

## A RESOURCE BASED THREE COMPARTMENT MODEL

J. CHATTOPADHYAY

*Embryology Research Unit, Indian Statistical Institute,  
203, B.T. Road, Calcutta 700-035, India*

A. K. SARKAR

*Department of Mathematics, Jadavpur University,  
Calcutta 700-032, India*

Received 30 August 1993

Revised 10 January 1994

### ABSTRACT

This paper examines a three compartment model which represents a resource-plant-herbivore system. It establishes that under certain conditions the system has a single interior (all positive) equilibrium and that when it exists is locally asymptotically stable. It has been shown that the reproduction rate of herbivore plays an important role in shaping the dynamics of the model.

*Keywords:* Plant-herbivore system, Poisson distribution, mortality, global stability.

### 1. Introduction

Modelling on plant-herbivore systems is based on an analogy to predator-prey systems [3]. The role of herbivore feeding in changing plant abundance by incorporating the mean number of attacking herbivores was studied by Crawley [4]. For natural dependence of plant and herbivore numbers, there are several theoretically possible outcomes [5]. The outcomes depend on the demographic parameters of the plant and herbivore populations [7]. Our main emphasis lies on the extent to which herbivore dynamics are determined by change in plant abundance and the degree to which these changes are brought about by the herbivore feeding. In a previous work one of the author of this article studied the role of herbivore attack patterns in the growth of plant populations and showed that the model possesses a simple steady-state which is either locally asymptotically stable or there exists a small amplitude oscillations due to the parameter of the distribution.

In this paper we consider a resource based plant herbivore model by incorporating the average number of herbivores attacking the plant following Poisson distribution. Actually, each plant does not suffer equally under herbivore when the herbivore attack is random. The model that follows the sessile herbivorous insects

is also equally applicable to mobile herbivores whose attack rate per plant is uneven for many reasons. Herbivore inflicted losses due to host plant death are of a non-linear type. It establishes that under certain conditions the system has a single interior (all positive) equilibrium and that when it exists this equilibrium is locally and globally stable.

## 2. The Model

Let  $S(t)$  be the amount of nutrient available in the soil for uptake,  $V(t)$  be the number of plants (for total plant biomass) and  $N(t)$  be the number of herbivores (or grazer biomass) at time  $t$  in a closed environment such as a field or enclosed pasture.

Let the specific rate of nutrient uptake per unit biomass of  $V$  in unit time be  $gS$ , and the supply rate of external nutrient input to the system be  $S_0$ . Nutrient involved in plant growth may be used with certain losses due to consumption and leaching at a rate  $gSV$  and  $aS$  respectively. Plant losses biomass due to litter-fall and herbivore grazing at the rate  $cV$  and  $fNV$  respectively. The reproduction rate of herbivore on plants is  $eNV$ .

Let us consider that  $N$  herbivores are distributed over  $V$  plants according to a Poisson distribution so that the probability of plants with  $i$  herbivores is  $p(i)$ .

Herbivores suffer losses from the following causes [4] namely

- (a) by natural mortality of herbivore at a rate  $bN$ ,
- (b) by natural mortality of their host plant at a rate  $hN$ ,
- (c) by their killing of the host plant that they are on at a rate  $ki$ .

This self-induced mortality occurs at a rate  $(Vki)$  ( $ip(i)$ ), and for the whole plant biomass it is  $kV \sum_{i=0}^{\infty} i^2 p(i)$ . Here  $\sum i^2 p(i)$  is the expectation of  $i^2$  and its value is  $(N/V + N^2/V^2)$  [4, p. 272]. Therefore, the rate of inflicted losses of herbivores through host plant death is  $kV(N/V + N^2/V^2) = k(N + \frac{N^2}{V})$ .

From the biological point of view, it is obvious that the plant biomass cannot be totally absent ( $V \neq 0$ ). It is assumed that for small plant biomass, herbivore numbers are also very small and the mean number of herbivore per plant, i.e., the ratio  $\frac{N}{V}$  is also very small.

Therefore, the rate equation of growth of  $S(t)$ ,  $V(t)$  and  $N(t)$  may be expressed as

$$\begin{aligned} dS/dt &= S_0 - aS - gSV \\ dV/dt &= V(gS - c - fN) \\ dN/dt &= N(eV - (b + h + k) - kN/V) \end{aligned} \tag{2.1}$$

where  $S(0) > 0$ ,  $V(0) > 0$  and  $N(0) > 0$ .

This model is actually a rather standard three compartment prey-predator-top-predator model with logistic prey growth and standard Lotka-Volterra dynamics at the other two levels. The model differs from the standard only in the inclusion

of a per capita mortality proportional to  $N/V$  in the top-predator dynamics. The inclusion of simple density dependence at this point is stabilizing, so our main interest lies in the inverse dependence on the prey density  $V$ .

System (2.1) can be non-dimensionalized by introduction of the variables

$$x = gS/c, \quad y = eV/c, \quad z = ekN/c^2, \quad T = ct, \quad \alpha = S_0g/c^2, \quad \beta = a/c, \\ \eta = (b + h + k)/c, \quad \sigma = fc/ek, \quad \text{and} \quad \gamma = g/e.$$

The transformed non-dimensional version of (2.1) is given by

$$\begin{aligned} dx/dT &= \alpha - \beta x - \gamma xy \\ dy/dT &= y(x - 1 - \sigma z) \\ dz/dT &= z(y - \eta - z/y) \end{aligned} \tag{2.2}$$

where  $x(0) = x_0 > 0$ ,  $y(0) = y_0 > 0$  and  $z(0) = z_0 > 0$ .

### 3. Boundedness of Solutions and Equilibria

**Lemma 3.1.** If  $\lambda < \min\{1, \beta, \eta\}$ , all the solutions of (2.2) which initiate in  $R_3^+$  are uniformly bounded for all  $(x_0, y_0, z_0) \in R_3^+$  as  $t \rightarrow \infty$ .

#### Proof

We define the function

$$W = x + \gamma y + \gamma \sigma z \tag{3.1}$$

The time derivative of  $W$  along the solutions of (2.2) is

$$\begin{aligned} \dot{W} &= \dot{x} + \gamma \dot{y} + \gamma \sigma \dot{z} \\ &= \alpha - \beta x - \gamma y - \gamma \sigma \eta z - \gamma \sigma z^2/y \end{aligned}$$

Therefore,

$$\dot{W} + \lambda W \leq \alpha + x(\lambda - \beta) + \gamma y(\lambda - 1) + \gamma \sigma z(\lambda - \eta). \tag{3.2}$$

Now, if we choose  $\lambda > 0$ , then the right hand side of (3.2) is bounded for all  $(x, y, z) \in R_3^+$ . Thus, we find a  $k > 0$  with  $\dot{W} + \lambda W \leq k$ . Now applying a theorem on differential inequality [1], we obtain,

$$0 \leq W(x, y, z) \leq k/\lambda + \{W(x(0), y(0), z(0)) - k/\lambda\} \exp(-\lambda t) \tag{3.3}$$

and for  $t \rightarrow \infty$ , we have  $0 \leq W(x, y, z) \leq k/\lambda$ .

Thus,  $B = \{(x, y, z) \in R_3^+ : W < k/\lambda + \theta, \text{ for any } \theta > 0\}$ . Hence, the result.

Now we consider the existence of equilibria of the system (2.2). The existence of planar and interior equilibria depend on the threshold value  $\alpha$ . The planar equilibrium  $E_1(x, y, 0)$ , where  $x = 1$  and  $y = \frac{(\alpha - \beta)}{\gamma}$  is feasible if  $\alpha > \beta$ . The interior equilibrium  $E_2(x^*, y^*, z^*)$ , where  $x^* = 1 + \sigma y^*(y^* - \eta)$  is feasible if  $\gamma > \eta$ . From the variational matrix of (2.2) it follows that  $E_1$  is locally stable in the  $x$ - $y$  plane, while the  $z$ -direction is stable or unstable according as  $\alpha < \beta + \gamma\eta$  or  $\alpha > \beta + \gamma\eta$  respectively.

#### 4. Local Stability

**Theorem 4.1.** Existence of interior equilibrium ensures its local asymptotic stability.

##### Proof

The interior equilibrium  $E_2(x^*, y^*, z^*)$  of the system (2.2) is feasible if  $\gamma > \eta$ .

The local behaviour of the interior equilibrium is determined by the sign of real parts of the eigenvalues of the characteristic equation of the Jacobian matrix at  $E_2(x^*, y^*, z^*)$ . The characteristic equation is given by

$$f(\delta) \equiv \delta^3 + a_1\delta^2 + a_2\delta + a_3 = 0,$$

where

$$a_1 = \beta + \gamma y^* + z/y^*$$

$$a_2 = \sigma(y^* z^* + z^{*2}/y^*) + \beta z^*/y^* + \gamma(x^* y^* + z^*)$$

$$a_3 = \sigma(\beta + \gamma y^*)(y^* z^* + z^{*2}/y^*) + \gamma x^* z^*.$$

Now it is evident that  $a_1, a_2, a_3 > 0$  and  $a_1 a_2 - a_3 > 0$ . Hence from Routh-Hurwitz criteria,  $E_2(x^*, y^*, z^*)$  is locally asymptotically stable. Hence the theorem.

#### 5. Global Stability

In the following theorem we shall prove that the interior equilibrium is globally asymptotically stable. Busenberg and Driessche [2] demonstrated a more general and flexible method which includes Bendixon and Dulac as special cases. The authors used in their application (see, Lemma 3.1 of Ref. 2)  $s + i + r = 1$  to rewrite  $f_1, f_2$  and  $f_3$  in their equivalent forms. But in our model system as  $S + V + N$  is not constant, so we are not able to rewrite our model system (2.2) in any equivalent forms. Hence, we use a straightforward approach in application of Theorem 4.1 of Busenberg and Driessche in our model system (2.2).

**Theorem 5.1.** The model system (2.2) has no periodic solutions, homoclinic loops, or oriented phase polygons inside the invariant region  $B$  if  $\sigma \leq 1$  and  $\gamma \leq 1$ .

**Proof**

Let  $g(x, y, z) = \{g_1(x, y, z), g_2(x, y, z), g_3(x, y, z)\}$  be a vector field which is piecewise smooth on compact subsets contained in the interior of  $B$  and which satisfy the conditions

$g \cdot f = 0$  and  $(\text{curl } g) \cdot n < 0$  on  $B_0 = B - vB$ , where  $vB$  is the boundary of  $B$ ,  $n$  is the unit normal to  $B_0$  and  $f = (f_1, f_2, f_3)$  is a Lipschitz continuous field on  $B_0$ . Then the differential equation system  $dx/dt = f_1$ ,  $dy/dt = f_2$ ,  $dz/dt = f_3$ , has no periodic solutions, homoclinic loops, or oriented phase polygons in  $B_0$ .

Let  $f_1, f_2, f_3$  denote the right hand side of (2.2) respectively and

$$\begin{aligned} g_1 &= (y^2 - \eta y - z - xy + y + \sigma yz)/xy \\ g_2 &= (\alpha y - \beta xy - \gamma xy^2 - xy^2 + \eta xy + xz)/xy^2 \\ g_3 &= (x^2 - x - \sigma xz - \alpha + \beta x + \gamma xy)/xz \end{aligned}$$

Clearly  $g \cdot f = 0$  on  $B_0$ . A few computation yield the expression

$$(\text{curl } g) \cdot n = -1/y^2 - \alpha/x^2 z - 1/xy - \alpha/x^2 y - z/xy^2 + (\gamma - 1)/z + (\sigma - 1)/x$$

which is negative definite if  $\sigma \leq 1$  and  $\gamma \leq 1$ . Hence, the theorem.

**6. Conclusion**

In this paper, we have considered a resource based plant herbivore model. The novelty of this model lies on the inverse dependence in the prey density  $V$ . We have shown that the existence of interior equilibrium implies its local asymptotic stability. We have also shown that the model system is globally asymptotically stable by Bendixon-Dulac criteria as a special case. We have observed that the reproduction rate ( $e$ ) of herbivore exceeds a certain threshold value, given by,  $e > \max. (fc/k, g)$ , for global stability. Thus, we may conclude that the reproduction rate of herbivore plays an important role in shaping the dynamics of the model, which is an interesting and important finding from the ecological point of view.

**References**

- [1] Birkhoff G. and Rota G. C., *Ordinary differential equation* (1982) Ginn, Boston.
- [2] Busenberg S. and Driessche Van den, Analysis of a disease transmission model in a population with varying size. *J. Math. Biol.* **28** (1990) pp. 257-270.
- [3] Caughley G. and Lawton J. H., Plant herbivore system. In *Theoretical Biol.*, ed. by May R. M., 2nd ed., (Sinauer Associates, Sunderland, 1981) pp. 132-166.
- [4] Crawley M. J., Herbivory: the dynamics of animal-plant interactions. *Studies in Ecology* **10** (Univ. of California Press, Berkeley, 1983).
- [5] May R. M., Simple mathematical models with very complicated dynamics. *Nature* **261** (1976) pp. 459-467.
- [6] Sarkar A. K. and Roy A. B., Role of herbivore attack pattern in growth of plant populations. *Ecol. Modelling* **45** (1989) pp. 307-316.
- [7] Stubbs M., Density dependence in the life cycles of animals and its importance in K- and R- strategies. *J. Animal Ecol.* **46** (1977) pp. 677-688.