THE RESPONSE OF THE BALSAM FIR FOREST TO A SPRUCE BUDWORM INVASION: A SIMPLE DYNAMICAL MODEL

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Foreword

In this research, a simple model of forest insect pest outbreaks is successfully tested with data obtained from the North American eastern spruce budworm forest system. The study is a collaborative effort amongst three scientists: Dr. R.A. Fleming, a Canadian forest pest modeller who visited IIASA in July 1987; Prof. M. Antonovsky, Chief Scientist of the IIASA Environment Program; and Dr. Y. Kuznetsov, one of the 1986 Peccei Award winners who returned to IIASA in the summer of 1987 to take up his Award. In this connection, IIASA has again demonstrated the important role that it plays as a facilitator of fruitful collaboration amongst scientists from the East and from the West.

R.E. Munn
Head, Environment Program

Abstract

The parameter values of a simple dynamical model of a non-even age forest-insect ecosystem are estimated for the case of balsam fir forests and the eastern spruce budworm. It is shown that, despite its extreme simplicity, the model can reproduce time series of a real budworm outbreak and can be considered a compact presentation of available forest data.

Strengths and weaknesses of the model are discussed and some directions for further research proposed.

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INTRODUCTION

In the paper of Antonovsky, Clark and Kuznetsov (1987) the following system of differential equations was proposed to describe non-even age forest-insect dynamics:

$$\begin{aligned} \dot{x} &= \rho y - \gamma(y)x - fx \\ \dot{y} &= fx - hy - Ayz \\ \dot{z} &= -\varepsilon z + Byz \end{aligned} \tag{1}$$

where x and y are densities of "young" and "old" tree (i.e., numbers of trees per square unit), z is insect density. Parameter ρ is reproductivity of the trees; h and f are death and aging rates. The function $\gamma(y)$ represents a dependence of "young" tree mortality on the density of "old" trees. It is supposed that some optimal value of "old" tree density exists for which "young" trees survive most successfully. In this case it is possible to choose $\gamma(y) = a(y-b)^2 + c$. Parameter ε is a rate of natural mortality of pests. Term $-Ayz$ describes pest-induced mortality of "old" trees, while term Byz corresponds to insect density growth due to old tree destruction.

In addition to model (1), the paper of Antonovsky, Clark and Kuznetsov (1987) deals with a model in which the pest attacks "young" trees. Actually, the paper mainly addressed the detailed analysis of this situation. In the present paper we study only model (1), but attempt to estimate their parameter values for the case of balsam fir forests in Canada where old trees are vulnerable to budworm.

PROPERTIES OF EQUATION (1)

By a linear change of variables, parameters and time, system (1) can be transformed into the form:

$$\begin{aligned} \dot{x} &= \rho y - (y-1)^2 x - sx \\ \dot{y} &= x - hy - yz \\ \dot{z} &= -\varepsilon z + Bxz , \end{aligned} \tag{2}$$

where the previous notations are preserved for new variables and parameters. For example, the new parameters can be presented in terms of the old ones as:

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$$\rho := \frac{f\rho}{a^2b^4}, \; s := \frac{(f+c)}{ab^2}, \; h := \frac{h}{ab^2},$$
$$\varepsilon := \frac{\varepsilon}{ab^2}, \; B := \frac{B}{ab}.$$

The system can have from one to four nonnegative equilibria:

$$E_0 = (0,0,0), E_{1,2} = (x_{1,2}, y_{1,2}, 0), E_3 = (x_3, y_3, z_3).$$

Equilibria $E_{1,2}$ in the invariant plane $z = 0$ have coordinates

$$y_{1,2} = 1 \pm (\frac{\rho}{h} - s)^{1/2}, \; x_{1,2} = hy_{1,2}\,.$$

and appear on line $D_1 = \{(\rho,h) : \rho = sh\}$.

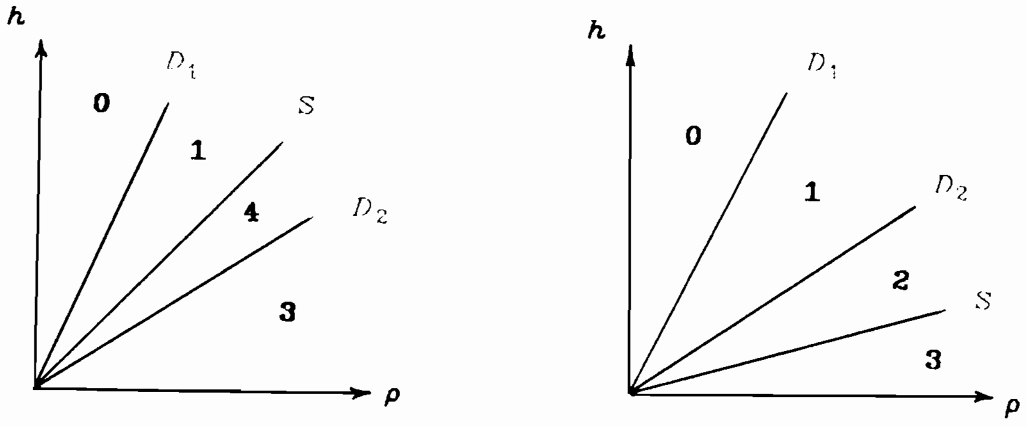
On line $D_2 = \{(\rho,h) : \rho = (s+1)h\}$ equilibrium E_1 coalesces together with equilibrium E_0 and becomes negative.

Equilibrium $E_3 = (\frac{\rho\varepsilon B}{(\varepsilon-B)^2+sB^2}, \frac{\varepsilon}{B}, \frac{\rho B^2}{(\varepsilon-B)^2+sB^2} - h)$

appears below line $S = \{(\rho,h) : h = \frac{\rho B^2}{(\varepsilon-B)^2+sB^2}\}$.

Equilibrium E_3 is always stable, but it could have either real or complex eigenvalues. Thus the character of the approach to E_3 by the system could be either monotonic or oscillatory.

The parametric portrait of system (2) is shown in Figure 1. It depends on the ε to B ratio. Corresponding phase portraits are presented in Figure 2.



$\varepsilon < 2B$ $\qquad$ $\varepsilon > 2B$

Figure 1: The parametric portraits of equation (2).

Let us consider in more detail the system behaviour in parameter region **3** where damped oscillations are possible. In the absence of pests (i.e. $z = 0$) the system tends to equilibria E_2 with constant densities of "young" and "old" trees. If a small number of pests then invades the forest, an outbreak occurs and the system moves to equilibria E_3 with lower tree densities and a low density insect popula-

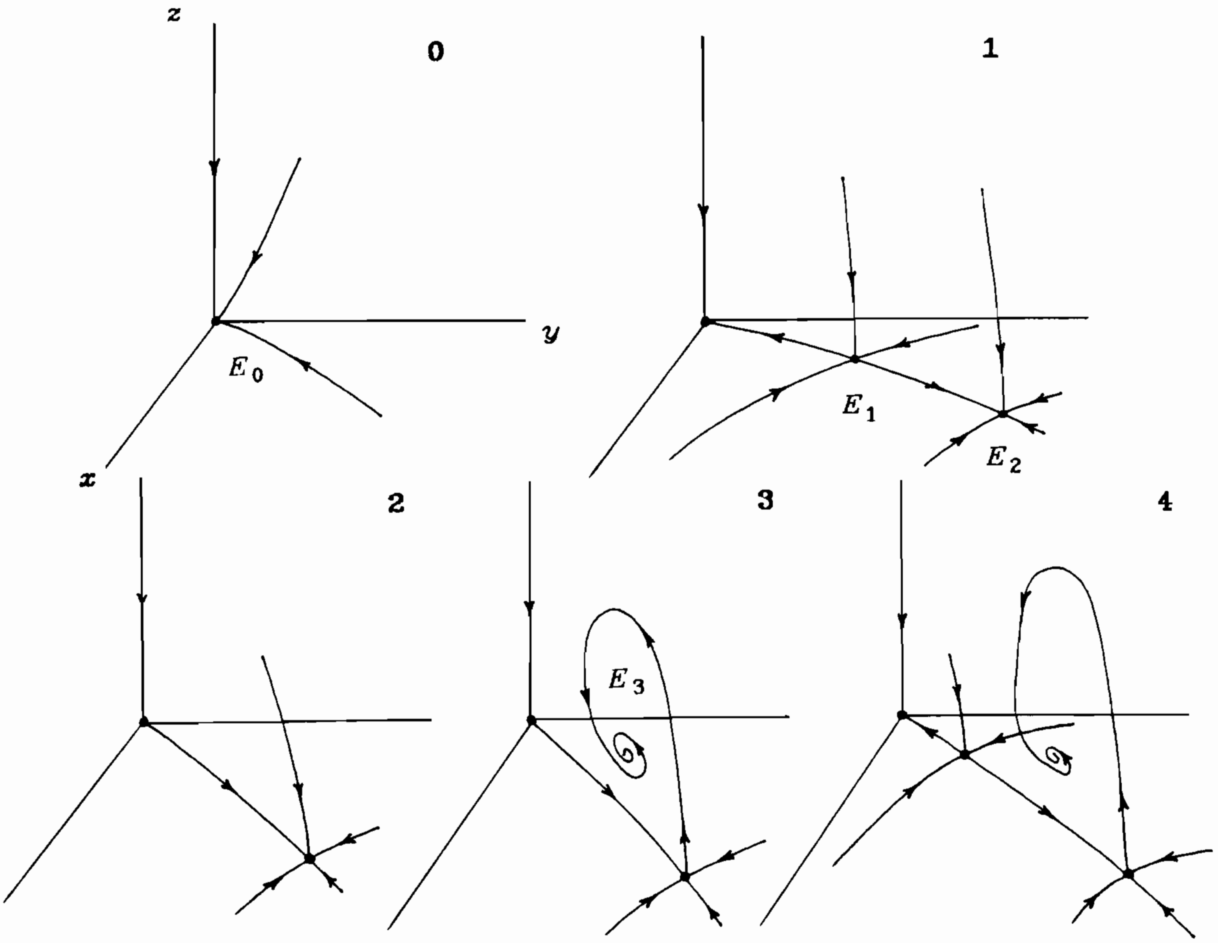


Figure 2: The phase portraits of system (2).

tion. The maximum insect density reached during the outbreak exceeds that of equilibrium E_3.

A potentially unexpected system behaviour can occur if the system is at equilibrium E_3 but the pest density then declines, perhaps due to pest control operations, epidemic disease, or random variation. As can be seen in Figure 3, a new pest outbreak results. Therefore, random declines in pest density may result in repeated outbreaks.

PARAMETER ESTIMATIONS

Our goal here is to demonstrate how the model might be applied to a real forest-pest ecosystem. This could lead to insight about the dynamics of the ecosystem or to a determination of the range of applicability of the model for describing the ecosystem's dynamics.

The eastern spruce budworm-forest system was picked as an appropriate candidate because of the availability of suitable information for many parts of the model, because of the similarity of the main model features with some key aspects of the budworm-forest system, and because previous models (e.g., Jones 1979, Stedinger 1984) of the budworm-forest system have emphasized different elements

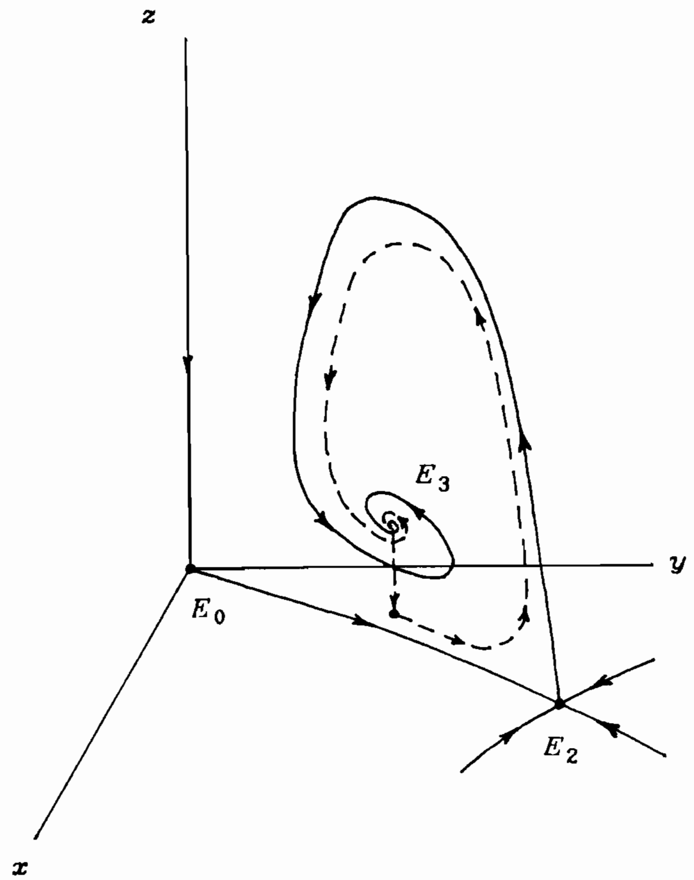


Figure 3: A small decrease in the pest density may result in an insect population outbreak.

(e.g., foliage, insect predators, insect dispersal) of this system.

The eastern spruce budworm, ***Choristoneura fumiferana*** (Clem.), is a naturally occurring defoliator of balsam fir *(Abies balsamea* [L.] Mill.) in the boreal forests of eastern North America. Outbreaking populations kill their host trees over wide areas. Outbreak cycles range from 26-40 years in length with outbreaks lasting for 6-15 years. During outbreaks, insect numbers can increase over four orders of magnitude in stands of mature and overmature balsam fir which are particularly vulnerable to attack.

In accordance with the simplistic nature of the model, which reduces the complex budworm-forest system to a system of three differential equations, we take a "broad brush" approach to parameter estimation. First we identify realistic ranges for the parameter values and then we select from the range to see how well the model can simulate the behaviour of the ecosystem.

We begin by estimating h, the natural mortality rate of old trees in equation (1). MacLean (1985) gives the "annual net probability of natural mortality (before outbreak)" as 1-3.8% for balsam fir. Hence, if n_a is the number of trees in a cohort of old trees of age a, then $n_{a+1} = n_a e^{-h}$, and $.01 \leq \frac{n_a - n_{a+1}}{n_a} \leq .038$.

Hence $$.01 \leq h \leq .04 \ yr^{-1} . \qquad (3)$$

The parameter f represents the aging of trees in the model. However, depending on how one defines "old" trees, f can take on different values. For instance, Bakuzis and Hansen (1965) report that balsam fir reaches sexual maturity at 30-35 years; becomes moderately susceptible to attack at over 40 years of age and becomes very susceptible at over 60 years of age. Moreover, stands are generally 40-60 years of age when established seedlings first appear. Thus we assume that trees spend a mean duration of 30-70 years in the physiologically young age group. If this duration has an exponential distribution with a mean of 30-70 years, then

$$1/70 \leq f \leq 1/30$$

or

$$.014 \leq f \leq .033 \; yr^{-1} . \tag{4}$$

The function $\gamma(y)$ describes the dependence of the natural mortality of young trees on y, the density of old trees. MacLean (1985) suggests that natural tree mortality might fall in the range .01 - .04 per year. Hence, since c = minimum of $\gamma(y)$, we approximate

$$c = .01 \; yr^{-1} . \tag{5}$$

The increased mortality at low y (old tree density) could be ascribed to competition with ferns, shrubs, and hardwoods (Bakuzis and Hansen 1965) invading sites opened up by the removal of the fir overstory. Competition with older trees accounts for the increase in young tree mortality at large y. Assuming that the interspecific competition is much less detrimental than the suppression by the older age group, then $b \ll y_{\max}$.

$$\begin{aligned} \text{Taking} \quad y_{\max} &\simeq 1 \; (\textit{in units of } 10^3 \textit{ trees / acre}) \\ &\approx 2.471 \; (\textit{in units of } 10^3 \textit{ trees / ha}) , \end{aligned}$$

indicating a fairly good site (Bakuzis and Hansen, 1965, Table 90), we arbitrarily set

$$\begin{aligned} b &\simeq .1 \times y_{\max} \simeq .1 \quad 10^3 \textit{ trees acre}^{-1} \\ &\approx .2471 \; (\textit{in units of } 10^3/ha) . \end{aligned} \tag{6}$$

Then, since $\gamma(y_{\max}) \simeq .4$ (MacLean 1985),

$$\gamma_{\max} = a\,(y_{\max} - b)^2 + c \simeq .04$$

Substituting with (5), (6), and then solving for a,

$$\begin{aligned} a &= .037 \; acre^2 \, (10^3 \; trees)^{-2} \, yr^{-1} \\ &= .00606 \; ha^2 (10^3 \; trees)^{-2} \, yr^{-1} . \end{aligned} \tag{7}$$

At this point we have estimates for all the parameters of the forest section of the model (1) except ρ, the rate of production of seedlings. This parameter combines fertility, germination rate, and survivorship well past the first year of life (i.e., into the middle of the range of ages of the 'young' age group). Hence, it is a difficult parameter to estimate.

Our approach is to solve the system (1) for ρ using reasonable x and y values for the equilibrium without pests. For instance, $\dot{y} = 0$ in system (1) with $z = 0$ when $x = yh/f$. From $y_{\max} \simeq 2.471$, and from Bakuzis and Hansen (1965, Table 90) the corresponding value of x lies in the range 4.94 - 7.42 10^3 trees/ha. Hence, if we choose $f = .017\ yr^{-1}$ say (after equation (4)) and $h = .04\ yr^{-1}$ after (3), then the value of x at the upper equilibrium (E_2 in Fig.2) is approximately

$$x_{\max} = 5.81\ 10^3\ trees\,/\,ha.$$

Since this is a reasonable value of $x_{\max}$ (Bakuzis and Hansen 1965 Table 90) we adopt

$$f = .017\ yr^{-1} \tag{8}$$

and

$$h = .04\ yr^{-1} \tag{9}$$

as reasonable initial guesses for these parameters.

For a forest equilibrium to occur near $(x_{\max}, y_{\max}) \simeq (5.81, 2.47)$ requires that the first equation in system (1) with $z = 0$ also meet equilibrium conditions at this point. Therefore, using (5), (6), (7) and (8)

$$\rho = .134\ yr^{-1}\,. \tag{10}$$

This completes the estimation of parameters for the forest section of the model and leaves only the parameters ε, A and B to be estimated. These three parameters represent the natural pest mortality and the interaction between the forest and the pest.

First we estimate ε, the instantaneous rate of pest mortality. After an outbreak there are often few mature and overmature balsam fir trees left. Hence, we assume y is small after an outbreak, so the pest equation in model (1) becomes approximately $\dot{z} \simeq -\varepsilon z$. This equation has the solution $z_{t+1}/z_t \simeq e^{-\varepsilon}$. Thus, after comparison it can be seen that ε corresponds to the negative part of the vertical axis of Royama's (1984) Fig.8. From the minimum of his smooth eye-drawn curve we estimate

$$1 \le \varepsilon \le 1.5\ yr^{-1}\,. \tag{11}$$

Next consider A, the instantaneous rate of tree mortality caused per pest. During outbreaks annual budworm-caused tree mortality peaks at 8 - 15% per year (MacLean 1985). Hence, considering budworm-caused tree mortality in isolation, $\dot{y} = -Ayz$. Then, at the peak of the outbreak, $y_{t+1}/y_t \approx e^{-Az}$. Hence, in analogy with the derivation of (3), $.08 \le 1 - e^{-Az} \le .15$. Since z peaks on the order of

$$z_{\max} \simeq 20\quad 10^3\ larvae\,/\,tree$$

(Miller 1975), this relationship becomes:

$$.00417 \leq A \leq .0081 \; in \; 10^3 \; trees \; larvae^{-1} \, yr^{-1} \qquad (12)$$

The per capita rate of pest increase per tree, B, remains to be estimated. When z is small and y is near its equilibrium density, y is relatively constant so the pest equation in system (1) gives $z_{t+1}/z_t \approx e^{-(By-\varepsilon)}$. In analogy with the derivation of (11), we note that $(By - \varepsilon)$ corresponds to the positive vertical axis of Royama's (1984) Fig.8. From the maximum of his curve we estimate

$$1 = By - \varepsilon \leq 2 \, .$$

Since $y \approx y_{\max} \simeq 1$ and substituting (11)

$$0.8 \leq B \leq 1.42 \;\; 10^3 \, ha \; tree^{-1} \, yr^{-1} \qquad (13)$$

We thus arrive at the following table of parameters for the model:

Table 1.

parameter	units	range	initial guess
a	ha^2 (10^3 trees)^2 yr^{-1}		.00606
b	10^3 trees/ha		.247
c	yr^{-1}		.01
ρ	yr^{-1}		.134
f	yr^{-1}	.014 - .03	.017
h	yr-1	.01 - .04	.04
ε	yr^{-1}	1 - 1.5	1.5
A	10^3 trees larvae^{-1} yr^{-1}	.004 - .008	.004
B	10^3 ha tree^{-1} yr^{-1}	2 - 3.5	10.8

Table 2.

initial conditions:	state variable	units	value
	x (young trees)	10^3 trees/ha	5.81
	y (old trees)	"	2.47
	z (insect larvae)	10^3 larvae/tree	.005

DISCUSSION

The results of model (1), numerically integrated by a computer, are presented in Figure 4. The parameters and initial conditions are chosen in accordance with Tables 1 and 2. It can be seen that the chosen parameter values belong to region **3** on the right parameter portrait in Figure 2, so the outbreak is expected. An outbreak is calculated with characteristics resembling real forest data. The outbreak length is equal to 15 years which coincides well with the observations of Royama (1984). So the model, despite its extreme simplicity, could reproduce time series of a real outbreak and can be considered as a compressed representation of available forest data.

There are two obvious differences between the computed outbreak shape and real forest outbreaks. First, the time of intensive tree mortality is different. In the model this takes place at the peak of the outbreak, while in the forest the mortality of trees comes after the insect peak. It may be the result of non-inclusion of a foliage role in equation (1). In reality the insects first defoliate trees and only then do trees begin to die due to defoliation. Nonetheless, this distinction is essentially a minor detail given the "broad brush" treatment of the problem employed here.

A more important problem with the model's behaviour as far as representing budworm-forest dynamics is the inability of the modelled stand to fully recover after the initial outbreak. For instance, in simulated years 50-60, the density of old trees (y) peaks at about 3.4 of its original (t=0) value. This behaviour (damped oscillation) is determined by the model's structure and parameter values which place the system (1) in phase portrait #3 of Figure 2. An obvious question is whether random variation within the given ranges of parameter values (Table 1), as might occur with changes in weather from year to year, could occasionally move the system into different phase portraits and thus maintain the oscillations.

Maintenance of the oscillations (perhaps as a limit cycle) might also be accomplished by a more accurate representation of the ecological processes considered in equation (1). An obvious starting point here would be with the term ρy in equation (1). This represents the rate of seedling establishment as a linear function of mature tree density. In fact, although a dense overstory of mature trees may produce many seeds, it can inhibit seedling establishment by limiting the available light. Hence, forest reproductivity, ρ , may be better described by a saturating function of mature tree density:

$$\rho(y) = [\rho^{-1} + y / (\dot{x}_{\max})]^{-1} .$$

Thus $\rho(y) \cdot y \longrightarrow \rho y$ when y *is small*,

$\longrightarrow (\dot{x}_{\max})$ when y *is large*.

Here $(\dot{x}_{\max})$, a constant, is the upper limit to seedling establishment when y is large.

Both the incorporation of random variation and the more accurate description of forest reproductivity as described above, are potentially fruitful avenues for further research. Another interesting direction is to analyze the propagation of the outbreak through a spatially continuous forest.

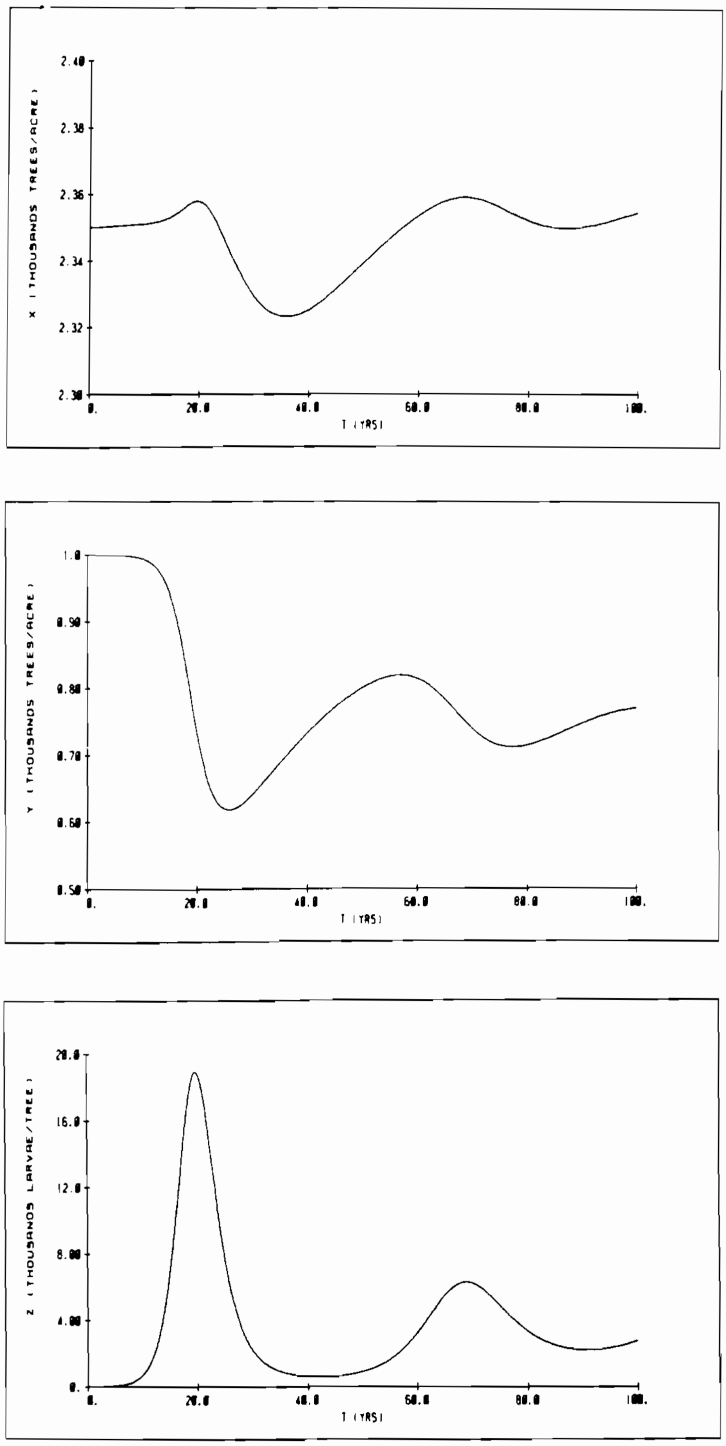


Figure 4: An outbreak time equation.

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