# COMPUTER SIMULATION IN BIOLOGY

## A BASIC Introduction

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## 13.2 Block Diagrams and Compartment Models

Block diagrams are useful conceptual tools for developing simulations of flow, with each component of the system represented by a rectangular block. The blocks are connected by arrows showing flow of energy or material between components, or between components and the environment. The system may include all biological components of a community, or only a portion, depending upon the modeler's definition of the system. Once the system has been defined, everything else is "environment". Inputs to the system are termed driving or forcing functions. Figure 13.2 is an example of a block diagram.

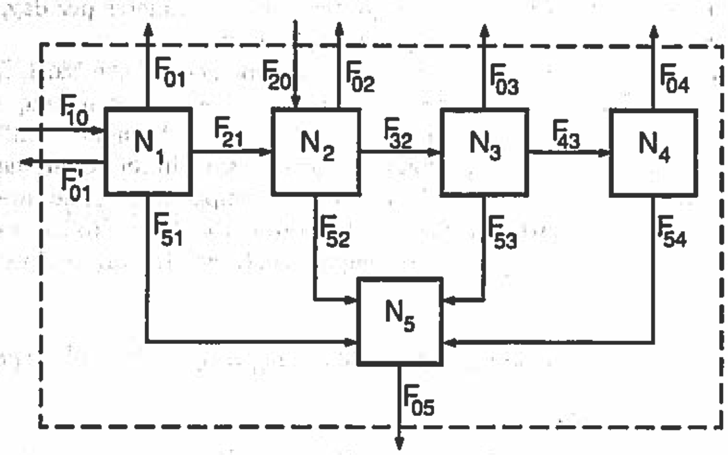


Figure 13.2. A simple block diagram of the Silver Springs energy flow compartmental model, modified from Patten (1971).

The blocks within a diagram may be defined with words. However, letters with subscripts to designate compartments, $N_1$ and $N_2$ for example, are more convenient because they may be used directly in writing computer programs. Between compartments, the flows $F_{12}$, $F_{32}$, etc., will have subscripts indicating receiving and donating blocks. Conventionally, a subscript of 0 indicates the environment. In this book, the first number in the subscript of a flow will represent the receiving compartment, and the second the source compartment. You should be aware that this subscript order may be reversed by different modelers working in different biological fields. No standardization exists.

In the Silver Springs model (Figure 13.2), $N_1$ = producers, $N_2$ = herbivores, $N_3$ = carnivores, $N_4$ = top carnivores, and $N_5$ = decomposers. $F_{10}$ and $F_{20}$ are the two driving flows from the environment. $F_{01}$, $F_{02}$, $F_{03}$,

$F_{04}$ and $F_{05}$ represent respiratory losses to the environment from the system. $F'_{01}$ represents the physical loss of plant biomass carried downstream and out of the system by water currents.

Under steady-state conditions, the sum of system inputs, $F_{10}$ and $F_{20}$, must equal the sum of the system outputs, $F_{01}$, $F_{02}$, $F_{03}$, $F_{04}$, $F_{05}$ and $F'_{01}$. Also at steady state, the sum of the inputs to any block must equal the sum of outputs from that block.

The units for the blocks will depend on the system. Usually they express mass or energy on the basis of volume or area. Typical units might be grams of dry weight per square meter, grams of organic carbon per cubic meter, or kilocalories per square meter. The flows will use the same units together with units of time, such as grams per square meter per day, or grams of organic carbon per square meter per year.

A compartmental model is a more formal statement of the block diagram, and includes the equations describing the flows between compartments. Sheppard (1948) apparently was the first to use "compartment" in this sense (Godfrey 1983). The flows or fluxes are used in the equations to provide an energy or material balance for each compartment. The rate of change for each compartment is found by adding the flows into the compartment and the flows out of the compartment. For the Silver Springs model these are

$$\frac{dN_1}{dt} = F_{10} - F_{21} - F_{01} - F_{51} - F'_{01} \tag{13.1}$$

$$\frac{dN_2}{dt} = F_{21} + F_{20} - F_{02} - F_{32} - F_{52} \tag{13.2}$$

$$\frac{dN_3}{dt} = F_{32} - F_{43} - F_{03} - F_{53} \tag{13.3}$$

$$\frac{dN_4}{dt} = F_{43} - F_{04} - F_{54} \tag{13.4}$$

$$\frac{dN_5}{dt} = F_{51} + F_{52} + F_{53} + F_{54} - F_{05} \tag{13.5}$$

Each flow is defined by an equation which usually involves a rate coefficient. We will designate the rate coefficients as $f_{ij}$. A large number of equations could be used to model flow between compartments, but only a few useful equations are encountered frequently. Some of these are described in Table 13.1. A variety of other examples may be found in Godfrey (1983).

| | |
|---|---|
| $F_{ij} = k$ | Flow from compartment $j$ to $i$ is constant, and is independent of time and system state. |
| $F_{ij} = f_{ij}N_j$ | Flow to $i$ is proportional to the content of $j$. This is a linear equation with control by the donor compartment only, with rate constant $f_{ij}$. |
| $F_{ij} = f_{ij}N_i$ | Flow to $i$ is proportional to the content of $i$. This is a linear equation describing control of flow by the receptor compartment. |
| $F_{ij} = f_{ij}N_iN_j$ | Flow to $i$ is controlled by both donor and receptor compartments in a cross-product manner. This is the mass-action approach. The equation is nonlinear. |
| $F_{ij} = f_{ij} \cdot f(\text{time})$ | Flow from $j$ to $i$ is a function of time. An example is a sine function (Equation 11.2). |
| $F_{ij} = f_{ij}N_i(1 - g_{ij}N_i)$ | Flow from $j$ to $i$ is controlled by a positive linear term and a negative non-linear term, much like the logistic equation. |
| $F_{ij} = \dfrac{f_{ij}N_i}{K + N_i}$ | Flow from $j$ to $i$ is limited with a hyperbolic term as in Michaelis-Menten kinetics. |

Table 13.1. Some useful equations for describing flow between compartments. $F_{ij}$ is the instantaneous flow to compartment $i$ from compartment $j$, and $f_{ij}$ is the rate coefficient. $N_i$ indicates the content of compartment $i$.

Compartment models of the type described here are often implemented on computers by solving the system of equations with matrix algebra. This method will be discussed in Chapter 16. For the present, we will solve the equations with a direct approach. Because most of the equations of flow are functions of the size of the compartments, it is necessary to use the two-stage numerical approach with Euler integration. For clarity of programming, the first stage should be separated into two parts as described in Section 6.2. That is, the various flows $F$ will all be calculated, and then the net changes of content for each compartment will be determined to complete the first stage. Then, following the usual second stage procedures, values of the compartments will be updated.

## 13.3 The Silver Springs Model

We will continue working with the Silver Springs model as an example. It is not better than similar and more recent models. However, it is familiar and relatively uncomplicated, and it still appears in general ecology textbooks. The set of equations given in this section define the flows in the block diagram of Figure 13.2, and have been modified from Odum (1957) and Patten (1971):

(A. Forcing:)

$$F_{10} = M + R\sin\left(2\pi\frac{(T-11)}{52}\right)$$

$$F_{20} = k$$

$F_{10}$ is the energy input from photosynthesis, assumed to be proportional to light intensity. $M$ is the annual mean photosynthesis, and $R$ is the range of the annual fluctuation around the mean. $F_{20}$ is the energy in 70 loaves of bread fed daily to catfish by the tourist concession at the springs.

(B. Feeding:)

$$F_{21} = \tau_{21}N_1$$

$$F_{32} = \tau_{32}N_2$$

$$F_{43} = \tau_{43}N_3$$

Feeding is donor-dependent in this system, with $\tau_{ij}$ the linear coefficient having units of inverse weeks ($\mathrm{wk}^{-1}$).

(C. Mortality:)

$$F_{51} = \mu_{51}N_1$$

$$F_{52} = \mu_{52}N_2$$

$$F_{53} = \mu_{53}N_3$$

$$F_{54} = \mu_{54}N_4$$

Here $\mu_{ij}$ is a coefficient of donor-dependent mortality, with units of $\mathrm{wk}^{-1}$.

(D. Respiration:)

$$F_{01} = \rho_{01} N_1$$

$$F_{02} = \rho_{02} N_2$$

$$F_{03} = \rho_{03} N_3$$

$$F_{04} = \rho_{04} N_4$$

$$F_{05} = \rho_{05} N_5$$

Here $\rho_{ij}$ is a coefficient of donor-dependent respiration, with units of $\mathrm{wk}^{-1}$.

(E. Export:)

$$F'_{01} = \lambda_{01} N_1$$

$\lambda_{01}$ is a coefficient of the loss downstream of small plants and pieces of plants that break loose from the plants that grow in the Silver Spring system. The coefficient has units of $\mathrm{wk}^{-1}$.

After the $F_{ij}$ values are calculated with the equations given above, the first stage in the two-stage Euler procedure is completed with the calculation of the $\Delta N_i$ values:

$$\Delta N_1 = (F_{10} - F_{21} - F_{51} - F_{01} - F'_{01})\,\Delta t$$

$$\Delta N_2 = (F_{20} + F_{21} - F_{32} - F_{52} - F_{02})\,\Delta t$$

$$\Delta N_3 = (F_{32} - F_{43} - F_{53} - F_{03})\,\Delta t$$

$$\Delta N_4 = (F_{43} - F_{54} - F_{04})\,\Delta t$$

$$\Delta N_5 = (F_{51} + F_{52} + F_{53} + F_{54} - F_{05})\,\Delta t$$

The second stage of the Euler integration is completed as usual, with

$$N_i \longleftarrow N_i + \Delta N_i$$

**Exercise 13-1:** Write and implement a program to simulate energy flow through Silver Springs using the model equations above. For the various compartment sizes and flows, use values given below derived from Odum (1957). The values of mean annual standing crop given in Figure 13.1 (units of kcal $m^{-2}$) are suitable for initial compartment sizes:

$N_1 = 2635 \quad N_2 = 213 \quad N_3 = 62 \quad N_4 = 9 \quad N_5 = 25$

The values of rate coefficients (units of $yr^{-1}$) can be calculated by inserting yearly values for the flows and for standing crops into the flow equations for mortality, feeding, respiration and export. This process yields coefficients as follows:

$\mu_{51} = 1.310 \quad \mu_{52} = 5.141 \quad \mu_{53} = 0.742 \quad \mu_{54} = 0.889$
$\tau_{21} = 1.094 \quad \tau_{32} = 1.798 \quad \tau_{43} = 0.339$
$\rho_{01} = 4.545 \quad \rho_{02} = 8.873 \quad \rho_{03} = 5.097 \quad \rho_{04} = 1.444$
$\rho_{05} = 184.0 \quad \lambda_{01} = 0.94$

For the driving functions, use the following values:

$$k = 486 \text{ kcal m}^{-2} \text{ yr}^{-1} \qquad R = 175 \text{ kcal m}^{-2} \text{ wk}^{-1}$$
$$M = 400 \text{ kcal m}^{-2} \text{ wk}^{-1}$$

Most of the rate coefficients above are based on annual flows through the system; weekly values may be found with division by 52. Use weeks as the time unit for your simulation, with $\Delta t = 0.1$ week as the unit for Euler integration. Larger $\Delta t$ values will produce unstable results.

Write your program to plot the contents of each compartment for each week, including initial values. Your output will be a graph with five separate lines, each showing the content of a model compartment.

After you have entered the program into your computer, make an initial trial run, setting $R = 0$. This procedure will keep $F_{10}$ constant. The system should tend rapidly to a steady-state condition. If it does not, then check your program for errors.

After this initial check, carry out a 3-year simulation, beginning with the first week in January. Set $R = 175$ kcal $m^{-2}$ $wk^{-1}$.

**Exercise 13-2:** A crude simulation of ecological succession may be obtained with the model above by setting the solar input to a constant value ($R = 0$) and reducing the starting size of all compartments to some minimum value (such as 5 kcal $m^{-2}$). Allow the simulation of the system to proceed for about 150 weeks to stabilize. Again use $\Delta t = 0.1$ week.

**Exercise 13-3:** Modify the Silver Springs model above by employing nonlinear feeding equations as follows:

$$F_{21} = \tau'_{21} N_1 N_2$$

$$F_{32} = \tau'_{32} N_2 N_3$$

$$F_{43} = \tau'_{43} N_3 N_4$$

Numerical values for the coefficients may be found by inserting the values for flows and standing crop sizes (Figure 13.1) and solving. This produces the following values for the coefficients:

$$\tau'_{21} = 0.00513 \qquad \tau'_{32} = 0.0290 \qquad \tau'_{43} = 0.0376$$ ...per yr

As in Exercise 13-1, run the simulation for a 3-year period, plotting the energy content of the five compartments. The larger excursions of the compartment contents produced by the nonlinear flows should be apparent.

## 13.4 Global Carbon-Cycle Model

The increased concentration of carbon dioxide that has been measured in the earth's atmosphere has caused concerns about global warming. There exist real controversies on the relative roles of burning fossil fuels and clearing tropical forests in producing the increase. The relative ability of terrestrial plants and the oceans to serve as reservoirs for the increase in carbon is also controversial. Complex compartmental models are important tools in working with analysis and prediction of the carbon cycle. Bolin (1981) has outlined a simple model of the carbon cycle that shows many of the expected characteristics of the cycle. We will use a modified version of this model as an introduction to the important subject of carbon cycle modeling, and as a further illustration of ecological compartment models.

In this model, carbon is distributed among seven compartments (Figure 13.3). The principal pool of the atmosphere can exchange carbon with both oceanic and terrestrial components. The oceans are represented by only two compartments, one for the mixed layers near the surface that come into contact with the atmosphere, and another for the deeper, more