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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   - Basic Mixing Problem - Water and Inert Salts
   - Mixing Problem Example
   - Pharmokinetic Problem
   - LSD Example

3. Nonlinear Applications of Systems of DEs
   - Model of Glucose and Insulin Control
   - Glucose Tolerance Test
   - Competition Model

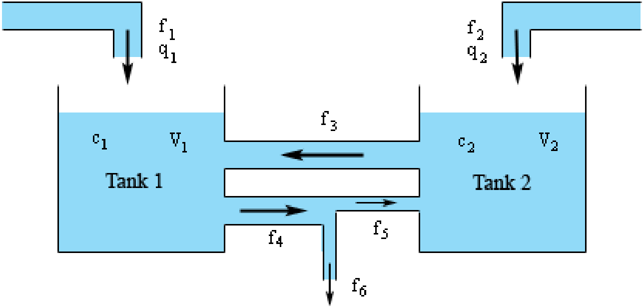
Introduction

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

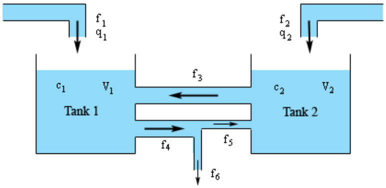


This problem examines the mixing of an **inert salt** in **two tanks**

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:

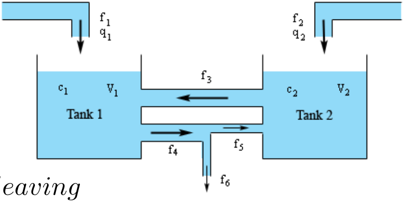
$$f_1 + f_2 = f_6 \qquad f_1 + f_3 = f_4$$
$$f_2 + f_5 = f_3 \qquad f_5 + f_6 = f_4$$

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

$$\begin{pmatrix} -\frac{f_4}{V_1} & \frac{f_3}{V_1} \\ \frac{f_5}{V_2} & -\frac{f_3}{V_2} \end{pmatrix} \begin{pmatrix} c_{1e} \\ c_{2e} \end{pmatrix} = \begin{pmatrix} -\frac{f_1 q_1}{V_1} \\ -\frac{f_2 q_2}{V_2} \end{pmatrix}$$

This has the general solution

$$\begin{pmatrix} c_{1e} \\ c_{2e} \end{pmatrix} = \begin{pmatrix} \frac{f_1 q_1 + f_2 q_2}{f_4 - f_5} \\ \frac{f_1 f_5 q_1 + f_2 f_4 q_2}{f_3 (f_4 - f_5)} \end{pmatrix}$$

Basic Mixing Problem

Eigenvalues: We find the eigenvalues by solving

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

or

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

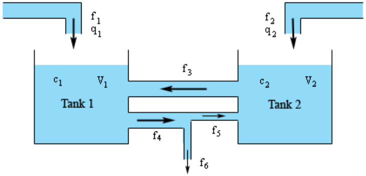
This has the **characteristic equation**

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

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

Mixing Problem Example 1

Mixing Problem Example



Assume the following parameters:

$$\begin{array}{ll} V_1 = 100 \text{ l}, & V_2 = 60 \text{ l}, \\ q_1 = 7 \text{ g/l}, & q_2 = 12 \text{ g/l}, \\ f_1 = 0.2 \text{ l/min}, & f_2 = 0.15 \text{ l/min}, \\ f_3 = 0.25 \text{ l/min}, & f_4 = 0.45 \text{ l/min}, \\ f_5 = 0.1 \text{ l/min}, & f_6 = 0.35 \text{ l/min} \end{array}$$

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

Mixing Problem Example

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:

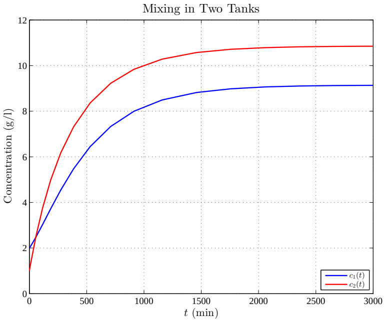
$$\begin{pmatrix} c_{1e} \\ c_{2e} \end{pmatrix} = \begin{pmatrix} 9.14286 \\ 10.85714 \end{pmatrix}$$

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

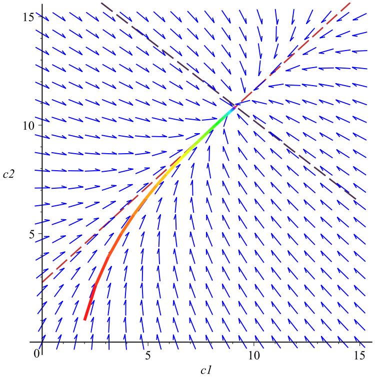
$$\xi_1 = \begin{pmatrix} 1 \\ -0.7525 \end{pmatrix} \quad \text{and} \quad \xi_2 = \begin{pmatrix} 1 \\ 0.8859 \end{pmatrix}$$

Mixing Problem Example

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

Pharmokinetic Problem 1

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

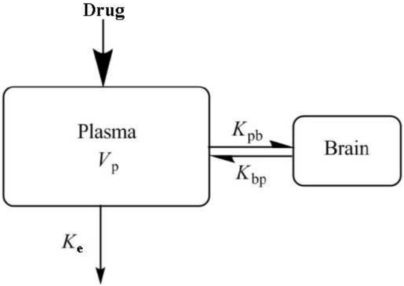
- This application examines a **drug** injected into the bloodstream
- The simplified model divides the body into a **Plasma compartment** and a **Brain compartment**
  - Track fraction of **drug** in each compartment, $d_1(t)$, in plasma and $d_2(t)$, in brain
  - Assume **linear transfer** between 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

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

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

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

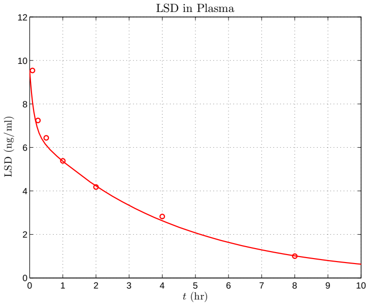
The sum of square errors is $J = 0.079948$

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

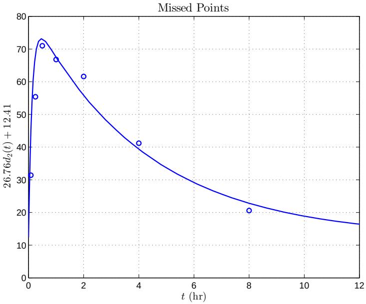
```
[t,L] = ode23(@LSD,[0,15],[9.5330;0],[],2.0580,5.6030,0.32904);
plot(t,L(:,1),'r-',td,L1,'ro');grid;
```

LSD Example

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

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:

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

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 1

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

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

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

Glucose Tolerance Test 2

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

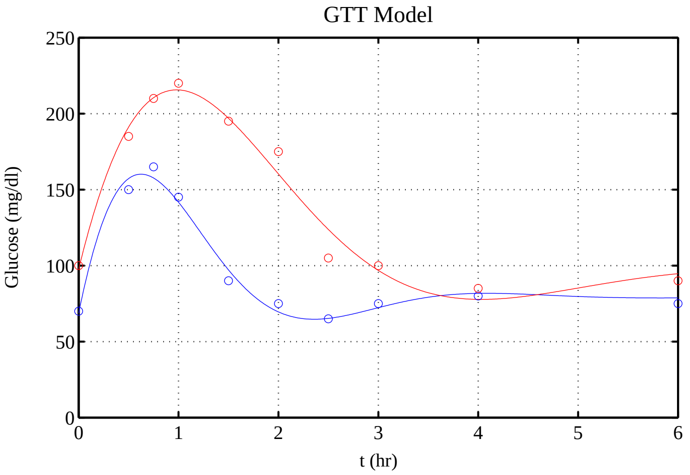
$$G_1(t) = 79.2 + 171.5e^{-0.99t}\cos(1.81(t - 0.901))$$

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 5

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

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,

$$\begin{aligned} a_1 X_e - a_2 X_e^2 - a_3 X_e Y_e &= 0, \\ b_1 Y_e - b_2 Y_e^2 - b_3 X_e Y_e &= 0. \end{aligned}$$

Factoring gives:

$$\begin{aligned} X_e(a_1 - a_2 X_e - a_3 Y_e) &= 0, \\ Y_e(b_1 - b_2 Y_e - b_3 X_e) &= 0. \end{aligned}$$

Competition Model – Analysis

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;
```

$$eq1 := Xe\,(-a2\,Xe - a3\,Ye + a1) = 0$$

$$eq2 := Ye\,(-b3\,Xe - b2\,Ye + b1) = 0 \qquad (1)$$

```
> solve({eq1, eq2}, {Xe, Ye});
```

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

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;
```

$$eq3 := Xe\,(0.2586 - 0.02030\,Xe - 0.05711\,Ye) = 0$$

$$eq4 := Ye\,(0.05744 - 0.009768\,Ye - 0.004803\,Xe) = 0 \qquad (3)$$

```
> solve({eq3, eq4}, {Xe, Ye});
```

$$\{Xe=0.,\ Ye=0.\},\ \{Xe=0.,\ Ye=5.880425880\},\ \{Xe=12.73891626,\ Ye=0.\},\ \{Xe=9.925065384,\ Ye=1.000195635\} \qquad (4)$$

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 $(2,4)$.

Linearization

Linearization: The competition model is below:

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

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

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

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***.

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:

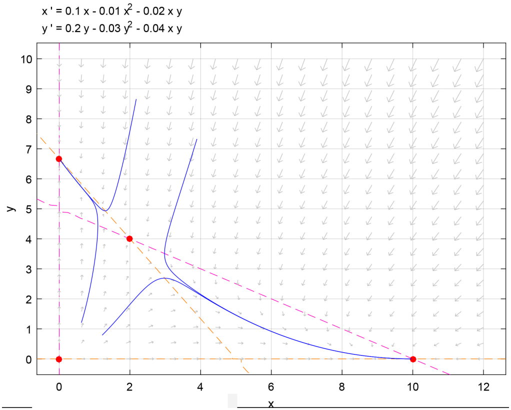
$$J(2, 4) = \begin{pmatrix} -0.02 & -0.04 \\ -0.16 & -0.12 \end{pmatrix}.$$

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***.

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 $(X_e, Y_e) = (10, 0)$.



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.https://jmahaffy.sdsu.edu/courses/f15/math337/beamer/LinSys2 04.pdf
  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 $(4,2)$.

Linearization

Linearization: The competition model is below:

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

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

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

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:

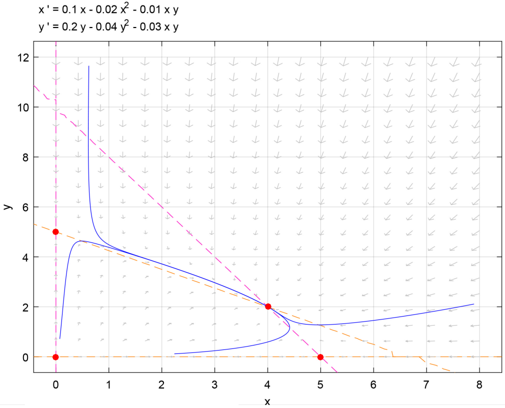
$$J(2,4) = \begin{pmatrix} -0.08 & -0.04 \\ -0.06 & -0.08 \end{pmatrix}.$$

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

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

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

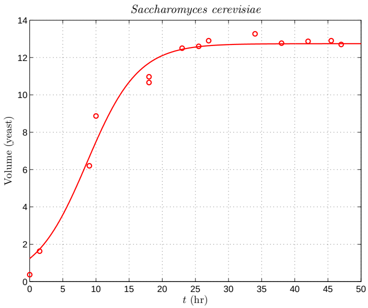
These models show that *S. cerevisiae* grows much faster than *S. kephir*

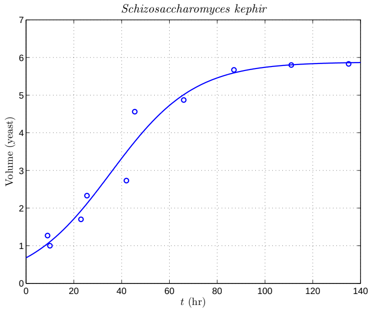
Monoculture Models 2

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

$$\begin{aligned} \frac{dY_c}{dt} &= a_1 Y_c - a_2 Y_c^2 - a_3 Y_c Y_k = f_1(Y_c, Y_k) \\ \frac{dY_k}{dt} &= b_1 Y_k - b_2 Y_k^2 - b_3 Y_k Y_c = f_2(Y_c, Y_k) \end{aligned}$$

- 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

Competition Model Parameters

Competition Model: Assume a competition model of the form

$$\begin{aligned}\frac{dY_c}{dt} &= a_1Y_c - a_2Y_c^2 - a_3Y_cY_k \\ \frac{dY_k}{dt} &= b_1Y_k - b_2Y_k^2 - b_3Y_kY_c\end{aligned}$$

- 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:

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

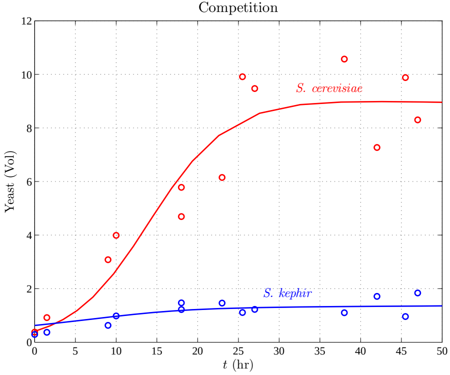
- More details for fitting a_3, b_3, $Y_c(0)$, and $Y_k(0)$ are available from **Math 636**

Competition Model Fit

Competition Model:

$$\frac{dY_c}{dt} = 0.25864Y_c - 0.020298Y_c^2 - 0.057015Y_cY_k, \qquad Y_c(0) = 0.41095$$

$$\frac{dY_k}{dt} = 0.057443Y_k - 0.0097689Y_k^2 - 0.0047581Y_kY_c, \qquad Y_k(0) = 0.62579$$



Equilibria for Competition Model

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

$$\begin{aligned} Y_{ce}(0.25864 - 0.020298Y_{ce} - 0.057015Y_{ke}) &= 0 \\ Y_{ke}(0.057443 - 0.0097689Y_{ke} - 0.0047581Y_{ce}) &= 0 \end{aligned}$$

- 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**

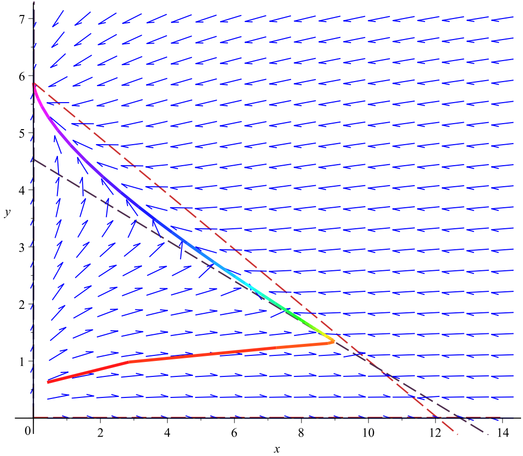
At the equilibrium, $(Y_{ce}, Y_{ke}) = (4.4407, 2.9554)$

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

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