CHAPTER VIII

STABILITY OF TWO - SPECIES COMPETITION SYSTEM:

THERMODYNAMIC AND STOCHASTIC APPROACHES
8.1. Introduction:

When two or more species live in proximity and share the basic requirements, they usually compete for resources, habitat or territory and in some way inhibit each other's growth. Sometimes only the strongest prevails driving the weaker competitor to extinction. This is the famous principle of competitive exclusion in population biology (Edelstein-Keshet, 1987). The first classical competition experiment in laboratory was due to Gause (1934) who based on Lotka-Volterra model also made the theoretical analysis of two competing yeast populations. Another classical competition experiment was that of Paré (1954) using metazoa. Tribolium confusum and T. Castaneum were used in a homogeneous environment with different temperature and humidity ranges. Some interesting phenomena have been found from the study of practical competition model. There are much current arguments and literature about the role of competition in determination of structure of an ecological community (Hsu et al., 1979).

In recent times great efforts are going on to develop a general non-equilibrium thermodynamic model of biological systems (Lamprecht and Zotin, 1983). We are, however, not interested here in the generality of the competition model.
Instead we shall consider a sample two-species competing system and study the stability of the system from the consideration of non-equilibrium thermodynamic and stochastic modelling of the system to see whether these modelings would result in any new conditions of stability in addition to those determined by the usual dynamical analysis of the deterministic model equations. The paper is a modification and extension of an earlier work [Ghosh and Chakrabarti, 1991].

8.2. Basic Dynamical Equations and Stability

Let us consider two competing species (for example, two yeast population in an alcohol medium). The equations governing their populations are given by

\[
\frac{dN_1}{dt} = e_1 N_1 - a_1 N_1 (N_1 + N_2) \quad \ldots \ldots \quad (8.1a)
\]

\[
\frac{dN_2}{dt} = e_2 N_2 - a_2 N_2 (N_1 + N_2) \quad \ldots \ldots \quad (8.1b)
\]

where \( N_1(t) \) and \( N_2(t) \) are the population sizes of the two species at any time \( t \); \( e_1 \) and \( e_2 \) are the species growth rates of the populations and are positive quantities.
There are three possible stationary points:

\((N_1^*, N_2^*) = (0, 0)\) (both species die out) \hspace{1cm} (8.2a)

\((N_1^*, N_2^*) = (0, \frac{e_2}{a_2})\) (only the first species dies out) \hspace{1cm} (8.2b)

\((N_1^*, N_2^*) = \left(\frac{e_1}{a_1}, 0\right)\) (only the second species dies out) \hspace{1cm} (8.2c)

The stationary point \((0, 0)\) is trivial and unstable. We shall not consider it.

Now we consider the stability (or instability) of the stationary point \((e_1/a_1, 0)\). We give a small perturbation \((x_1, x_2)\) about it:

\[N = \frac{e_1}{a_1} + x_1, \quad N_2 = 0 + x_2\]

The equation (8.1a) and (8.1b) are then linearized to

\[\frac{dx_1}{dt} = -e_1(x_1 + x_2)\]

\[\frac{dx_2}{dt} = \left(\frac{e_2}{a_2} - \frac{e_1}{a_1}\right)x_2\]

The eigenvalues for the system of equations (8.3) are given by

\[\lambda = -e_1, \quad e_2 - a_2 \frac{e_1}{a_1}\]
So the position \( \left( \frac{e_i}{a_i}, 0 \right) \) is stable if

\[
e_i > 0, \quad a_2 e_i - a_1 e_2 > 0 \quad \ldots \ldots (8.5a)
\]

and unstable if

\[
e_i < 0, \quad a_2 e_i - a_1 e_2 > 0 \quad \ldots \ldots (8.5b)
\]

8.3. **Non-Equilibrium Thermodynamic Model and Stability**

To develop thermodynamic model of the linearized systems described by the equations we have to choose the thermodynamic fluxes and forces properly consistent with the basic requirements namely the linear phenomenological relations between the thermodynamic fluxes and forces and Prigogine's principle of minimum-entropy production for stationary state of the system. We choose the thermodynamic fluxes as the growth rates or rates of change of biomass

\[
J_i = \frac{dx_i}{dt} \quad (i = 1, 2) \quad \ldots \ldots (8.6)
\]

and the thermodynamic forces as the deviation from the stationary state [Assimacoupoulis, 1987]
\[ X_i = N_i^* - N_i \quad (i = 1, 2) \quad \ldots \ldots \quad (8.7) \]

Then the system of equations (8.3) can be written in the form of phenomenological linear relations:

\[ J_1 = L_{11} X_1 + L_{12} X_2, \quad J_2 = L_{21} X_1 + L_{22} X_2 \quad \ldots \ldots \quad (8.8) \]

where

\[
\begin{bmatrix}
L_{11} = e_1, & L_{12} = e_1 \\
L_{21} = 0, & L_{22} = -\left( e_2 - \frac{e_1}{a_1} \right)
\end{bmatrix}
\quad \ldots \ldots \quad (8.9)
\]

are the phenomenological coefficients.

Let \( S \) be the entropy of the system. For the system near to the stationary equilibrium state \( (e_1/a_1, 0) \), \( S \) can be expanded about the stationary equilibrium state as,

\[ S = S_{eq} + (\delta S)_{eq} + \frac{1}{2} (\delta^2 S)_{eq} \quad \ldots \ldots \quad (8.10) \]

Then the criteria of thermodynamic stability of the stationary equilibrium state is given by [Glansdorff and Prigogine, 1971]
Using the phenomenological relations (8.8), we have

\[ \frac{\partial}{\partial t} \left( \frac{1}{2} \delta^2 \theta \right)_{\theta q} = \sum_{i=1}^{2} \delta X_i \delta J_i \quad 0 \quad \ldots \ldots (8.11) \]

Using the phenomenological relations (8.8), we have

\[ \sum_{i=1}^{2} \delta X_i \delta J_i = L_{11} (\delta X_{11})^2 + (L_{12} + L_{21}) \delta X_{1} \delta X_{2} + L_{22} (\delta X_{22})^2 \]

\[ \ldots \ldots (8.12) \]

where \( L_{11}, L_{12}, L_{21}, L_{22} \) are given by (8.9).

For stability of the stationary state \((e_1/a_1, 0)\), the expression (8.12) must be a positive-definite. The necessary and sufficient condition of the positive definiteness of (8.12) are

\[ L_{11} > 0, L_{22} > 0 \text{ and } (L_{11} L_{22} - L_{12} L_{21}) > 0. \]

implying

\[ e_1 > 0, \left[ e_2 - a_2 \frac{e_1}{a_1} \right] > 0 \quad \ldots \ldots (8.13a) \]

and \( e_1 \left\{ - \left[ e_2 - a_2 \frac{e_1}{a_1} \right] \right\} - e_1.0 > 0 \quad \ldots \ldots (8.13b) \)

Since (8.13a) implies (8.13b), the thermodynamic criteria of stability of the stationary point \( \left( \frac{e_1}{a_1}, 0 \right) \) are,
We note that the thermodynamic criteria of stability (8.14) are the same as criteria of stability (8.5a) obtained directly from the dynamical equation.

8.4. Stochastic Model and Stability

Let us now consider the stochastic model of the system. This can be achieved by addition of a random perturbation term to the r.h.s. of the system of equations (8.1). We have the Matrosov type of system described by the stochastic differential equations

\[
\frac{dN}{dt} = f_i(N) + \epsilon_i(t) \quad \ldots \ldots \ldots \ldots \ldots \ldots (8.15)
\]

where

\[
f_i(N) = N_i \left[ e_i - a_i (N_1 + N_2) \right] \quad \ldots \ldots \ldots \ldots \ldots \ldots (8.16)
\]

for \( N = (N_1, N_2) \) and \( i = 1, 2 \)

The random perturbation \( \epsilon_i(t) \) are assumed to be white-noises characterized by

\[
\langle \epsilon_i(t) \rangle = 0, \quad \langle \epsilon_i(t_1) \epsilon_j(t_2) \rangle = D_{ij} \delta(t_2 - t_1) \quad \ldots \ldots \ldots \ldots \ldots \ldots (8.17)
\]
Let \( P(N, t) \) be the probability density of \( N = (N_1 + N_2) \). Due to the Markovian character of the process \( N(t) \), the probability density \( P(N, t) \) satisfies the Fokker-Planck equation

\[
\frac{\partial}{\partial t} P(N, t) = -\sum_i \frac{\partial}{\partial N_i} \left\{ f_i(N), P(N, t) \right\} + \frac{1}{2} \sum_{i,j} D_{ij} \frac{\partial^2 P(N, t)}{\partial N_i \partial N_j} \quad \ldots \ldots (8.18)
\]

We define the stochastic entropy \( S(t) \) by

\[
S(t) = -\int_{-\infty}^{\infty} P(N, t) \ln P(N, t) dN \quad \ldots \ldots (8.19)
\]

It can then be shown that [Platonov, 1988]

\[
S(t) = \sum_i \int_{-\infty}^{\infty} \left( \frac{\partial f_i(N)}{\partial N_i} \right) P(N, t) \, dN
\]

\[
+ \frac{1}{2} \sum_{i,j} D_{ij} \int_{-\infty}^{\infty} \left( \frac{\partial \ln P(N, t)}{\partial N_i} \right) \left( \frac{\partial \ln P(N, t)}{\partial N_j} \right) \, dN
\]

\[
= \sum_i \frac{\partial f_i(N, t)}{\partial N_i} \, dN + \frac{1}{2} \sum_{i,j} D_{ij} \frac{\partial \ln P(N, t)}{\partial N_i} \cdot \frac{\partial \ln P(N, t)}{\partial N_j}
\]

\[
= S_d + S_r \quad \ldots \ldots (8.20)
\]
where \( \langle \rangle \) denotes the average over the probability distribution \( P(N, t) \). We thus see that the entropy-rate \( S \) can be decomposed into two parts: \( S_d \) and \( S_n \). The first part is due to drift term and can be positive or negative. The second term is the contribution of the stochasticity or noises and it is always non-negative, since we can write it as

\[
\sum_{i,j} D_{ij} \left( \frac{\partial \ln P(N, t)}{\partial N_i} - \frac{\partial \ln P(N, t)}{\partial N_j} \right) \geq 0 \quad \ldots \ldots (8.21)
\]

where \( \eta_i \) are random quantities whose moments are equal to \( \langle \eta_i \eta_j \rangle = D_{ij} \). The non-negativity of the second term also shows that the entropy of a generalized conservative system i.e. for system in which

\[
\text{div } f(N) = \sum_l \frac{\partial f(N)}{\partial N_l} = 0 \quad \ldots \ldots (8.22)
\]

always increases due to the presence of noises.

We now expand the entropy \( S(t) \) about a stationary state as

\[
S(t) = S_{st} + \delta S \bigg|_{st} + \frac{1}{2} \delta^2 S \bigg|_{st} \quad \ldots \ldots (8.23)
\]
Since $\delta^2 S \neq 0$, we have

$$\left. \dot{S} \right|_{\text{st}} = - \frac{\partial}{\partial t} (\delta^2 S) \left|_{\text{st}} \right. \quad \ldots \ldots (8.24)$$

The criteria of stability of the stationary state now becomes

$$\left. \dot{S} \right|_{\text{st}} = 0 \quad \ldots \ldots (8.25)$$

We now consider the stability of the stationary state

$$\left( \frac{e_1}{a_1}, 0 \right).$$

By (8.20) we have

$$S_d = \sum_i \frac{\partial f (N)}{\partial N_i} = \left( e_2 - a_2 \frac{e_1}{a_1} \right) - e_1 \quad \ldots \ldots (8.26)$$

so that

$$\left. \dot{S} \right| \left( \frac{e_1}{a_1}, 0 \right) = \left\{ \left( e_2 - a_2 \frac{e_1}{a_1} \right) - e_1 \right\} + \left( S \right)_{\text{st}} \quad \ldots \ldots (8.27)$$

where the positive contribution due to noises is proportional to the noise intensity $D_{ij}$. We are not determining $(S)_{\text{st}}$ explicitly which will not, however, hamper the qualitative analysis of stability of the system. The deterministic and non-equilibrium thermodynamic criteria of stability impose constraints.
\[ e_i > 0, \text{ and } \left( e_2 - a \frac{e_i}{a_i} \right) > 0 \quad \ldots \ldots (8.28) \]

so that the first term \((S)_d\) in \((8.26)\)

\[ \dot{(S)}_d = \left\{ \left( e_2 - a_2 \frac{e_i}{a_i} \right) - e_i \right\} > 0 \quad \ldots \ldots (8.29) \]

However, the stability of the stochastic system i.e. the system under random noises will depend on the non-negative part \((S)_r\) which is proportional to the noise intensity \(D_{ij}\). Thus if the random noise \(e_{1i}(t)\) be of so low intensity that

\[ \left\{ \left( e_2 - a_2 \frac{e_i}{a_i} \right) - e_i \right\} + (S)_r > 0 \quad \ldots \ldots (8.30) \]

then the stochastic system is stable at the stationary point

\[ \left( \frac{e_i}{a_i}, 0 \right) \]. However, if the noise intensity be so large (in comparison to both \(e_i\) and \(e_2 - a_2 \frac{e_i}{a_i}\)) as to make the l.h.s. of \((8.30)\) positive, then the system becomes unstable. So the eigenvalues \(e_i\) and \(e_2 - a_2 \frac{e_i}{a_i}\) in the deterministic analysis of stability and the noise intensity \(D_{ij}\) are the factors which determine the stability of the stochastic system.
8.5. Conclusion

Interesting biological phenomena of population extinction, survival, persistence, co-existence, succession and stability are associated with biological communities with competition. Although deterministic and stochastic differential equations analysis of such phenomena has progressed considerably in recent times [Hsu, 1979; Hallam, 1980; Gard, 1984], the non-equilibrium thermodynamic analysis of biological system, particularly of competition system has progressed comparatively a little. An entropic theory of succession, stability and evolution of a generalized ecosystem on the basis of a generalized measure of entropy-production has been attempted recently [Chalrabarti, 1994]. The present chapter is an attempt, limited in its scope and field, in the entropic (both thermodynamic and stochastic) analysis of stability only. Here we see that although the deterministic and non-equilibrium thermodynamic modelling lead to the same criteria of stability or instability, the stochastic model sets different criteria of stability. The result is in qualitative agreement with the stability analysis of May [1973].