Plant Propagation

Consider plants that produce seeds each August. Seeds can germinate only one or two years later.

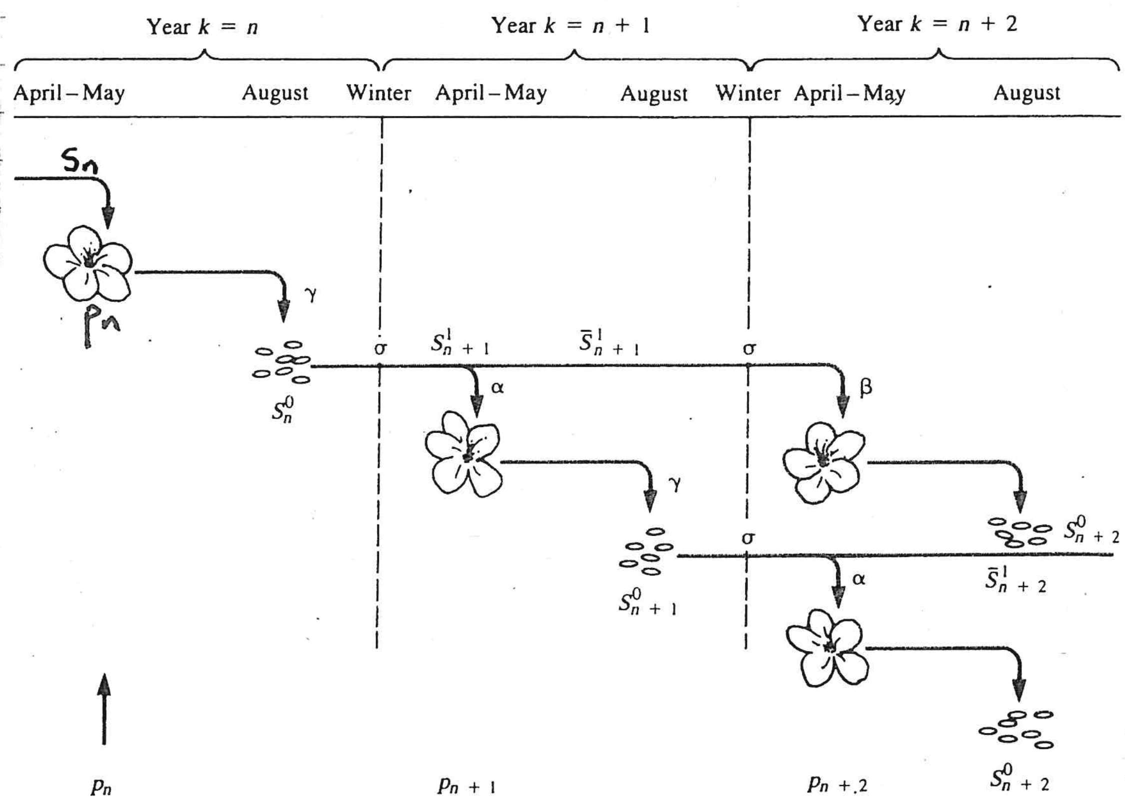


Figure 1.2 Annual plants produce γ seeds per plant each summer. The seeds can remain in the ground for up to two years before they germinate in the springtime. Fractions α of the one-year-old and β of the two-year-old seeds give rise to a new plant generation. Over the winter seeds age, and a certain proportion of them die. The model for this system is discussed in Section 1.2.

γ = # seeds per plant in August

α = fraction of 1-yr old seeds germinate

β = fraction of 2-yr old seeds germinate

σ = fraction of seeds survive winter.

Variable Defns (year n)

p_n = number of plants (May)

S_n^1 = number of 1yr old seeds before April germ.

$\bar{S}_n^1$ = number of 1yr old seeds left in May after germ.

S_n^2 = number of 2yr old seeds before April germ.

$\bar{S}_n^2$ = number of 2yr old seeds left in May after germ

S_n^0 = number new seeds produced in August

Parameter Defns

γ = # seeds per plant in August

α = fraction of 1yr old seeds that germinate

β = fraction of 2yr old seeds that germinate

σ = fraction of seeds that survive winter.

Relation between variables (at year n)

(1) $$p_n = \alpha S_n^1 + \beta S_n^2$$

These plants will produce seeds in August.

(2) $$\bar{S}_n^1 = (1-\alpha) S_n^1$$

(3) $$\bar{S}_n^2 = (1-\beta) S_n^2$$

Seeds produced by plants in August

(4) $$S_n^0 = \gamma p_n$$

Winter mortality

(5) $$S_{n+1}^1 = \sigma S_n^0$$

(6) $$S_{n+1}^2 = \sigma \bar{S}_n^1$$

Simplify system

$$p_{n+1} = \alpha S^1_{n+1} + \beta S^2_{n+1}$$

use (4)-(5)

$$p_{n+1} = \alpha\gamma\sigma p_n + \beta S^2_{n+1}$$

use (2), (6)

(7) $$p_{n+1} = \alpha\gamma\sigma p_n + \beta\sigma(1-\alpha) S^1_n$$

Eqns (7) and (5) can then be written as a system of two first order difference equations

$$\boxed{\begin{aligned} p_{n+1} &= \alpha\gamma\sigma p_n + \beta\sigma(1-\alpha)S^1_n \\ S^1_{n+1} &= \gamma\sigma p_n \end{aligned}}$$

system of 1st order diff. eqns

Given we know initial values p_0, S^1_0 then (p_n, S^1_n) can be found

To determine fate of population is easier to eliminate S^1_n noting

(4), (5) $$S^1_n = \gamma\sigma p_{n-1}$$

hence

$$\boxed{p_{n+1} = \alpha\gamma\sigma p_n + \beta\sigma^2(1-\alpha)\gamma p_{n-1}}$$

second order difference eqn.

Need to know math for solving this.

Plant model as a system

$$\boxed{\begin{aligned} p_{n+1} &= \alpha\gamma\sigma\, p_n + \beta\sigma(1-\alpha)\, s_n^1 \\ s_{n+1}^1 &= \gamma\sigma\, p_n \end{aligned}}$$

is equivalent to the system

(1) $$X_{n+1} = A X_n \qquad X_n \in \mathbb{R}^2,\ A \in \mathbb{R}^{2\times 2}$$

$$X_n = \begin{pmatrix} p_n \\ s_n^1 \end{pmatrix} \qquad A = \begin{bmatrix} \alpha\gamma\sigma & \beta\sigma(1-\alpha) \\ \gamma\sigma & 0 \end{bmatrix}$$

Plant model as 2nd order difference equation

$$\boxed{p_{n+1} - \alpha\gamma\sigma\, p_n - \beta\sigma^2(1-\alpha)\gamma\, p_{n-1} = 0}$$

is equivalent to

(2) $$a x_{n+1} + b x_n + c x_{n-1} = 0$$

$$a = 1$$

$$b = -\alpha\gamma\sigma$$

$$c = \beta\sigma^2(1-\alpha)\gamma$$

$$x_n = p_n$$

$$\boxed{\text{Mathematics of second order difference equations}}$$

Second Order Difference Equations

(1) $$\boxed{a x_{n+1} + b x_n + c x_{n-1} = 0}$$

Seek solutions of the form

(2) $$x_n = \lambda^n \qquad \lambda \in \mathbb{C} \text{ (complex)}$$

Substitute (2) into (1) and simplify

$$a\lambda^{n+1} + b\lambda^n + c\lambda^{n-1} = 0$$

$$\lambda^{n-1} \underbrace{(a\lambda^2 + b\lambda + c)}_{\text{must vanish}} = 0$$

Hence $x_n = \lambda^n$ is a solution only if λ is a root of the characteristic polynomial

$$\boxed{P(\lambda) \doteq a\lambda^2 + b\lambda + c}$$

Solutions depend on whether roots of $P(\lambda)$ are real, equal, complex.

General Solutions (without proof)

Categorized by roots λ_k of $P(\lambda)$

$\lambda_1 \neq \lambda_2$ real $\qquad x_n = c_1\lambda_1^n + c_2\lambda_2^n$

$\lambda_1 = \lambda_2$ real $\qquad x_n = (c_1 + c_2 n)\lambda_1^n$

$\lambda = re^{i\theta}$ complex $\qquad x_n = c_1 r^n \cos(n\theta) + c_2 r^n \sin(n\theta)$

Conversion in complex case

Complex roots of $P(\lambda)$ can be written

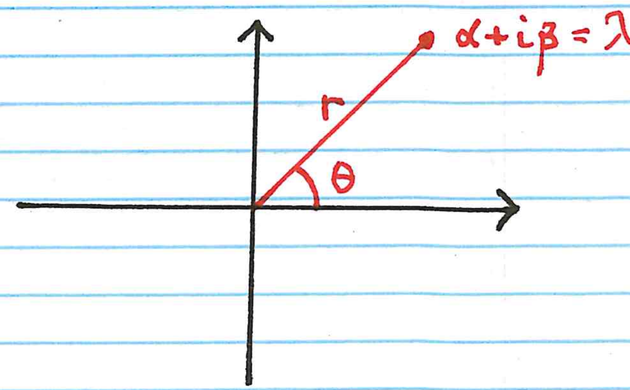
(1) $\qquad \lambda = \alpha + i\beta \qquad \alpha, \beta \in \mathbb{R}$

To convert λ to polar note

(2) $\qquad \lambda = re^{i\theta} = r\cos\theta + i r\sin\theta$

Compare (1) and (2)

$$\underbrace{\boxed{\begin{aligned} r\cos\theta &= \alpha \\ r\sin\theta &= \beta \end{aligned}}}_{\text{solve for } (r,\theta)}$$



More on complex solutions

$$L(z_n) = a z_{n+2} + b z_{n+1} + c z_n = 0$$

Solutions may be complex even if a, b, c real

$$z_n = x_n + i y_n$$

where x_n, y_n are both real. From (1) it is easy to see

$$L(z_n) = L(x_n) + i L(y_n) = 0$$

which is true only if both $L(x_n) = 0$ and $L(y_n) = 0$.

Thus, real and complex parts of z_n are each solutions of the difference eqn.

$$z_n = (\alpha + i\beta)^n$$

$$z_n = (re^{i\theta})^n$$

$$z_n = r^n e^{in\theta}$$

$$z_n = r^n(\underbrace{\cos(n\theta)}_{x_n} + i \underbrace{\sin(n\theta)}_{y_n})$$

Hence general solution is

$$x_n = c_1 r^n \cos(n\theta) + c_2 r^n \sin(n\theta)$$

EXAMPLE $\boxed{x_{n+2} - 5x_{n+1} + 6x_n = 0}$

Let $x_n = \lambda^n$ ultimately yields chacteristic eqn

$$\lambda^2 - 5\lambda + 6 = 0$$

which has two real roots:

$$\lambda_1 = 2 \qquad \lambda_2 = 3$$

General solution of difference eqn is:

(1) $$x_n = c_1 2^n + c_2 3^n$$

where c_K are arbitrary constants.

If one also stipulates initial conditions these constants can be found. For instance

(2) $$x_{n+1} - 5x_n + 6x_{n-1} = 0 \qquad x_0 = 1 \quad x_1 = 2$$

Use gen. soln (1) to find c_K

$n=0$ $\quad x_0 = c_1 2^0 + c_2 3^0 = 1$

$n=1$ $\quad x_1 = c_1 2^1 + c_2 3^1 = 2$

Solving these $\Rightarrow$ $c_1 = 1$, $c_2 = 0$.

$$x_n = 2^n$$

EXAMPLE $\quad x_{n+2} - 6x_{n+1} + 9x_n = 0 \quad$ (repeated)

$$\lambda^2 - 6\lambda + 9 = 0$$

Hence $\lambda = 3$ repeated yields a gen. soln.

$$x_n = (c_1 + c_2 n)\, 3^n$$

EXAMPLE $\quad x_{n+2} - x_{n+1} + x_n = 0 \quad$ (complex)

$$\lambda^2 - \lambda + 1 = 0$$

has complex roots $\lambda = \frac{1}{2} \pm \frac{\sqrt{3}}{2} i$

$$\lambda = re^{i\theta} = r\cos\theta + ir\sin\theta = \frac{1}{2} + \frac{\sqrt{3}}{2} i$$

hence

$$r\cos\theta = 1/2$$
$$r\sin\theta = \sqrt{3}/2$$

whose soln: $\quad r = 1, \quad \theta = \pi/3$

$$= c_1 (1)^n \cos\left(\frac{n\pi}{3}\right) + c_2 (1)^n \sin\left(\frac{n\pi}{3}\right)$$

Asymptotic Behavior

$$a x_{n+1} + b x_n + c x_{n-1} = 0$$

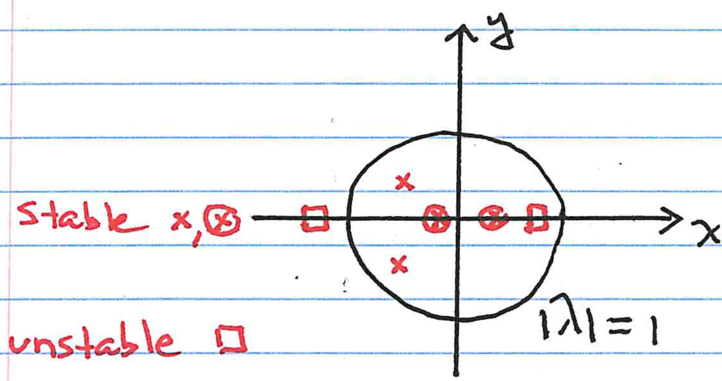
The general solution is $(\lambda_1 \neq \lambda_2)$

$$x_n = c_1 \lambda_1^n + c_2 \lambda_2^n$$

Even when λ_k are complex, very simple conditions determine the large n asymptotic behavior of x_n.

stable $|\lambda_1| < 1$ and $|\lambda_2| < 1$ $\Rightarrow$ $|x_n| \to 0$

unstable $|\lambda_k| > 1$ for some k $\Rightarrow$ $|x_n| \to \infty$



complex plane
$\lambda = x + iy$

Systems of Difference Equations

$$(1) \qquad x_{n+1} = a_{11} x_n + a_{12} y_n$$

$$(2) \qquad y_{n+1} = a_{21} x_n + a_{22} y_n$$

Can be re-expressed in vector form

$$(3) \qquad \mathbf{X}_{n+1} = A \mathbf{X}_n$$

where

$$\mathbf{X}_n = \begin{pmatrix} x_n \\ y_n \end{pmatrix} \qquad A = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \in \mathbb{R}^{2\times 2}$$

An example of the solution of (3)

Suppose $\lambda_i, \vec{\xi}_i$ are eigenvalue/vector pairs of A

$$A \vec{\xi}_i = \lambda_i \vec{\xi}_i \qquad i = 1, 2$$

General solution of (3) is

$$\mathbf{X}_n = c_1 \lambda_1^n \vec{\xi}_1 + c_2 \lambda_2^n \vec{\xi}_2 \qquad \lambda_1 \neq \lambda_2$$

<u>Proof:</u>

$$\begin{aligned} A\mathbf{X}_n &= c_1 \lambda_1^n \overbrace{A\vec{\xi}_1} + c_2 \lambda_2^n \overbrace{A\vec{\xi}_2} \\ &= c_1 \lambda_1^n \cdot \lambda_1 \vec{\xi}_1 + c_2 \lambda_2^n \cdot \lambda_2 \vec{\xi}_2 \\ &= c_1 \lambda_1^{n+1} \vec{\xi}_1 + c_2 \lambda_2^{n+1} \vec{\xi}_2 = \mathbf{X}_{n+1} \qquad \square \end{aligned}$$

EXAMPLE $\quad \mathbf{X}_{n+1} = A\mathbf{X}_n \qquad A = \begin{bmatrix} -10 & -4 \\ 24 & 10 \end{bmatrix}$

First find eigenvalues of A. Characteristic Polynomial

$$P(\lambda) = \det(A - \lambda I) = \lambda^2 - 4$$

Roots of $P(\lambda)$ are eigenvalues of A

$$\lambda_1 = 2 \qquad \lambda_2 = -2$$

Now find eigenvectors for λ_1 and λ_2

$$A - \lambda_1 I = \begin{bmatrix} -12 & -4 \\ 24 & 8 \end{bmatrix} \sim \begin{bmatrix} 3 & 1 \\ 0 & 0 \end{bmatrix} \qquad \vec{\xi}_1 = \begin{pmatrix} 1 \\ -3 \end{pmatrix}$$

$$A - \lambda_2 I = \begin{bmatrix} -8 & -4 \\ 24 & 12 \end{bmatrix} \sim \begin{bmatrix} 2 & 1 \\ 0 & 0 \end{bmatrix} \qquad \vec{\xi}_2 = \begin{pmatrix} 1 \\ -2 \end{pmatrix}$$

Given we now know $\lambda_i, \vec{\xi}_i$ we have

$$\mathbf{X}_n = c_1 2^n \begin{pmatrix} 1 \\ -3 \end{pmatrix} + c_2 (-2)^n \begin{pmatrix} 1 \\ -2 \end{pmatrix} \qquad \square$$

Remarks

General solutions when λ_i are repeated or complex are not shown here.

Analysis of Plant Model

Plant model revisited

Recall the plant population p_n at year n satisfies the second order difference equation

$$(1) \quad \boxed{\begin{aligned} p_{n+1} - \alpha\gamma\sigma\, p_n - \beta\sigma^2(1-\alpha)\gamma\, p_{n-1} &= 0 \\ p_{n+1} - a\, p_n - b\, p_{n-1} &= 0 \end{aligned}}$$

where

α = fraction of 1-yr old seeds that germinate

β = fraction of 2-yr old seeds that germinate

σ = fraction of seeds that survive winter

γ = number of seeds per plant in August

Wish to answer the simple question:

do the plants thrive (survive)?

To answer we note the solution to (1) is

$$(2) \quad \boxed{\begin{aligned} p_n &= c_1 \lambda_-^n + c_2 \lambda_+^n \\ \lambda_\pm &= \tfrac{1}{2}\left(a \pm \sqrt{a^2+4b}\right) \end{aligned}}$$

<u>Note</u>: Both eigenvalues $\lambda_\pm$ are real. Does not preclude oscillations if $\lambda_- < 0$ though.

We make a few observations

$$\sqrt{a^2+4b} > a > 0$$

Consequently

$$\lambda_+ = \frac{1}{2}\left(a + \sqrt{a^2+4b}\right) > a > 0$$

$$\lambda_- = \frac{1}{2}\left(a - \sqrt{a^2+4b}\right) < 0$$

Summarize

$$\boxed{\lambda_- < 0 < \lambda_+}$$

$|\lambda_+| > |\lambda_-|$

Thus the term λ_-^n in (2) does oscillate.

A necessary condition for the plant population to survive is

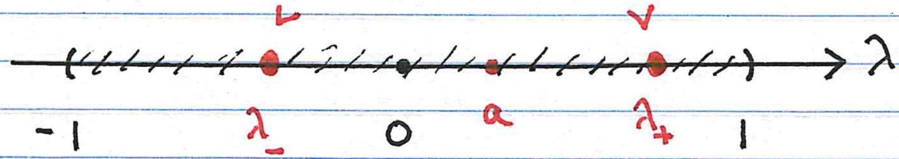
$$\boxed{\lambda_+ > 1}$$

Were this not true $p_n \to 0$ as $n \to \infty$

$$p_n = c_1 \lambda_-^n + c_2 \lambda_+^n$$

decay oscillation

decay



Necessary Condition $\lambda_+ > 1$

We will first determine when $\lambda_+ < 1 \Rightarrow p_n \to 0$.
Same as

$$a + \sqrt{a^2 + 4b} < 2$$

$$\sqrt{a^2 + 4b} < 2 - a$$

$$a^2 + 4b < (2-a)^2$$

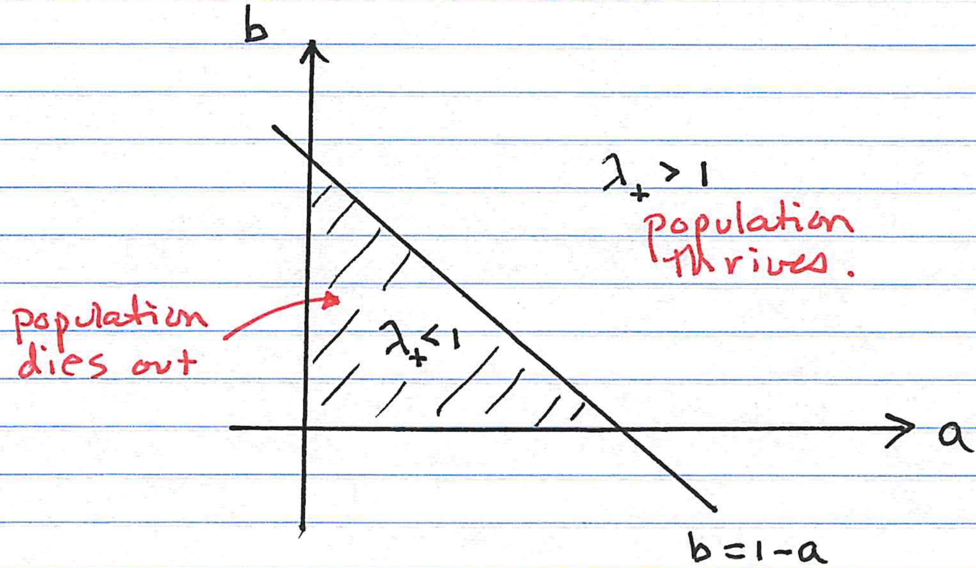
$$\cancel{a^2} + 4b < 4 - 4a + \cancel{a^2}$$

$$4b < 4 - 4a$$

Conclude $\lambda_+ < 1$ only if

$$b < 1 - a$$

* For all other (a, b) positive $\lambda_+ > 1$



Survival $\lambda_+ > 1$

Given the definitions for (a, b)

$$a = \alpha \gamma \sigma$$

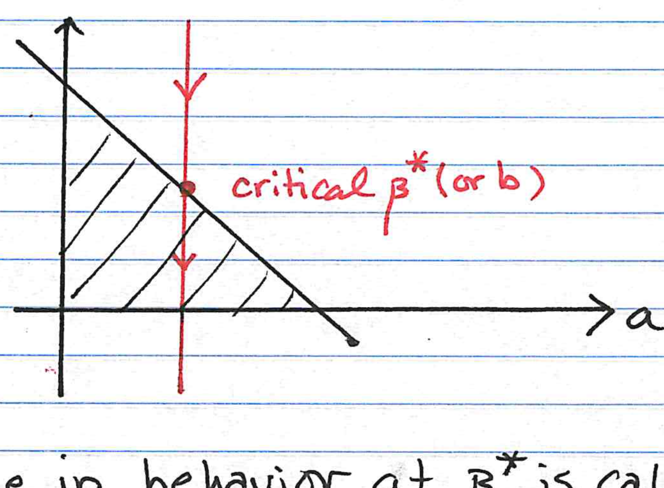
$$b = \beta \sigma^2 (1-\alpha)\gamma$$

the condition $b > 1 - a$ is equivalent to

$$(3) \qquad \boxed{\gamma > \frac{1}{\alpha\sigma + \beta\sigma^2(1-\alpha)}}$$

Decreasing β (2nd yr seeds)

Note only b of (a, b) contains "β".
Decreasing β in (a,b)-plane with
other parameters fixed



The change in behavior at β^* is called
a <u>bifurcation</u>

Approximations

Condition (3) is hard to understand.
But, when

$$(4) \qquad \varepsilon \equiv \frac{\beta}{\alpha} \ll 1$$

is small, an approximation can be derived.
Using (4) in (3)

$$\gamma > \frac{1}{\alpha\sigma\left(1 + \varepsilon\sigma(1-\alpha)\right)}$$

$$\gamma > \frac{1}{\alpha\sigma} f(\varepsilon)$$

which has a Taylor Series approximation

$$\gamma > \frac{1}{\alpha\sigma}\left(\underbrace{f(0)}_{1} + \underbrace{\varepsilon f'(0)}_{\text{small}} + \underbrace{O(\varepsilon^2)}_{\text{smaller}} \right)$$

The first term yields

$$\boxed{\gamma > \frac{1}{\alpha\sigma} \qquad \text{if} \quad \beta \ll \alpha}$$

Problem 2: A Schematic Model of Red Blood Cell Production

The following problem[5] deals with the number of red blood cells (RBCs) circulating in the blood. Here we will present it as a discrete problem to be modeled by difference equations, though a different approach is clearly possible.

In the circulatory system, the red blood cells (RBCs) are constantly being destroyed and replaced. Since these cells carry oxygen throughout the body, their number must be maintained at some fixed level. Assume that the spleen filters out and destroys a certain fraction of the cells daily and that the bone marrow produces a number proportional to the number lost on the previous day. What would be the cell count on the nth day?

To approach this problem, consider defining the following quantities:

$$\begin{aligned} R_n &= \text{number of RBCs in circulation on day } n, \\ M_n &= \text{number of RBCs produced by marrow on day } n, \\ f &= \text{fraction RBCs removed by spleen}, \\ \gamma &= \text{production constant (number produced per number lost)}. \end{aligned}$$

It follows that equations for R_n and M_n are

$$\begin{aligned} R_{n+1} &= (1-f)R_n + M_n, \\ M_{n+1} &= \gamma f R_n. \end{aligned} \tag{47}$$

Problem 16 discusses this model. By solving the equations it can be shown that the only way to maintain a nearly constant cell count is to assume that $\gamma = 1$. Moreover, it transpires that the delayed response of the marrow leads to some fluctuations in the red cell population.

As in problem 2, we apply a discrete approach to a physiological situation in which a somewhat more accurate description might be that of an underlying continuous process with a time delay. (Aside from practice at formulating the equations of a discrete model, this will provide a further example of difference equations analysis.)