Algebraic and Discrete Methods in Biology

Nikolaj Popov

Research Institute for Symbolic Computation
popov@risc.uni-linz.ac.at

Difference Equations II

Difference Equations

- Equations defined by a recursive relation are commonly called *difference equations*.

$$F_n = F_{n-1} + F_{n-2}$$

Propagation of Annual Plants

- Annual plants produce seeds at the end of a summer. The flowering plants wilt and die, leaving their progeny in the seeds that must survive a winter to give rise to a new generation.
- The following spring a certain fraction of these seeds germinate. Some seeds might remain passive for a year or more before reviving.
- Others might be lost due to disease or weather.

Propagation of Annual Plants

- But in order for the plants to survive as a species, a sufficiently large population must be renewed from year to year.
- We formulate a model to describe the propagation of annual plants. Complicating the problem is the fact that annual plants produce seeds that may stay passive for several years before germinating.

Propagation of Annual Plants

- Stage 1: Statement of the Problem

  Plants produce seeds at the end of their growth season (say August), after which they die.

  A fraction of these seeds survive the winter, and some of these germinate at the beginning of the season (say May), giving rise to the new generation of plants.

  The fraction that germinates depends on the age of the seeds.

Propagation of Annual Plants

- Stage 2: Definitions and Assumptions

  We first collect all the parameters and constants specified in the problem.

  Next we define the variables.

Propagation of Annual Plants

- Parameters:

γ – number of seeds produced per plant in August,

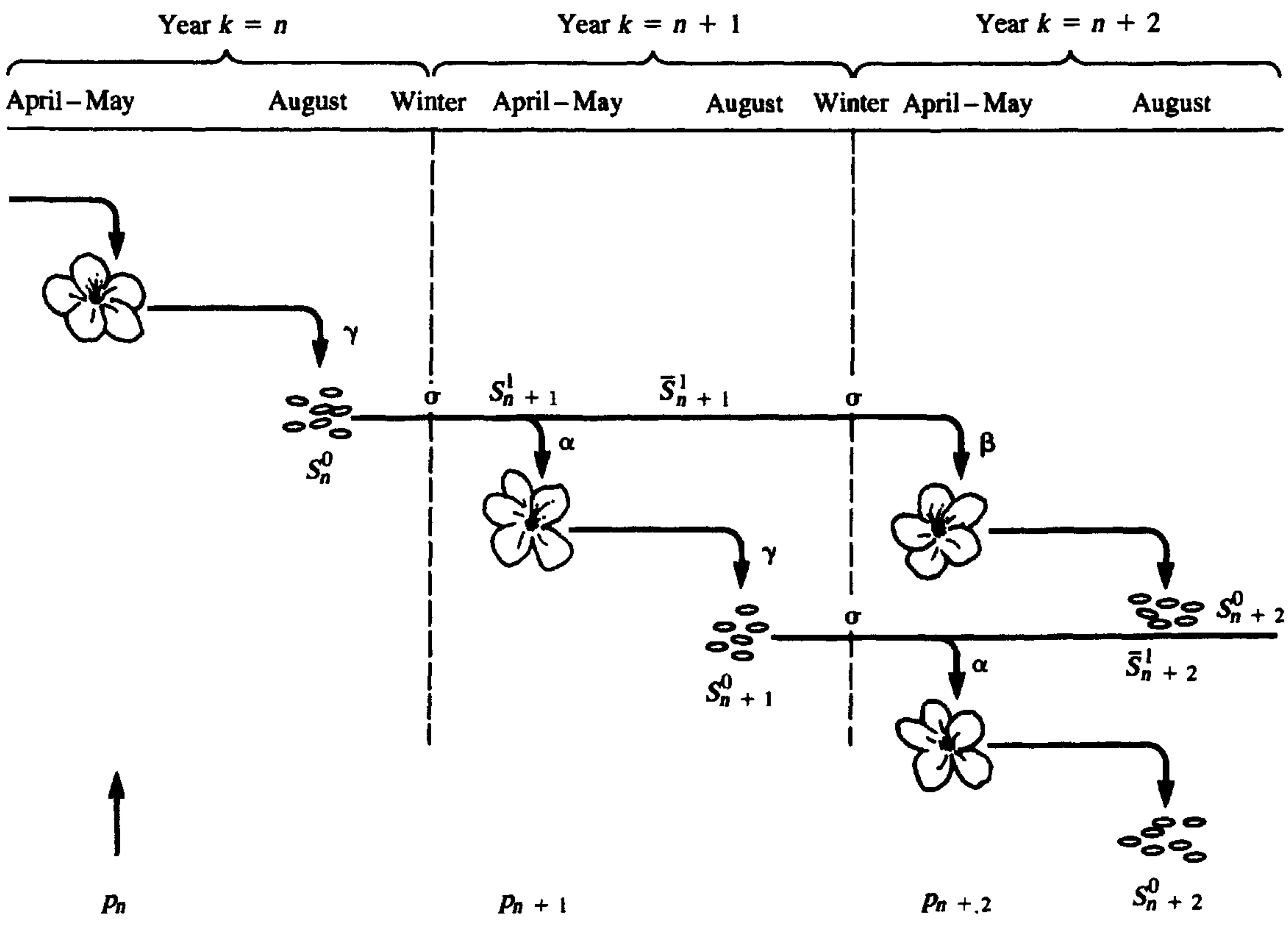
α – fraction of one-year-old seeds that germinate in May,

β – fraction of two-year-old seeds that germinate in May,

σ – fraction of seeds that survive a given winter.

Seeds older than two years are no longer alive and can be neglected.

Propagation of Annual Plants



Propagation of Annual Plants

Keep track of the various quantities by defining:

- p_n – number of plants in generation n,
- $S_{1,n}$ – number of one-year-old seeds in April
- $S_{2,n}$ – number of two-year-old seeds in April
- $\hat{S}_{1,n}$ – number of one-year-old seeds left in May
- $\hat{S}_{2,n}$ – number of two-year-old seeds left in May
- $S_{0,n}$ – number of new seeds produced in August.

Propagation of Annual Plants

Stage 3: The Equations:

In May, a fraction of α one-year-old and β of two-year-old seeds produce the plants.

Thus $p_n =$ (plants from one-year-old seeds) + + (plants from two-year-old seeds)

$$p_n = \alpha S_{1,n} + \beta S_{2,n} \qquad \text{(a)}$$

Propagation of Annual Plants

Stage 3: The Equations:

The seed bank is reduced as a result of this germination. Indeed, for each age class, we have

seeds left = (fraction not germinated) x x (original number of seeds in April)

$$\hat{S}_{1,n} = (1 - \alpha)\, S_{1,n} \qquad \text{(b)}$$

$$\hat{S}_{2,n} = (1 - \beta)\, S_{2,n} \qquad \text{(c)}$$

Propagation of Annual Plants

Stage 3: The Equations:

In August, new (0-year-old) seeds are produced at the rate of γ per plant:

$$S_{0,n} = \gamma\, p_n \qquad \text{(d)}$$

Propagation of Annual Plants

Stage 3: The Equations:

Over the winter the seed bank changes by mortality and aging. Seeds that were new in generation *n* will be one year old in the next generation, *n + 1*. Thus we have:

$S_{1,n+1} = \sigma\, S_{0,n}$ (e)

$S_{2,n+1} = \sigma\, \hat{S}_{1,n}$ (f)

Propagation of Annual Plants

Stage 4: Condensing the Equations:

We now use information from equations (a- f) to recover a set of two equations linking successive plant and seed generations.

We observe that by using equation (d) we can simplify (e) to the following:

$$S_{1,n+1} = \sigma (\gamma p_n) \qquad (10)$$

Propagation of Annual Plants

Stage 4: Condensing the Equations:

Similarly, from equation (b) equation (f) becomes

$$S_{2,n+1} = \sigma\,(1 - \alpha)\,S_{1,n} \qquad (11)$$

Rewriting equation (a) for generation $n + 1$:

$$p_{n+1} = \alpha\,S_{1,n+1} + \beta\,S_{2,n+1} \qquad (12)$$

Propagation of Annual Plants

Stage 4: Condensing the Equations:

Using (10), (11), and (12) we arrive at a system of two equations in which plants and one-year-old seeds are coupled:

$$p_{n+1} = \alpha \sigma \gamma p_n + \beta \sigma (1 - \alpha) S_{1,n} \qquad (13a)$$

$$S_{1,n+1} = \sigma \gamma p_n \qquad (13b)$$

Propagation of Annual Plants

Stage 4: Condensing the Equations:

Notice that it is also possible to eliminate the seed variable altogether by first rewriting equation (13b) as:

$$S_{1,n} = \sigma \gamma p_{n-1} \qquad (14)$$

and then substituting it into equation (13a) to get

$$p_{n+1} = \alpha \sigma \gamma p_n + \beta \sigma^2 (1 - \alpha) \gamma p_{n-1} \qquad (15)$$

Propagation of Annual Plants

Stage 4: Condensing the Equations:

We observe that the model can be formulated in a number of alternative ways, as a system of two first-order equations or as one second-order equation (15).

Equation (15) is linear since no multiples $p_n p_m$ or terms that are nonlinear in p_n occur; it is second order since two previous generations are implicated in determining the present generation.

Propagation of Annual Plants

Stage 4: Check

To be on the safe side, we shall further explore equation (15) by interpreting one of the terms on its right hand side.

Rewriting it for the n-th generation and reading from right to left we see that p_n is given by:

Propagation of Annual Plants

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

seeds produced two years ago

which then survived first winter

and failed to germinate last year

survived last winter

and were among the fraction of two-year-old seeds that germinated

Systems of Linear Difference Equations

- The problem of annual plant reproduction leads to a system of two first-order difference equations (10,13), or equivalently a single second-order equation (15).
- General form:

$$x_{n+1} = a_{1,1}\, x_n + a_{1,2}\, y_n \qquad (16a)$$

$$y_{n+1} = a_{2,1}\, x_n + a_{2,2}\, y_n \qquad (16b)$$

Systems of Linear Difference Equations

- As before, this can be converted to a single higher-order equation.
- Starting with (16a) and using (16b) to eliminate y_{n+1} we have:

$$x_{n+2} = a_{1,1}\ x_{n+1} + a_{1,2}\ y_{n+1} =$$
$$= a_{1,1}\ x_{n+1} + a_{1,2}(a_{2,1}\ x_n + a_{2,2}\ y_n)$$

- And from (16a)

$$a_{1,2}\ y_n = x_{n+1} - a_{1,1}\ x_n$$

Systems of Linear Difference Equations

- Now eliminating y_n we conclude that

$$x_{n+2} = a_{1,1}\, x_{n+1} + a_{1,2}\, a_{2,1}\, x_n + a_{2,2}(x_{n+1} - a_{1,1}\, x_n)$$

that is:

$$x_{n+2} - (a_{1,1} + a_{2,2})\, x_{n+1} + (a_{2,2}\, a_{1,1} - a_{1,2}\, a_{2,1})\, x_n = 0 \qquad (17)$$

Systems of Linear Difference Equations

- Recall what we had when defining the number of cells in each generation with:

$$M_1, M_2, \ldots, M_n$$

- and the equation relating successive generations:

$$M_{n+1} = a\, M_n$$

- we obtained the closed form:

$$M_n = a^n M_0$$

Systems of Linear Difference Equations

- First-order linear difference equations are in general of the form

$$x_n = C\,\lambda^n \qquad (18)$$

- While the notation has been changed slightly, the form is still the same: constant depending on initial conditions times some number raised to the power *n*.
- Could this type of solution work for higher-order linear equations such as (17)?

Systems of Linear Difference Equations

- We proceed to test this idea by substituting the expression $x_n = C\lambda^n$ in the form of

  $x_{n+1} = C\lambda^{n+1}$ and $x_{n+2} = C\lambda^{n+2}$ into (17)

$$C\lambda^{n+2} - (a_{1,1} + a_{2,2})\, C\lambda^{n+1} + (a_{2,2}a_{1,1} - a_{1,2}a_{2,1})\, C\lambda^n = 0$$

- Cancel the common factor $C\lambda^n$

$$\lambda^2 - (a_{1,1} + a_{2,2})\,\lambda + (a_{2,2}a_{1,1} - a_{1,2}a_{2,1}) = 0 \qquad (19)$$

Systems of Linear Difference Equations

- Thus a solution of the form (18) would in fact work, provided that λ satisfies the quadratic equation (19), which is generally called the characteristic equation of (17).

- To simplify notation we label the coefficients appearing in equation (19) :

$$\beta = (a_{1,1} + a_{2,2})$$
$$\gamma = (a_{2,2}\, a_{1,1} - a_{1,2}\, a_{2,1})$$

Systems of Linear Difference Equations

- The solutions to the characteristic equation (there are two of them) are then:

$$\lambda_{1,2} = \frac{\beta \pm \sqrt{\beta^2 - 4\gamma}}{2}$$

- These numbers are called eigenvalues, and their properties will uniquely determine the behavior of solutions to equation (17).

Systems of Linear Difference Equations

- Equation (17) is linear – it contains only scalar multiples of the variables—no quadratic, exponential, or other nonlinear expressions.

- For such equations, the principle of linear superposition holds: *if several different solutions are known, then any linear combination of these is again a solution*.

Systems of Linear Difference Equations

- Since we have just determined that λ_1 and λ_2 are two solutions to (17), we can conclude that a general solution is

$$x_n = A_1 \lambda_1^n + A_2 \lambda_2^n \qquad (22)$$

provided $\lambda_1 \neq \lambda_2$

Systems of Linear Difference Equations

- This involves two arbitrary scalars, A_1 and A_2, whose values are not specified by the difference equation (17) itself. They depend on separate constraints, such as particular known values attained by x.

- Note that specifying any two x values uniquely determines A_1 and A_2.

Systems of Linear Difference Equations

- Most commonly, x_0 and x_1, the levels of a population in the first two successive generations, are given as initial conditions.

- A_1 and A_2 are determined by solving the two resulting linear algebraic equations.

Will Plants Be Successful?

- The central question that the model should resolve is how many seeds a given plant should produce in order to ensure survival of the species.

Will Plants Be Successful?

- To simplify notation, let
  $a = \alpha \sigma \gamma$ and $b = \beta \sigma^2 (1 - \alpha) \gamma$
- Then the equation (15)
  $p_{n+1} = \alpha \sigma \gamma p_n + \beta \sigma^2 (1 - \alpha) \gamma p_{n-1}$
  becomes
  $p_{n+1} - a p_n - b p_{n-1} = 0$
  with characteristic equation
  $\lambda^2 - a \lambda - b = 0$

Will Plants Be Successful?

- Eigenvalues are:

$$\lambda_{1,2} = \frac{1}{2}(a \pm \sqrt{a^2 + 4b})$$

$$= \frac{\sigma\gamma\alpha}{2}(1 \pm \sqrt{1 + \delta})$$

where $\delta = \frac{4\beta(1 - \alpha)}{\gamma\alpha^2} = \frac{4}{\gamma}\frac{\beta}{\alpha}\left(\frac{1}{\alpha} - 1\right)$

is a positive quantity since $\alpha < 1$

Will Plants Be Successful?

- We arrived at a rather complicated expression for the eigenvalues. The following rough approximation will give us an estimate of their magnitudes.

- Initially we consider a special case. Suppose few two-year-old seeds germinate in comparison with the one-year-old seeds. Then β/α is very small, making δ small relative to 1.

Will Plants Be Successful?

- This means that at the very least, the positive eigenvalue λ_1 has magnitude

$$\lambda_1 \approx \frac{\sigma\gamma\alpha}{2}(1 + \sqrt{1}) = 2\,\frac{\sigma\gamma\alpha}{2} = \sigma\gamma\alpha$$

- Thus, to ensure propagation we need the following conditions:

$$\lambda_1 > 0\,, \quad \sigma\gamma\alpha > 1\,, \quad \gamma > 1/\sigma\alpha$$

Will Plants Be Successful?

- By this reasoning we may conclude that the population will grow if the number of seeds per plant is greater than $1/\sigma\alpha$.

- To give some biological meaning to this inequality, we observe that the quantity $\sigma\gamma\alpha$ represents the number of seeds produced by a given plant that actually survive and germinate the following year.

Conclusions

Linear difference equations find applications in

- Population growth
- Cell division
- An insect population
- Propagation of annual plants
- Growth of segmental organisms
- Schematic model of red blood cell production

Conclusions

Models based on linear difference equations are very convenient for performing computations – they are recursive programs.