Scaled and shifted $d_2(t)$

The graph on the right shows the strong correlation between missed points on the test and the amount of LSD in the **Tissue compartment**

Scores are vertically shifted to account for points missed without LSD

Modeling Diabetes

Diabetes (diabetes mellitus) is a disease characterized by excessive glucose in the blood

- There are **3 forms**
  - **Type 1** or **juvenile diabetes** is an autoimmune disorder, where the β-cells in the pancreas are destroyed, so insulin cannot be produced
  - **Type 2** or **adult onset diabetes** is where cells become insulin resistant, often caused by excessive weight and poor exercise
  - **Gestational diabetes** happens in some pregnant women
- This study concentrates on **Type 1** diabetes
- Affects 4-20 per 100,000 with peak occurrence around 14 years of age
- Causes serious health conditions, especially heart disease and nerve damage

Glucose Metabolism

Glucose Metabolism

- Ingest food for nutrients and energy
  - **Carbohydrates** are broken into simple sugars
  - Sugars are absorbed into the blood
  - Cells access blood sugar for energy
- Glucose Control in Blood
  - **High glucose** levels are bad for tissues (osmotic pressure?)
  - β-cells in pancreas sense high levels and release **insulin**
  - Insulin facilitates glucose entering tissues (skeletal muscle, esp.)
  - Convert glucose to glycogen to store in liver
  - Negative feedback control
- Many other controlling hormones

Modeling Glucose Metabolism

General Glucose Control Model Let $G(t)$ be the blood glucose level and $I(t)$ be the blood insulin level

A general differential equation describing this system is

$$\begin{aligned}\frac{dG}{dt} &= f_1(G,I) + J(t),\\ \frac{dI}{dt} &= f_2(G,I),\end{aligned}$$

where $J(t)$ is the external uptake of glucose (a **control function**)

Many significantly more complex models exist

The body wants to maintain homeostasis, so assume an equilibrium (G_0, I_0) or

$$f_1(G_0,I_0) = 0 \qquad \text{and} \qquad f_2(G_0,I_0) = 0.$$

We examine the translated variables (about equilibrium)

$$g(t) = G(t) - G_0 \qquad \text{and} \qquad i(t) = I(t) - I_0$$

Linearization 1

Taylor's Theorem for Two Variables allows the expansion of the functions $f_1(G,I)$ and $f_2(G,I)$:

$$\begin{aligned}f_1(G,I) &= f_1(G_0,I_0) + \frac{\partial f_1(G_0,I_0)}{\partial G}(G-G_0) + \frac{\partial f_1(G_0,I_0)}{\partial I}(I-I_0) + h.o.t.\\ f_2(G,I) &= f_2(G_0,I_0) + \frac{\partial f_2(G_0,I_0)}{\partial G}(G-G_0) + \frac{\partial f_2(G_0,I_0)}{\partial I}(I-I_0) + h.o.t.,\end{aligned}$$

where $h.o.t.$ represents all higher order terms greater than linear

Recall that $f_1(G_0,I_0) = 0$ and $f_2(G_0,I_0) = 0$ (**Equilibrium**).

Also, $g(t) = G(t) - G_0$ and $i(t) = I(t) - I_0$,
which gives $\frac{dG}{dt} = \frac{dg}{dt}$ and $\frac{dI}{dt} = \frac{di}{dt}$

Linearization 2

Linear Terms from Taylor's Expansion: We carefully analyze each **linear term**

Begin with the **glucose dynamics**, $f_1(G,I)$

- Consider $\frac{\partial f_1(G_0,I_0)}{\partial G}$
  - Increases of glucose in the blood stimulates tissues to uptake glucose and liver to store glycogen
  - Thus, this term is negative or $\frac{\partial f_1(G_0,I_0)}{\partial G} = -a_{11} < 0$
- Consider $\frac{\partial f_1(G_0,I_0)}{\partial I}$
  - Increases of insulin in the blood facilitates uptake of glucose in the tissues and liver
  - Thus, this term is negative or $\frac{\partial f_1(G_0,I_0)}{\partial I} = -a_{12} < 0$

Linearization 3

Analysis of Linear Terms from Taylor's Expansion: We continue with the **insulin dynamics**, $f_2(G,I)$

- Consider $\frac{\partial f_2(G_0,I_0)}{\partial G}$
  - Increases of glucose in the blood stimulates production of insulin from the β-cells
  - Thus, this term is positive or $\frac{\partial f_2(G_0,I_0)}{\partial G} = a_{21} > 0$
- Consider $\frac{\partial f_2(G_0,I_0)}{\partial I}$
  - Increases of insulin in the blood results in increased metabolism of the insulin
  - Thus, this term is negative or $\frac{\partial f_2(G_0,I_0)}{\partial I} = -a_{22} < 0$

Linearized Glucose Model

Linearized Glucose Model: In the translated coordinates $g(t) = G(t) - G_0$ and $i(t) = I(t) - I_0$, the model

$$\begin{aligned} \frac{dG}{dt} &= f_1(G, I) + J(t), \\ \frac{dI}{dt} &= f_2(G, I), \end{aligned}$$

can be written in **linearized form**, where the $h.o.t$ terms are dropped along with the **control function**, $J(t)$

The **linearized model** is

$$\begin{pmatrix} \frac{dg}{dt} \\ \frac{di}{dt} \end{pmatrix} = \begin{pmatrix} -a_{11} & -a_{12} \\ a_{21} & -a_{22} \end{pmatrix} \begin{pmatrix} g \\ i \end{pmatrix}$$

Analysis of Linearized Glucose Model

Analysis of Linearized Glucose Model:

$$\dot{\mathbf{z}} = \begin{pmatrix} \frac{dg}{dt} \\ \frac{di}{dt} \end{pmatrix} = \begin{pmatrix} -a_{11} & -a_{12} \\ a_{21} & -a_{22} \end{pmatrix} \begin{pmatrix} g \\ i \end{pmatrix} = \mathbf{Az},$$

where $\mathbf{z} = [g, i]^T$

Eigenvalues are found from the **characteristic equation**, $\det|\mathbf{A} - \lambda\mathbf{I}| = 0$ or

$$\begin{vmatrix} -a_{11} - \lambda & -a_{12} \\ a_{21} & -a_{22} - \lambda \end{vmatrix} = \lambda^2 + (a_{11} + a_{22})\lambda + a_{11}a_{22} + a_{12}a_{21} = 0$$

Since this **characteristic equation** has only positive coefficients (or $tr(A) < 0$ and $\det(A) > 0$), the **equilibrium** is **asymptotically stable**

Simplified Glucose Model

Simplified Glucose Model: Only the blood sugar is measured, so only need to track $g(t)$

The typical situation is that one is hungry after a period of time, indicating blood sugar drops below equilibrium and suggesting a damped oscillator solution or $\lambda = -\alpha \pm i\omega$

$$\begin{aligned} g(t) &= c_1 e^{-\alpha t}\cos(\omega t) + c_2 e^{-\alpha t}\sin(\omega t) \\ g(t) &= A e^{-\alpha t}\cos(\omega(t - \delta)), \end{aligned}$$

where $A = \sqrt{c_1^2 + c_2^2}$ and $\delta = \frac{1}{\omega}\arctan\left(\frac{c_2}{c_1}\right)$

These results give the simplified **Ackerman model** for blood glucose

$$G(t) = G_0 + A e^{-\alpha t}\cos(\omega(t - \delta)),$$

which is widely used to test for **diabetes**

Glucose Tolerance Test

Glucose Tolerance Test (GTT) and **Ackerman Model**

- **GTT**
  - Patient fasts for 12 hours
  - Patient drinks 1.75 mg of glucose/kg of body weight
  - Glucose levels in blood is monitored for 4-6 hours
- **Ackerman Model**
  - Compartmental model for glucose and insulin in the body
  - Model tracks glucose in the blood
  - Model given by equation

$$G(t) = G_0 + A e^{-\alpha t}\cos(\omega(t - \delta))$$

  - **5 parameters** fit to GTT blood data
  - Use parameters α and ω to detect diabetes

Glucose Tolerance Test

Data for a **Normal Subject A** and **Diabetic Subject B**

t (hr)	**A**	**B**	t (hr)	**A**	**B**
0	70	100	2	75	175
0.5	150	185	2.5	65	105
0.75	165	210	3	75	100
1	145	220	4	80	85
1.5	90	195	6	75	90

Model for **Normal Patient** with best parameters

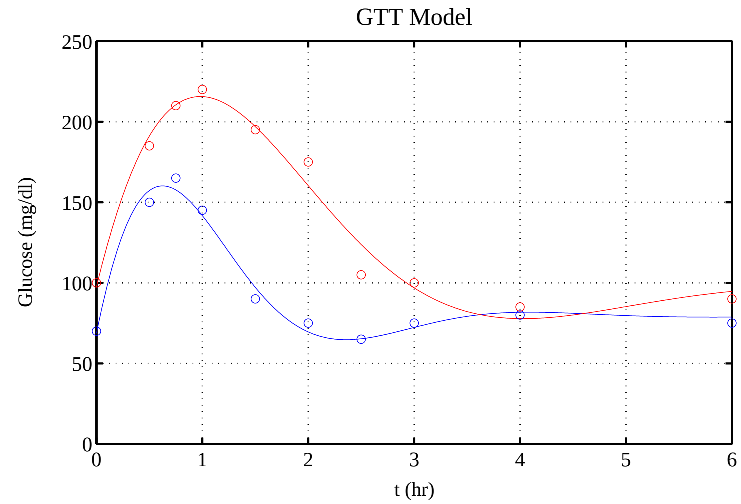
$$G_1(t) = 79.2 + 171.5e^{-0.99t}\cos(1.81(t-0.901))$$

Model for **Diabetic Patient** with best parameters

$$G_2(t) = 95.2 + 263.2e^{-0.63t}\cos(1.03(t-1.52))$$

Glucose Tolerance Test

Graph of data and models



Glucose Tolerance Test

Model for **Normal Patient** with best parameters is

$$G_1(t) = 79.2 + 171.5e^{-0.99t}\cos(1.81(t-0.901))$$

Calculus techniques show a **maximum** at $t_{max} = 0.624$ hr with $G_1(t_{max}) = 160.3$ ng/dl and a **minimum** at $t_{min} = 2.360$ hr with $G_1(t_{min}) = 64.7$ ng/dl

Model for **Diabetic Patient** with best parameters is

$$G_2(t) = 95.2 + 263.2e^{-0.63t}\cos(1.03(t-1.52)),$$

Similar calculations give the maximum at $t_{max} = 0.987$ hr with $G_2(t_{max}) = 215.8$ ng/dl and a **minimum** at $t_{min} = 4.037$ hr with $G_2(t_{min}) = 77.6$ ng/dl

Glucose Tolerance Test

The **Ackerman Test** examines the **natural frequency**, ω_0, (study in next chapter) and period, T_0, of the models, where

$$\omega_0^2 = \alpha^2 + \omega^2 \qquad \text{and} \qquad T_0 = \frac{2\pi}{\omega_0}$$

Our models give the **normal subject**

$$\omega_0 = 2.067 \qquad \text{and} \qquad T_0 = 3.04 \text{ hr}$$

and the **diabetic subject**

$$\omega_0 = 1.210 \qquad \text{and} \qquad T_0 = 5.19 \text{ hr}$$

Note: $T_0 > 4$ suggests diabetes

Two Species Competition Model 1

Two Species Competition Model: Let $X(t)$ be the density of one species of yeast and $Y(t)$ be the density of another species of yeast.

- Assume each species follows the ***logistic growth model*** for interactions within the species.
  - Model has a ***Malthusian growth term***.
  - Model has a term for ***intraspecies competition***.
- The differential equation for each species has a loss term for ***interspecies competition***.
- Assume ***interspecies competition*** is represented by the product of the two species.

If two species compete for a single resource, then
1. **Competitive Exclusion** - one species out competes the other and becomes the only survivor
2. **Coexistence** - both species coexist around a stable equilibrium

Two Species Competition Model 2

Two Species Competition Model: The system of ordinary differential equations (ODEs) for $X(t)$ and $Y(t)$:

$$\begin{aligned} \frac{dX}{dt} &= a_1X - a_2X^2 - a_3XY = f_1(X,Y) \\ \frac{dY}{dt} &= b_1Y - b_2Y^2 - b_3YX = f_2(X,Y) \end{aligned}$$

- First terms with a_1 and b_1 represent the exponential or **Malthusian growth** at low densities
- The terms a_2 and b_2 represent **intraspecies competition** from crowding by the same species
- The terms a_3 and b_3 represent **interspecies competition** from the second species

Unlike the ***logistic growth model***, this system of ODEs does not have an analytic solution, so we must turn to other analyses.

Competition Model – Analysis 1

Competition Model: Analysis always begins finding *equilibria*, which requires:

$$\frac{dX}{dt} = 0 \qquad \text{and} \qquad \frac{dY}{dt} = 0,$$

in the model system of ODEs.

Thus,

$$\begin{aligned} a_1X_e - a_2X_e^2 - a_3X_eY_e &= 0, \\ b_1Y_e - b_2Y_e^2 - b_3X_eY_e &= 0. \end{aligned}$$

Factoring gives:

$$\begin{aligned} X_e(a_1 - a_2X_e - a_3Y_e) &= 0, \\ Y_e(b_1 - b_2Y_e - b_3X_e) &= 0. \end{aligned}$$

Competition Model – Analysis 2

The *equilibria* of the *competition model* satisfy:

$$\begin{aligned} X_e(a_1 - a_2X_e - a_3Y_e) &= 0, \\ Y_e(b_1 - b_2Y_e - b_3X_e) &= 0. \end{aligned}$$

This system of equations must be solved simultaneously. The first equation gives: $X_e = 0$ or $a_1 - a_2X_e - a_3Y_e = 0$.

If $X_e = 0$, then from the second equation we have either the *extinction equilibrium*,

$$(X_e, Y_e) = (0, 0)$$

or the *competitive exclusion equilibrium* (with Y winning):

$$(X_e, Y_e) = \left(0, \frac{b_1}{b_2}\right),$$

where Y_e is at *carrying capacity*.

Competition Model – Analysis 3

Continuing the ***equilibria*** of the ***competition model***: If $a_1 - a_2X_e - a_3Y_e = 0$ from the first equation, then from the second equation we have either the ***competitive exclusion equilibrium*** (with X winning):

$$(X_e, Y_e) = \left(\frac{a_1}{a_2}, 0\right),$$

where X_e is at ***carrying capacity*** or the **nonzero equilibrium**:

$$(X_e, Y_e) = \left(\frac{a_1b_2 - a_3b_1}{a_2b_2 - a_3b_3}, \frac{a_2b_1 - a_1b_3}{a_2b_2 - a_3b_3}\right).$$

If $X_e > 0$ and $Y_e > 0$, then we obtain the ***cooperative equilibrium*** with neither species going extinct.

Note: This last ***equilibrium*** could have a negative X_e or Y_e, depending on the values of the parameters.

Maple Equilibrium

Maple can readily be used to find ***equilibria***:

```
> eq1 := Xe·(a1 - a2·Xe - a3·Ye) = 0;
  eq2 := Ye·(b1 - b2·Ye - b3·Xe) = 0;
                eq1 := Xe (-a2 Xe - a3 Ye + a1) = 0
                eq2 := Ye (-b3 Xe - b2 Ye + b1) = 0                    (1)
> solve({eq1, eq2}, {Xe, Ye});
```

$\{Xe = 0, Ye = 0\}, \left\{Xe = 0, Ye = \frac{b1}{b2}\right\}, \left\{Xe = \frac{a1}{a2}, Ye = 0\right\}, \left\{Xe = \frac{a1\ b2 - a3\ b1}{a2\ b2 - a3\ b3}, Ye = -\frac{a1\ b3 - b1\ a2}{a2\ b2 - a3\ b3}\right\}$ (2)

Later we find the numerical values of the parameters, so **Maple** easily finds all equilibria:

```
> eq3 := Xe·(0.2586 - 0.02030·Xe - 0.05711·Ye) = 0;
  eq4 := Ye·(0.05744 - 0.009768·Ye - 0.004803·Xe) = 0;
          eq3 := Xe (0.2586 - 0.02030 Xe - 0.05711 Ye) = 0
          eq4 := Ye (0.05744 - 0.009768 Ye - 0.004803 Xe) = 0         (3)
> solve({eq3, eq4}, {Xe, Ye});
{Xe = 0., Ye = 0.}, {Xe = 0., Ye = 5.880425880}, {Xe = 12.73891626, Ye = 0.}, {Xe   (4)
    = 9.925065384, Ye = 1.000195635}
```

Note: The ***positive equilibrium*** is close to the late data points.

Nullclines 1

Equilibrium analysis shows there are always the ***extinction*** and two ***competitive exclusion*** equilibria with the latter going to ***carrying capacity*** for one of the species.

Provided $a_2b_2 - a_3b_3 \neq 0$, there is another equilibrium, and it satisfies: 1. $X_e \leq 0$ and $Y_e > 0$ or 2. $X_e > 0$ and $Y_e \leq 0$ or 3. $X_e > 0$ and $Y_e > 0$.

We concentrate our studies on Case 3, where there exists a ***positive cooperative equilibrium***.

Finding ***equilibia*** can be done **geometrically** using ***nullclines***.

Nullclines are simply curves where

$$\frac{dX}{dt} = 0 \qquad \text{and} \qquad \frac{dY}{dt} = 0.$$

Nullclines 2

For the ***competition model***, the ***nullclines*** satisfy:

$$\frac{dX}{dt} = X(a_1 - a_2X - a_3Y) = 0 \quad \text{and} \quad \frac{dY}{dt} = Y(b_1 - b_2Y - b_3X) = 0,$$

where the first equation has solutions only flowing in the Y-direction and the second equation has solutions only flowing in the X-direction.

Equilibria occur where the curves intersect.

The ***nullclines*** for the ***competition model*** are only straight lines:

- The $\frac{dX}{dt} = 0$ has $X = 0$ or the Y-axis preventing solutions in X from becoming negative.
- The $\frac{dY}{dt} = 0$ has $Y = 0$ or the X-axis preventing solutions in Y from becoming negative.
- The other ***two nullclines*** are straight lines with negative slopes passing through the positive quadrant, $X > 0$ and $Y > 0$.

Nullclines

Example 1: Consider the ***competition model***:

$$\frac{dX}{dt} = 0.1\,X - 0.01\,X^2 - 0.02\,XY,$$
$$\frac{dY}{dt} = 0.2\,Y - 0.03\,Y^2 - 0.04\,XY.$$

- ***Nullclines*** where $\frac{dX}{dt} = 0$ are
  1. $X = 0$.
  2. $0.1 - 0.01\,X - 0.02\,Y = 0$ or $Y = 5 - 0.5\,X$.
- ***Nullclines*** where $\frac{dY}{dt} = 0$ are
  1. $Y = 0$.
  2. $0.2 - 0.03\,Y - 0.04\,X = 0$ or $Y = \frac{20}{3} - \frac{4}{3}X$.

Equilibria occur at intersections of a ***nullcline*** with $\frac{dX}{dt} = 0$ and one with $\frac{dY}{dt} = 0$.

The ***4 equilibria*** are $(0,0)$, $\left(0, \frac{20}{3}\right)$, $(10,0)$, and $(2,4)$.

SDSU

Linearization

Linearization: The competition model is below:

$$\frac{dX}{dt} = 0.1\,X - 0.01\,X^2 - 0.02\,XY = f_1(X,Y),$$
$$\frac{dY}{dt} = 0.2\,Y - 0.03\,Y^2 - 0.04\,XY = f_2(X,Y),$$

and the linearization about the equilibria is found by evaluating the ***Jacobian matrix*** at the equilibria:

$$J(X,Y) = \begin{pmatrix} \frac{\partial f_1(X,Y)}{\partial X} & \frac{\partial f_1(X,Y)}{\partial Y} \\ \frac{\partial f_2(X,Y)}{\partial X} & \frac{\partial f_2(X,Y)}{\partial Y} \end{pmatrix} = \begin{pmatrix} 0.1 - 0.02X - 0.02Y & -0.02X \\ -0.04Y & 0.2 - 0.06Y - 0.04X \end{pmatrix}.$$

SDSU

Linearization and Equilibria

Linearization: Consider the ***extinction equilibrium***, $(X_e, Y_e) = (0,0)$, the Jacobian satisfies:

$$J(0,0) = \begin{pmatrix} 0.1 & 0 \\ 0 & 0.2 \end{pmatrix}.$$

This has ***eigenvalues*** $\lambda_1 = 0.1$ ($\xi_1 = [1,0]^T$) and $\lambda_2 = 0.2$ ($\xi_1 = [0,1]^T$).

This is an ***unstable node***, as we'd expect for low populations.

At the X_e ***carrying capacity equilibrium***, $(X_e, Y_e) = (10,0)$, the Jacobian satisfies:

$$J(10,0) = \begin{pmatrix} -0.1 & -0.2 \\ 0 & -0.2 \end{pmatrix}.$$

This has ***eigenvalues*** $\lambda_1 = -0.1$ ($\xi_1 = [1,0]^T$) and $\lambda_2 = -0.2$ ($\xi_1 = [2,1]^T$).

This is a ***stable node***.

SDSU

Linearization and Equilibria

Linearization: At the Y_e ***carrying capacity equilibrium***, $(X_e, Y_e) = (0, 20/3)$, the Jacobian satisfies:

$$J(0, 20/3) = \begin{pmatrix} -0.03333 & 0 \\ -0.2667 & -0.2 \end{pmatrix}.$$

This has ***eigenvalues*** $\lambda_1 = -0.03333$ ($\xi_1 = [1, -1.6]^T$) and $\lambda_2 = -0.2$ ($\xi_1 = [0,1]^T$).

This is a ***stable node***.

At the ***cooperative equilibrium***, $(X_e, Y_e) = (2,4)$, the Jacobian satisfies:

$$J(2,4) = \begin{pmatrix} -0.02 & -0.04 \\ -0.16 & -0.12 \end{pmatrix}.$$

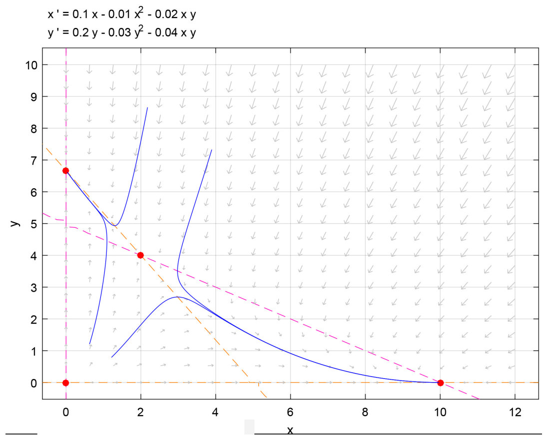
This has ***eigenvalues*** $\lambda_1 = -0.1643$ ($\xi_1 = [1, 3.609]^T$) and $\lambda_2 = 0.02434$ ($\xi_1 = [1, -1.1085]^T$).

This is a ***saddle node***.

SDSU

Phase Portrait

The figure below was generated with `pplane8` and shows that **Example 1** exhibits ***competitive exclusion*** with all solutions going to either the ***carrying capacity equilibria***, $(X_e, Y_e) = \left(0, \frac{20}{3}\right)$ or $(X_e, Y_e) = (10, 0)$.



Introduction
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Example/Equilibria

Example 2: Consider the ***competition model***:

$$\frac{dX}{dt} = 0.1\,X - 0.02\,X^2 - 0.01\,XY,$$
$$\frac{dY}{dt} = 0.2\,Y - 0.04\,Y^2 - 0.03\,XY.$$

- ***Nullclines*** where $\frac{dX}{dt} = 0$ are
  1. $X = 0$.
  2. $0.1 - 0.02\,X - 0.01\,Y = 0$ or $Y = 10 - 2\,X$.
- ***Nullclines*** where $\frac{dY}{dt} = 0$ are
  1. $Y = 0$.
  2. $0.2 - 0.04\,Y - 0.03\,X = 0$ or $Y = 5 - 0.75\,X$.

Equilibria occur at intersections of a ***nullcline*** with $\frac{dX}{dt} = 0$ and one with $\frac{dY}{dt} = 0$.

The ***4 equilibria*** are $(0,0)$, $(0,5)$, $(5,0)$, and $(4,2)$.

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Linearization

Linearization: The competition model is below:

$$\frac{dX}{dt} = 0.1\,X - 0.02\,X^2 - 0.01\,XY = f_1(X,Y),,$$
$$\frac{dY}{dt} = 0.2\,Y - 0.04\,Y^2 - 0.03\,XY = f_2(X,Y),$$

and the linearization about the equilibria is found by evaluating the ***Jacobian matrix*** at the equilibria:

$$J(X,Y) = \begin{pmatrix} \frac{\partial f_1(X,Y)}{\partial X} & \frac{\partial f_1(X,Y)}{\partial Y} \\ \frac{\partial f_2(X,Y)}{\partial X} & \frac{\partial f_2(X,Y)}{\partial Y} \end{pmatrix} = \begin{pmatrix} 0.1 - 0.04X - 0.01Y & -0.01X \\ -0.03Y & 0.2 - 0.08Y - 0.03X \end{pmatrix}.$$

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Linearization and Equilibria

Linearization: Consider the ***extinction equilibrium***, $(X_e, Y_e) = (0,0)$, the Jacobian satisfies:

$$J(0,0) = \begin{pmatrix} 0.1 & 0 \\ 0 & 0.2 \end{pmatrix}.$$

This has ***eigenvalues*** $\lambda_1 = 0.1$ ($\xi_1 = [1,0]^T$) and $\lambda_2 = 0.2$ ($\xi_1 = [0,1]^T$).

This is an ***unstable node***, as we'd expect for low populations.

At the X_e ***carrying capacity equilibrium***, $(X_e, Y_e) = (5,0)$, the Jacobian satisfies:

$$J(5,0) = \begin{pmatrix} -0.1 & -0.05 \\ 0 & 0.05 \end{pmatrix}.$$

This has ***eigenvalues*** $\lambda_1 = -0.1$ ($\xi_1 = [1,0]^T$) and $\lambda_2 = 0.05$ ($\xi_1 = [1,-3]^T$).

This is a ***saddle node***.

Linearization and Equilibria

Linearization: At the Y_e *carrying capacity equilibrium*, $(X_e, Y_e) = (0, 5)$, the Jacobian satisfies:

$$J(0,5) = \begin{pmatrix} 0.05 & 0 \\ -0.15 & -0.2 \end{pmatrix}.$$

This has *eigenvalues* $\lambda_1 = 0.05$ ($\xi_1 = [5, -3]^T$) and $\lambda_2 = -0.2$ ($\xi_1 = [0, 1]^T$).

This is a *saddle node*.

At the *cooperative equilibrium*, $(X_e, Y_e) = (4, 2)$, the Jacobian satisfies:

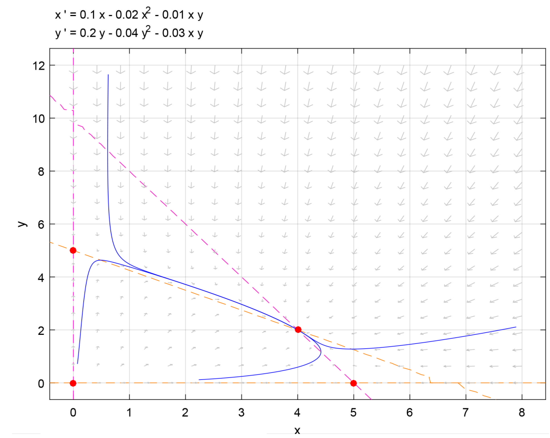
$$J(2,4) = \begin{pmatrix} -0.08 & -0.04 \\ -0.06 & -0.08 \end{pmatrix}.$$

This has *eigenvalues* $\lambda_1 = -0.129$ ($\xi_1 = [1, 1.2247]^T$) and $\lambda_2 = -0.031$ ($\xi_1 = [1, -1.2247]^T$).

This is a *stable node*.

Phase Portrait

The figure below was generated with `pplane8` and shows that **Example 2** exhibits ***cooperation*** with all solutions going toward the ***nonzero equilibrium***, $(X_e, Y_e) = (4, 2)$.



Yeast Competition Model 1

Competition Model: Competition is ubiquitous in ecological studies and many other fields

- Craft beer is a very important part of the San Diego economy
- Researchers at UCSD created a company that provides brewers with one of the best selections of diverse cultures of different strains of the yeast, *Saccharomyces cerevisiae*
- Different strains are cultivated for particular flavors
- Often *S. cerevisiae* is maintained in a continuous chemostat for constant quality - large beer manufacturers
- Large cultures can become contaminated with other species of yeast
- It can be very expensive to start a new pure culture
- We examine a **competition model** for different species of yeast

Yeast Competition Model 2

Yeast Experiment: G. F. Gause [2,3] studied competing species of yeast, *Saccharomyces cerevisiae* and a common contaminant species *Schizosaccharomyces kephir*

The experiments examined growth in monocultures for individual growth laws and in mixed cultures to observe **competition**

Below is a table combining two experimental studies of *S. cerevisiae*

Time (hr)	0	1.5	9	10	18	18	23
Volume	0.37	1.63	6.2	8.87	10.66	10.97	12.5
Time (hr)	25.5	27	34	38	42	45.5	47
Volume	12.6	12.9	13.27	12.77	12.87	12.9	12.7

Below is a table combining two experimental studies of *S. kephir*

Time (hr)	9	10	23	25.5	42	45.5	66	87	111	135
Volume	1.27	1	1.7	2.33	2.73	4.56	4.87	5.67	5.8	5.83

[2] G. F. Gause, *Struggle for Existence*, Hafner, New York, 1934.
[3] G. F. Gause (1932), Experimental studies on the struggle for existence. I. Mixed populations of two species of yeast, *J. Exp. Biol.* **9**, p. 389.

Monoculture Models 1

Monoculture Model: Previous slide gave data for monocultures, which should satisfy **logistic growth model**

$$\frac{dY}{dt} = rY\left(1 - \frac{Y}{M}\right), \qquad Y(0) = Y_0,$$

which has the solution

$$Y(t) = \frac{MY_0}{Y_0 + (M - Y_0)e^{-rt}}$$

Use MatLab to fit parameters to the data, and the results for *Saccharomyces cerevisiae* are

$$r = 0.25864 \qquad M = 12.742 \qquad Y_0 = 1.2343$$

The results for *Schizosaccharomyces kephir* are

$$r = 0.057443 \qquad M = 5.8802 \qquad Y_0 = 0.67805$$

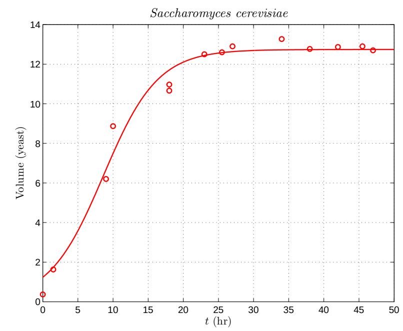
These models show that *S. cerevisiae* grows much faster than *S. kephir*

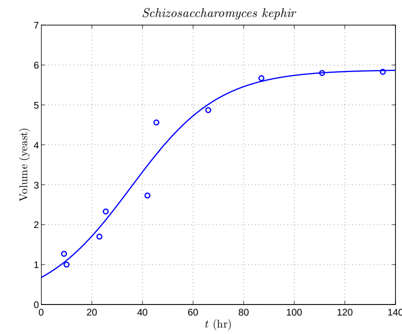
Monoculture Models 2

Monoculture Models and Data:

$$Y_c(t) = \frac{12.742}{1 + 9.3230e^{-0.25864t}} \quad \text{and} \quad Y_k(t) = \frac{5.8802}{1 + 7.6723e^{-0.057443t}}$$

Graphs show the best fitting logistic models for the two species with the Gause experiment data





Competition Experiment

Competition Experiment: G. F. Gause ran experiments (same nutrient conditions) mixing the cultures of *S. cerevisiae* and *S. kephir*

Table combining two experimental studies of the mixed culture

t (hr)	0	1.5	9	10	18	18	23
Y_c	0.375	0.92	3.08	3.99	4.69	5.78	6.15
Y_k	0.29	0.37	0.63	0.98	1.47	1.22	1.46
t (hr)	25.5	27	38	42	45.5	47	
Y_c	9.91	9.47	10.57	7.27	9.88	8.3	
Y_k	1.11	1.225	1.1	1.71	0.96	1.84	

The data show the populations are increasing, but the *S. cerevisiae* population is significantly below the carrying capacity

If two species compete for a single resource, then
1. **Competitive Exclusion** - one species out competes the other and becomes the only survivor
2. **Coexistence** - both species coexist around a stable equilibrium

Competition Model

Competition Model: Assume a competition model of the form

$$\frac{dY_c}{dt} = a_1Y_c - a_2Y_c^2 - a_3Y_cY_k = f_1(Y_c, Y_k)$$
$$\frac{dY_k}{dt} = b_1Y_k - b_2Y_k^2 - b_3Y_kY_c = f_2(Y_c, Y_k)$$

- First terms with a_1 and b_1 represent the exponential or **Malthusian growth** at low densities
- The terms a_2 and b_2 represent **intraspecies competition** from crowding by the same species
- The terms a_3 and b_3 represent **interspecies competition** from the second species

Competition Model Parameters

Competition Model: Assume a competition model of the form

$$\frac{dY_c}{dt} = a_1 Y_c - a_2 Y_c^2 - a_3 Y_c Y_k$$
$$\frac{dY_k}{dt} = b_1 Y_k - b_2 Y_k^2 - b_3 Y_k Y_c$$

- The monoculture experiments give the values:

$$a_1 = 0.25864 \quad a_2 = 0.020298 \quad b_1 = 0.057443 \quad b_2 = 0.0097689$$

- The competition experiments give the best interspecies competition parameters

$$a_3 = 0.057015 \qquad b_3 = 0.0047581$$

- These experiments also fit the best initial conditions:

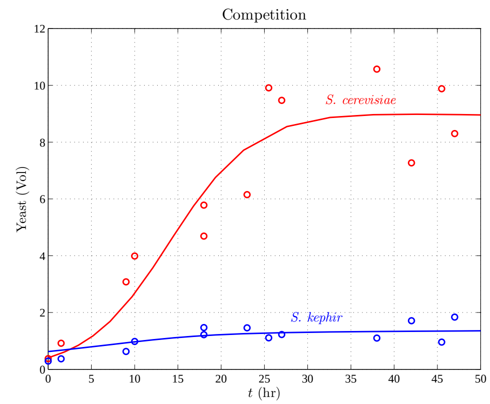
$$Y_c(0) = 0.41095 \qquad Y_k(0) = 0.62579$$

- More details for fitting a_3, b_3, $Y_c(0)$, and $Y_k(0)$ are available from **Math 636**

Competition Model Fit

Competition Model:

$$\frac{dY_c}{dt} = 0.25864 Y_c - 0.020298 Y_c^2 - 0.057015 Y_c Y_k, \qquad Y_c(0) = 0.41095$$
$$\frac{dY_k}{dt} = 0.057443 Y_k - 0.0097689 Y_k^2 - 0.0047581 Y_k Y_c, \qquad Y_k(0) = 0.62579$$



Equilibria for Competition Model

Equilibria for Competition Model: Let the equilibria for *S. cerevisiae* and *S. kephir* be Y_{ce} and Y_{ke}, respectively

$$Y_{ce}(0.25864 - 0.020298 Y_{ce} - 0.057015 Y_{ke}) = 0$$
$$Y_{ke}(0.057443 - 0.0097689 Y_{ke} - 0.0047581 Y_{ce}) = 0$$

- Must solve the above equations simultaneously, giving 4 equilibria
- **Extinction equilibrium**, $(Y_{ce}, Y_{ke}) = (0, 0)$
- **Carrying capacity equilibria**, $(Y_{ce}, Y_{ke}) = (12.742, 0)$ and $(Y_{ce}, Y_{ke}) = (0, 5.8802)$
- **Coexistence equilibrium**, $(Y_{ce}, Y_{ke}) = (4.4407, 2.9554)$

Linearization of Competition Model

Linearization of Competition Model: With equilibria Y_{ce} and Y_{ke}, let $u = Y_c - Y_{ce}$ and $v = Y_k - Y_{ke}$

$$\begin{pmatrix} \dot{u} \\ \dot{v} \end{pmatrix} = \begin{pmatrix} \frac{\partial f_1(Y_{ce},Y_{ke})}{\partial u} & \frac{\partial f_1(Y_{ce},Y_{ke})}{\partial v} \\ \frac{\partial f_2(Y_{ce},Y_{ke})}{\partial u} & \frac{\partial f_2(Y_{ce},Y_{ke})}{\partial v} \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}$$

so the linear system is

$$\begin{pmatrix} \dot{u} \\ \dot{v} \end{pmatrix} = \begin{pmatrix} a_1 - 2a_2 Y_{ce} - a_3 Y_{ke} & a_3 Y_{ce} \\ b_3 Y_{ke} & b_1 - 2b_2 Y_{ke} - b_3 Y_{ce} \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix},$$

where

$$a_1 = 0.25864 \qquad a_2 = 0.020298 \qquad a_3 = 0.057015$$
$$b_1 = 0.057443 \qquad b_2 = 0.0097689 \qquad b_3 = 0.0047581$$

Local Stability of Competition Model

Local Stability of Competition Model: At the equilibrium, $(Y_{ce}, Y_{ke}) = (0, 0)$

$$\begin{pmatrix} \dot{u} \\ \dot{v} \end{pmatrix} = \begin{pmatrix} 0.25864 & 0 \\ 0 & 0.057443 \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix},$$

which has eigenvalues $\lambda_1 = 0.25864$ and $\lambda_2 = 0.057443$, so this **equilibrium** is an **Unstable Node**

At the equilibrium, $(Y_{ce}, Y_{ke}) = (12.742, 0)$

$$\begin{pmatrix} \dot{u} \\ \dot{v} \end{pmatrix} = \begin{pmatrix} -0.25864 & 0.72649 \\ 0 & -0.0031847 \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix},$$

which has eigenvalues $\lambda_1 = -0.25864$ and $\lambda_2 = -0.0031847$, so this **equilibrium** is a **Stable Node**

Local Stability of Competition Model

Local Stability of Competition Model: At the equilibrium, $(Y_{ce}, Y_{ke}) = (0, 5.8802)$

$$\begin{pmatrix} \dot{u} \\ \dot{v} \end{pmatrix} = \begin{pmatrix} -0.076620 & 0 \\ 0.027979 & -0.057443 \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix},$$

which has eigenvalues $\lambda_1 = -0.07662$ and $\lambda_2 = -0.057443$, so this **equilibrium** is a **Stable Node**

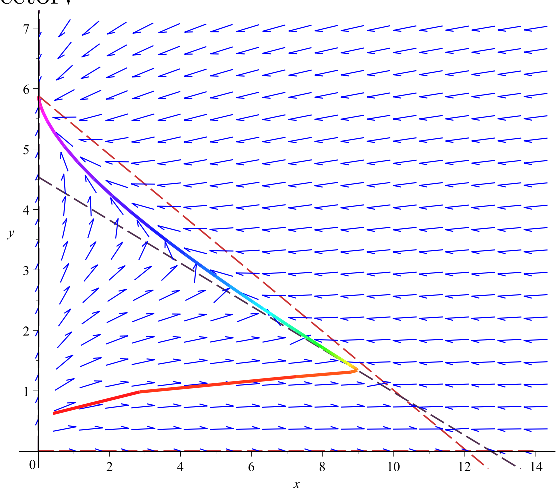
At the equilibrium, $(Y_{ce}, Y_{ke}) = (4.4407, 2.9554)$

$$\begin{pmatrix} \dot{u} \\ \dot{v} \end{pmatrix} = \begin{pmatrix} -0.090137 & 0.25319 \\ 0.014062 & -0.021428 \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix},$$

which has eigenvalues $\lambda_1 = -0.1246$ and $\lambda_2 = 0.01307$, so this **equilibrium** is a **Saddle Node**

Competition Model

Competition Model Phase Portrait: Plot shows nullclines and solution trajectory



Competition Model

Competition Model Time Series: Plot shows the solution trajectories