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SMR.648 - 60

# SECOND AUTUMN WORKSHOP ON MATHEMATICAL ECOLOGY

(2 - 20 November 1992)

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# "Stability Problems in Chemostat Equations with Delayed Nutrient Recycling"

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**These are preliminary lecture notes, intended only for distribution to participants.**

# CHEMOSTAT EQUATIONS WITH DELAYED NUTRIENT RECYCLING.

Models based on chemostat-type equations to simulate the growth of planktonic communities of unicellular algae have been studied by many authors (e.g. Hsu et al. (1977), Waltman et al. (1980), Di Liddo-Rinaldi, (1986)).
An important difference between a "chemostat" situation and a "lake" situation appears to be in the fact that lakes generally have residence time measured in years (Powell and Richerson, (1985))


- Hsu, S.B., Hubbel, S., Waltman, P. : A mathematical theory for single-nutrient competition of micro-organisms. SIAM J. Appl. Math. 32, 366-383 (1977).
- Waltman, P., Hubbel, S.P., Hsu, S.B. : Theoretical and experimental investigations of microbial competition in continuos culture. In : Burton, T.(ed.) MODELING AND DIFF. EQ.NS IN BIOLOGY. N.Y. DEKKER, (1980)
- Di Liddo, A. ; Rinaldi, F. : L'effetto del recycling di nutriente in un modello di crescita di un microorganismo. Rapporto Interno I.R.M.A.-C.N.R., (1986).
- Powell, T., Richerson, P.J. : Temporal variation, spatial heterogeneity and competition for resources in plankton system: a theoretical model. Am. Nat. 125, 431-464, (1985)

This implies that in models of natural systems a smaller wash-out rate constant and regeneration of nutrient due to bacterial decomposition of dead biomass must be considered (Svirezhev and Logofet, (1983)).

The effect of material recycling on ecosystem stability has been mainly studied for closed systems (Nisbet and Gurney (1976), Nisbet et al. (1983), Ulanowicz, (1972)).

Powell and Richerson (1985) and Nisbet and Gurney (1976), considered nutrient recycling as an instantaneous term thus neglecting the time required to regenerate nutrient from dead biomass by bacterial decomposition.


- Svirezhev, Y.M., Logofet, D.O.: Stability of Biological Communities. Moscow, MIR (1983).
- Nisbet, R.M., Gurney, W.S.C.: Model of material cycling in a closed ecosystem. Nature, 264, 633-635, (1976).
- Nisbet, R.M., McKinstry, J., Gurney, W.S.C.: A strategic model of material cycling in a closed ecosystem. Math. Biosc. 64, 99-113, (1983).
- Ulanowicz, R.E.: Mass and energy flow in closed ecosystems. J. Theor. Biol. 34, 239-253, (1972).

- Such a delay in nutrient recycling is always present in a natural system and increases for decreasing temperature (Whittaker, (1985)).
- In the following will be considered a model with a single species feeding on a limiting nutrient which is partially recycled after the death of the organisms and we insert a distributed time lag in order to study the effect of a delayed recycling on the stability of the positive equilibrium.
- The population may be any planktonic community of unicellular algae, and the nutrient in question may be phosphorous, nitrogen or even a vitamin such as $B_{12}$.

The model variables are

$N_1$ nutrient concentration in the chemostat $[mol/\ell]$

$N_2 := Q\,N$ ; $Q$ is the average content of nutrient for cell $[mol/cell]$. $N$ is the algae concentration in the chemostat. $[cell/\ell]$.

$N_2$ represents the nutrient stored into the algae $[mol/\ell]$

We do the crude assumption that $Q$ is independent of time.


- Whittaker, R.H.: Communities and ecosystems. N.Y., Macmillan (1975).

- To account for the growth of algae concentration in the chemostat even when the nutrient concentration has dropped to small levels, we insert a distributed delay in growth response to nutrient uptake (Nisbet and Gurney, (1982); Cunningham and Nisbet, (1980)).
- We assume the following general hypotheses on the nutrient uptake function (Hale and Somolinos, (1983)):
  (i) the function is non-negative, increasing, and vanishes when there is no nutrient,
  (ii) there is a saturation effect when the nutrient is very abundant.

  This class of functions includes both Michaelis-Menten and Monod functions.


- Nisbet, R.M., Gurney, W.S.C.: <u>Modelling Fluctuating Populations</u>. J. Wiley & Sons, (1982)
- Cunningham, A. and Nisbet, R.M.: <u>Time lag and co-operativity in the transient growth dynamics of Microalgae</u>. J. Theor. Biol., <u>84</u>, 189-203, (1980).
- Hale, J.K., Somolinos, A.S.: <u>Competition for fluctuating nutrient</u>. J. Math. Biol., <u>18</u>, 255-280, (1983)

$$\begin{cases} \dot{N}_1 = D(N_1^0 - N_1) - aU(N_1)N_2 + b\gamma \int_0^{+\infty} f(s)\, N_2(t-s)\, ds \\ \dot{N}_2 = -(\gamma + D) N_2 + c N_2 \int_0^{+\infty} g(s)\, U(N_1(t-s))\, ds \end{cases} \qquad (1)$$

$N_1^0$ constant input concentration of the limiting nutrient; $N_1^0 \in \mathbb{R}_+ := (0,+\infty)$;

$a \in \mathbb{R}_+$ maximum uptake rate of nutrient; $[T^{-1}]$

$c \in \mathbb{R}_+$, $c < a$, maximum specific growth rate of the biotic species; $[T^{-1}]$

$\gamma \in \mathbb{R}_+$ death constant rate for the biotic species; $[T^{-1}]$

$b \in (0,1)$ fraction of dead biomass recycled as a new nutrient;

$D = \frac{v}{V}$ dilution constant rate of the chemostat; $[T^{-1}]$ (ratio between volumetric input-output rate $v$ and chemostat volume $V$.)

$U = U(N_1)$ saturation law for nutrient uptake:

(i) $U : \mathbb{R}_{+0} := [0,+\infty) \to [0,1)$; $U \in C^1(\mathbb{R}_{+0})$.

(ii) $U'(N_1) > 0 \quad \forall N_1 \in \mathbb{R}_+$

(iii) $U(0) = 0$, $\lim_{N_1 \to +\infty} U(N_1) = 1$

Delay Kernels

"f" for nutrient recycling;

"g" for growth delayed rensponse to nutrientuptake.

(a) $f, g : \mathbb{R}_{+0} \to \mathbb{R}_{+0}$ (biological meaning)

(b) $\int_0^{+\infty} s^i f(s)\, ds < +\infty$, $\int_0^{+\infty} s^i g(s)\, ds < +\infty$, $i = 0, 1, 2$,

$$\int_0^{+\infty} f(s)\, ds = \int_0^{+\infty} g(s)\, ds = 1$$

$$T_r = \int_0^{+\infty} s f(s)\, ds \quad , \quad T_g = \int_0^{+\infty} s g(s)\, ds$$

where

$T_r$ : average time delay in recycling process;

$T_g$ : average time delay in growth response.

Initial conditions for (1).

For any $t \geqslant t_0$ denote by

$$N_{i_t} = N_i(t+\theta) \ , \ \theta \in (-\infty, 0] \ , \ i = 1, 2 \ ,$$

with "$t_0$" initial time for (1).

By "$X_H(t)$" we mean the space of continuous bounded functions $\underline{X}_t = (N_{1t}, N_{2t})^T$ such that $\underline{X}_t : (-\infty, t] \to \mathbb{R}^2$ with $\| \underline{X}_t \| < H$, $H \in \mathbb{R}_+$.

$$\| \underline{X}_t \| = \sup_{\theta \in (-\infty, 0]} | \underline{X}(t+\theta) | \qquad (2)$$

where $| \cdot |$ is any norm on $\mathbb{R}^2$.

Then, the i.c. are:

$$N_{i\,t_0} = N_i(t_0+\theta) := \phi_i(\theta) \quad , \theta \in (-\infty, 0], i=1,2, \qquad (3)$$

where we assume

$$\phi_i \geq 0 \quad , i = 1,2$$

because of their biological meaning. Hence

$$\underline{X}_{t_0} = \underline{\phi} \in \mathcal{Q}_H \quad , \qquad (4)$$

where $\mathcal{Q}_H := \underline{X}_H(t_0)$.

- System (1) can be rewritten:

$$\dot{\underline{X}} = \underline{F}(\underline{X}_t) \quad , t \geq t_0 \qquad (5)$$

where

$$\underline{F}(\underline{X}_t) = \begin{pmatrix} F_1(\underline{X}_t) \\ F_2(\underline{X}_t) \end{pmatrix} := \begin{pmatrix} D(N_1^0 - N_1) - aU(N_1)N_2 + b\gamma \int_0^{+\infty} f(s) N_2(t-s)\,ds \\ -(\gamma + D)N_2 + cN_2 \int_0^{+\infty} g(s)\, U(N_1(t-s))\,ds \end{pmatrix} \qquad (6)$$

i.e. is an <u>autonomous</u> system of functional differential equations.

1. <u>$\underline{F}$ is locally Lipschitzian</u>.

For any $\underline{\phi}, \underline{\psi} \in \mathcal{Q}_H$ a constant $K$ exists such that:

$$\left| \underline{F}(\underline{\phi}) - \underline{F}(\underline{\psi}) \right|_1 \leq K \left\| \underline{\phi} - \underline{\psi} \right\| \qquad (7)$$

where $|\underline{X}|_1 := |X_1| + |X_2|$.

Let be $J = [t_0, \delta + t_0)$, $\delta \in \mathbb{R}_+$ the maximum existence interval for a solution

$$\underline{X}(t) = \underline{X}(t, \underline{\phi}) \quad , \quad \underline{\phi} \in \mathcal{Q}_H \; , \forall t \in J \qquad (8)$$

of (1).

Then, given $\underline{\phi} \in \mathcal{Q}_H$ the solution (8) is "unique" and continuously depending upon $\underline{\phi} \in \mathcal{Q}_H$.
(J.K. Hale - J. Diff. Eq.ns, 1, 452-482, (1965)).

2. Positive invariance of $\mathbb{R}^2_{+0} := \{(N_1, N_2) \in \mathbb{R}^2 \mid N_i \geq 0, i=1,2\}$

From (1) and for all $t \geq t_0$

$$\dot{N}_2(t) = N_2\left[-(\gamma + D) + c\int_0^{+\infty} g(s)\, U(N_1(t-s))\, ds\right],$$

$$N_2(t_0) = \phi_2(0) \geq 0$$

gives:

$$N_2(t) = \phi_2(0) \exp\left\{\int_{t_0}^{t}\left[-(\gamma+D) + c\int_0^{+\infty} g(s)\, U(N_1(\tau - s))\, ds\right] d\tau\right\} \geq 0$$

Hence:

$$\dot{N}_1(t) = D(N_1^0 - N_1) - a\, U(N_1) N_2 + b\gamma \int_0^{+\infty} f(s) N_2(t-s)\, ds \geq$$

$$\geq D(N_1^0 - N_1) - a\, U(N_1) N_2$$

Now, observe that whenever $N_1 = 0$ then

$$\dot{N}_1(t) \geq D N_1^0 > 0 \; .$$

Continuation on $[t_0,+\infty)$ of a solution $\underline{X}=\underline{X}(t,\underline{\phi})$ of (1) with its properties of uniqueness and continuous dependence on $\underline{\phi}\in Q_H$ is ensured by the boundedness of solutions:

Theorem 1. If $T_g$ satisfies that

$$T_g \leqslant \frac{(a-bc)}{ac} \tag{9}$$

then all the solutions of (1) are uniform bounded in $\mathbb{R}^2_{+0}$.

Proof. Consider the functional

$$W(\underline{X}_t) = N_1 + bN_2 + b\gamma\int_0^{+\infty} f(s)\int_{t-s}^{t} N_2(u)\,du\,ds + $$

$$+ aN_2\int_0^{+\infty} g(s)\int_{t-s}^{t} U(N_1(u))\,du\,ds \quad . \tag{10}$$

Chosen as norm in $\mathbb{R}^2$ $|\underline{X}(t)|_1 = |N_1(t)|+|N_2(t)|$, because of the positive invariance of $\mathbb{R}^2_{+0}$, the following holds for a constant

$$\kappa = \min\{1,b\} > 0 \quad : \tag{11}$$

$$\kappa\,|\underline{X}(t)|_1 \leqslant W(\underline{X}_t) \quad , \forall\, t \geqslant t_0 . \tag{12}$$

Denote by

$$0 \leqslant \nu_i := \sup_{\theta \in (-\infty, 0]} |\phi_i(\theta)| \;, i = 1,2 \quad . \tag{13}$$

Then at $t = t_0$

$$W(\underline{X}_{t_0}) = W(\underline{\phi}) = \phi_1(0) + b\,\phi_2(0) + b\gamma \int_0^{+\infty} f(s) \int_{t_0 - s}^{t_0} \phi_2(u)\,du\,ds$$
$$+ a\,\phi_2(0) \int_0^{+\infty} g(s) \int_{t_0-s}^{t_0} U(\phi_1(u))\,du\,ds \,. \tag{14}$$

Since $0 \leqslant U < 1$, then:

$$W(\underline{\phi}) \leqslant \phi_1(0) + b\,\phi_2(0) + b\gamma\,\nu_2 T_r + a\,\phi_2(0) T_g \leqslant$$
$$\leqslant \nu_1 + (b + b\gamma T_r + a T_g)\,\nu_2 \tag{15}$$

Let be

$$\eta := \max\{1,\; b + b\gamma T_r + a T_g\} \quad . \tag{16}$$

From (15) we obtain:

$$W(\underline{\phi}) \leqslant \eta\,(\nu_1 + \nu_2) \leqslant 2\eta \sup_{\theta \in (-\infty, 0]} |\underline{\phi}(\theta)|_1 = 2\eta \|\underline{\phi}\|$$

Hence, for each $\underline{\phi} \in \Omega_H$ a positive constant $\beta$ exists (independent of $t_0$) such that:

$$W(\underline{\phi}) \leqslant \beta \quad , \quad \beta = 2\eta H \tag{17}$$

Time derivative of $W(\underline{X}_t)$ along the solutions of (1) :

$$\dot{W}(\underline{X}_t)_{(1)} = \dot{N}_1 + b\dot{N}_2 + b\gamma N_2 - b\gamma \int_0^{+\infty} f(s) N_2(t-s)\, ds + a N_2 U(N_1) - a N_2 \int_0^{+\infty} g(s)\, U(N_1(t-s))\, ds + a\dot{N}_2 \int_0^{+\infty} g(s) \int_{t-s}^{t} U(N_1(u))\, du\, ds \quad (18)$$

By substitution of eq.ns (1) in (18) we have

$$\dot{W}(\underline{X}_t)_{(1)} = D(N_1^0 - N_1) - bDN_2 - a(\gamma+D)N_2 \int_0^{+\infty} g(s) \int_{t-s}^{t} U(N_1(u))\, du\, ds - \left\{ a - bc - ac \int_0^{+\infty} g(s) \int_{t-s}^{t} U(N_1(u))\, du\, ds \right\} N_2 \int_0^{+\infty} g(s)\, U(N_1(t-s))\, ds$$

Noting that :

$$T_g = \int_0^{+\infty} s\, g(s)\, ds \geq \int_0^{+\infty} g(s) \int_{t-s}^{t} U(N_1(u))\, du\, ds$$

and that by the hypothesis : $a - bc - acT_g \geq 0$, the following holds :

$$\dot{W}(\underline{X}_t)_{(1)} \leq D(N_1^0 - N_1) - bDN_2 \quad (19)$$

- By integration of (19) from "$t_0$" to "$t$" we obtain:

$$W(\underline{X}_t) \leq W(\underline{\phi}) + DN_1^0(t-t_0) - D\int_{t_0}^{t} (N_1(\tau) + bN_2(\tau))\, d\tau \leq \beta + DN_1^0(t-t_0) - \kappa D \int_{t_0}^{t} |\underline{X}(\tau)|_1\, d\tau \quad (20)$$

where $\kappa = \min\{1, b\}$.

Since $W(\underline{X}_t) \geq \kappa |\underline{X}(t)|_1 \quad \forall\, t \geq t_0$, from (20) we obtain

$$|\underline{X}(t)|_1 \leq K(t) + \int_{t_0}^{t} u(\tau)\, |\underline{X}(\tau)|_1 \, d\tau \qquad (21)$$

where

$$K(t) = \frac{\beta + D N_1^\circ (t - t_0)}{\kappa} \;, \quad u(\tau) \equiv -D \,.$$

Then, by Gronwall inequality

$$|\underline{X}(t)|_1 \leq \left( \frac{\beta - N_1^\circ}{\kappa} \right) e^{-D(t-t_0)} + \frac{N_1^\circ}{\kappa} \qquad \forall\, t \geq t_0 \quad (22).$$

Hence, if $\beta \leq N_1^\circ$ then we have the estimate

$$|\underline{X}(t)|_1 \leq \frac{N_1^\circ}{\kappa} \qquad \forall\, t \geq t_0 \qquad (23)$$

whereas if $\beta > N_1^\circ$, then

$$|\underline{X}(t)|_1 \leq \frac{\beta}{\kappa} \qquad \forall\, t \geq t_0 \,. \qquad (24)$$

Since the bounds in (23), (24) are independent of $t_0$, the solutions of (1), in their **existence** interval, are uniform bounded. ■

REMARKS

(i) We assumed $a > c > 0$ and $1 > b > 0$. **Hence** "$a > bc$", which is necessary for "$T_g$" to satisfy the hypothesis $T_g \leq \frac{a - bc}{ac}$, holds true.

## REMARKS

(ii) On $[t_0, +\infty)$, the solutions of (1) have the <u>attractive domain</u>

$$\Omega = \left\{ \underline{X} \in \mathbb{R}^2_{+0} \;\middle|\; N_1 + N_2 \leq \frac{N_1^0}{b} \right\}$$

This follows from (22) as $t \to +\infty$.

(iii) If $g(s) = \delta(s)$ (i.e. no delay in growth response to nutrient uptake), then $T_g = 0$, and we expect that solutions of (1) are uniform bounded for any $T_r \geq 0$.

<u>Positive equilibrium of (1).</u>

We look for positive constant solutions of (1), i.e.

$$N_i(t) = N_i^* \quad , \quad t \in (-\infty, +\infty) \quad , i = 1, 2,$$

which we call "<u>positive equilibrium</u>" of (1). From (1)

$$\begin{cases} \dot{N}_1 = D(N_1^0 - N_1) - aU(N_1)N_2 + b\gamma \int_0^{+\infty} f(s)\, N_2(t-s)\, ds \\ \dot{N}_2 = -(\gamma + D) N_2 + c N_2 \int_0^{+\infty} g(s)\, U(N_1(t-s))\, ds \end{cases}$$

the positive equilibrium $\underline{X}^* = (N_1^*, N_2^*)$ has **components**

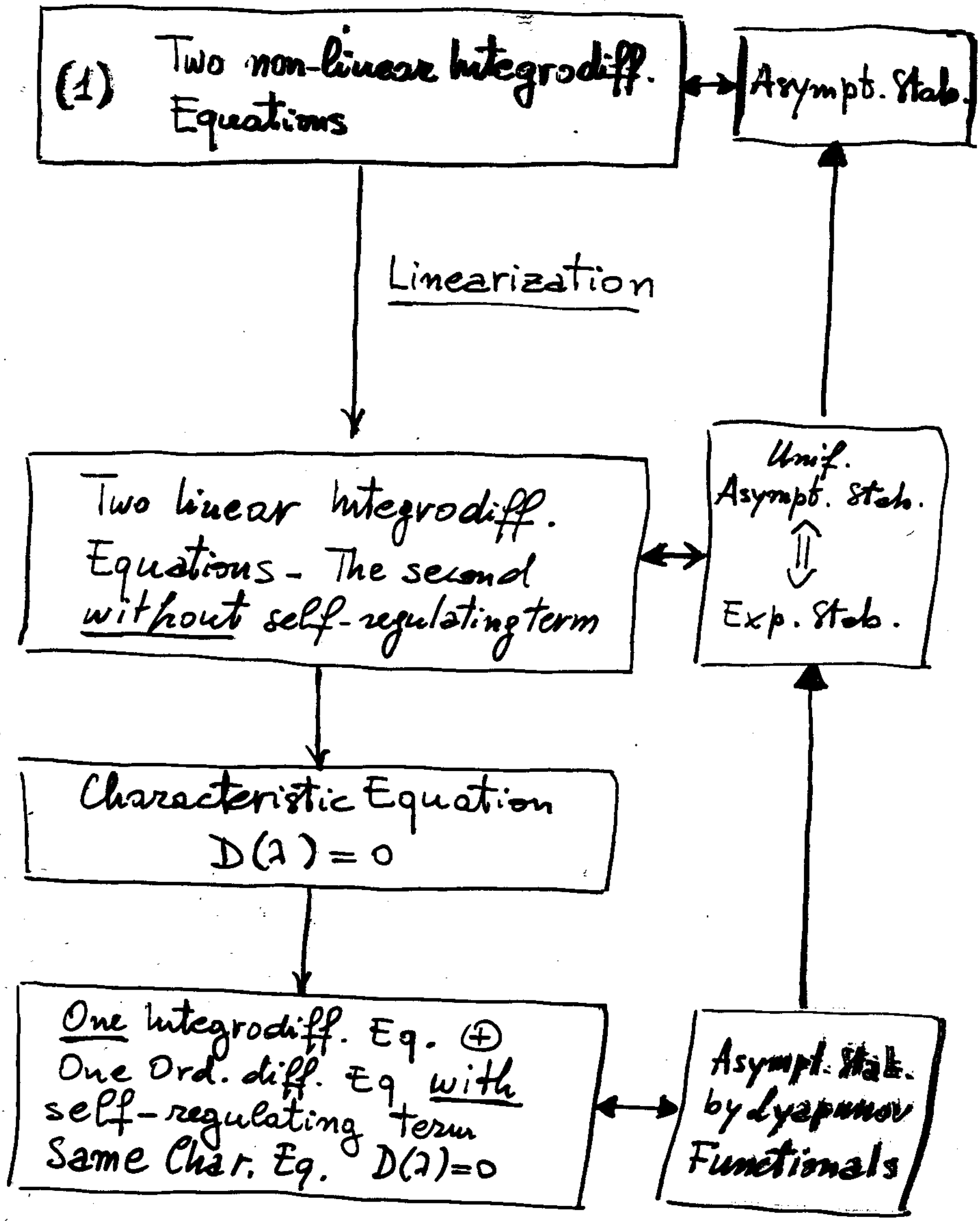
$$N_1^* = U^{-1}\left(\frac{\gamma + D}{c}\right) \quad , \quad N_2^* = \frac{D(N_1^0 - N_1^*)}{aU^* - b\gamma} \qquad (25)$$

<u>provided</u> <u>that</u> "$\frac{\gamma + D}{c} < 1$", and $N_1^* < N_1^0$.

(Observe that "$aU^* - b\gamma = \frac{a}{c} D + \gamma\left(\frac{a}{c} - b\right) > 0$". Hence "$N_1^* < N_1^0$" in order that "$N_2^* > 0$".)

<u>Furthermore</u> $\underline{X}^* \in \Omega$. (This is ensured by $N_1^* < N_1^0$).

# STABILITY OF THE POSITIVE EQUILIBRIUM.



We study the **stability of the** trivial solution of the linearized system

$$\underline{\dot{x}} = \underline{L}(\underline{x}_t) \tag{38}$$

with i.c. $\underline{x}_{t_0} = \underline{\varphi} \in Q_H$.

In fact

a) both the linear (38) and complete equations (32) are autonomous;

b) for autonomous R.F.D.E. (38), the asymptotic stability of the trivial solution is uniform;

c) the uniform asymptotic stability of the trivial solution of (38) is equivalent to its exponential stability;

d) the exponential stability of the trivial solution of (38) implies the asymptotic stability of the trivial solution of the complete equations (32).

(see: V. B. Kolmanovskii and V. R. Nosov - Stability of Functional Differential Equations - Academic Press, Inc., 1986)

# STABILITY OF THE POSITIVE EQUILIBRIUM.

By the help of the equilibrium components

$$U^* = \frac{\gamma + D}{c}, \qquad N_2^* = \frac{D(N_1^0 - N_1^*)}{aU^* - b\gamma}$$

we rewrite equations (1) centred around the positive equilibrium:

$$\dot N_1 = -D(N_1 - N_1^*) - a N_2 \left(U(N_1) - U(N_1^*)\right) - aU(N_1^*)(N_2 - N_2^*) + b\gamma \int_0^{+\infty} f(s)\,(N_2(t-s) - N_2^*)\,ds$$

$$\dot N_2 = c N_2 \int_0^{+\infty} g(s)\left(U(N_1(t-s)) - U(N_1^*)\right) ds . \qquad (26)$$

By introducing

$$x_i = N_i - N_i^*, \quad -N_i^* \leq x_i < +\infty, \quad i = 1,2, \qquad (27)$$

and the function

$$\xi(x_1) := U(N_1) - U(N_1^*), \quad -U(N_1^*) \leq \xi(x_1) < 1 - U(N_1^*) \qquad (28)$$

(observe that $\xi(x_1)x_1 \geq 0 \ \forall x_1$, and $\xi(x_1)x_1 = 0$ iff $x_1 = 0$)

equations (26) become:

$$\begin{cases} \dot x_1 = -Dx_1 - a(x_2 + N_2^*)\xi(x_1) - aU^* x_2 + b\gamma \int_0^{+\infty} f(s)\,x_2(t-s)\,ds \\ \dot x_2 = c(x_2 + N_2^*) \int_0^{+\infty} g(s)\,\xi(x_1(t-s))\,ds \end{cases} \qquad (29)$$

supplemented with i.c.

$$\varphi_i(\theta) = \phi_i(\theta) - N_i^*, \quad \theta \in (-\infty, 0], \ i = 1,2 \qquad (30)$$

where the positive equilibrium corresponds to the trivial solution of (29):

$$x_1(t) = x_2(t) = 0 \quad \text{for all } t \in (-\infty, \infty). \qquad (31)$$

By introducing the nomenclature

$$\underline{x}_t = (x_1(t+\theta), \dot{x}_2(t+\theta))^T, \theta \in (-\infty, 0], t \in \mathbb{R}$$

such that

$$\underline{x}_{t_0} = (\varphi_1(\theta), \varphi_2(\theta))^T = \underline{\varphi}(\theta), \quad \theta \in (-\infty, 0]$$

are the i.c., and the vector

$$\underline{x}(t) = (x_1(t), x_2(t))^T, -N_i^* \le x_i < +\infty, i=1,2,$$

system (29) can be rewritten:

$$\dot{\underline{x}}(t) = \underline{f}(\underline{x}_t), \qquad \underline{x}_{t_0} = \underline{\varphi}(\theta) \in \mathcal{C}_H, \theta \in (-\infty, 0]. \quad (32)$$

i.e. are autonomous R.F.D.E., where

$$\underline{f}(\underline{x}_t) = \begin{pmatrix} -Dx_1 - aN_2^* \xi(x_1) - aU^* x_2 + b\gamma \int_0^{+\infty} f(s) x_2(t-s)\,ds - a x_2 \xi(x_1) \\ cN_2^* \int_0^{+\infty} g(s)\, \xi(x_1(t-s))\,ds + c x_2 \int_0^{+\infty} g(s)\, \xi(x_1(t-s))\,ds \end{pmatrix}$$

System (32) can be linearized around the trivial solution by taking the linear part of the function

$$\xi(x_1) \simeq U'(N_1^*)\, x_1 \quad (33)$$

and neglecting the terms "$O(x_1)$".

By substituting (33) in $\underline{f}(\underline{x}_t)$ we obtain:

$$\underline{f}(\underline{x}_t) = \underline{L}(\underline{x}_t) + \underline{u}(\underline{x}_t); \quad (34)$$

$$\underline{L}(\underline{X}_t) := \underline{\underline{L}}\, \underline{x} + \int_0^{+\infty} \underline{\underline{K}}(s)\, \underline{x}(t-s)\,ds \quad (35)$$

where:

$$\underline{\underline{L}} = \begin{pmatrix} -(D + aN_2^* U'(N_1^*)) & -aU^* \\ 0 & 0 \end{pmatrix} \quad (36)$$

$$\underline{\underline{K}}(s) = \begin{pmatrix} 0 & b\gamma f(s) \\ cN_2^* U'(N_1^*) g(s) & 0 \end{pmatrix} \quad (37)$$

The linearized system (38) is

$$\underline{\dot{x}}(t) = \underline{L}(\underline{x}_t)$$

$$\underline{L}(\underline{x}_t) = \underline{\underline{L}}\,\underline{x}(t) + \int_0^{+\infty} \underline{\underline{K}}(s)\,\underline{x}(t-s)\,ds$$

$$\underline{\underline{L}} = \begin{pmatrix} -(D + aN_2^* U'(N_1^*)) & -aU^* \\ 0 & 0 \end{pmatrix}, \quad \underline{\underline{K}}(s) = \begin{pmatrix} 0 & b\gamma f(s) \\ cN_2^* U'(N_1^*) g(s) & 0 \end{pmatrix}.$$

The characteristic equation for (38) is:

$$D(\lambda) = 0$$

where

$$D(\lambda) := \det\left[\lambda \underline{\underline{I}} - \underline{\underline{L}} - \int_0^{+\infty} \underline{\underline{K}}(s)\, e^{-\lambda s}\, ds\right]$$

"The trivial solution of (38) $\underline{x} = \underline{0}$ is asymptotically stable if and only if in the complex plane $D(\lambda) \neq 0$ whenever $\Re e(\lambda) \geq 0$."

$$D(\lambda) = \det\begin{pmatrix} \lambda + (D + aN_2^* U'(N_1^*)) & aU^* - b\gamma \int_0^{+\infty} f(s) e^{-\lambda s} ds \\ -cN_2^* U'(N_1^*) \int_0^{+\infty} g(s) e^{-\lambda s} ds & \lambda \end{pmatrix}$$

$$F(\lambda) := \int_0^{+\infty} f(s)\, e^{-\lambda s}\, ds \quad ; \quad G(\lambda) := \int_0^{+\infty} g(s)\, e^{-\lambda s}\, ds$$

$$A := D + aN_2^* U'(N_1^*), \quad B := acN_2^* U^* U'(N_1^*), \quad C := b\gamma c N_2^* U'(N_1^*)$$

Hence:

$$D(\lambda) = \lambda^2 + A\lambda + G(\lambda)(B - CF(\lambda)) = 0$$

is the characteristic equation.

$$D(\lambda) = \lambda^2 + A\lambda + G(\lambda)(B - C\,F(\lambda)) = 0 \qquad (39)$$

If we write

$$D(\lambda) = \det \begin{pmatrix} \lambda + \underline{\underline{\delta}} & C\,G(\lambda)F(\lambda) - B\,G(\lambda) + \underline{\underline{\delta\varepsilon}} \\ 1 & \lambda + \underline{\underline{\varepsilon}} \end{pmatrix}$$

where "$\delta, \varepsilon$" are <u>non-negative</u> parameters satisfying

$$\delta + \varepsilon = A \qquad (40)$$

then $D(\lambda) = 0$ provides the <u>same characteristic equation as in (39).</u>

The convolution Kernels

$$\int_0^s g(s-\nu)\,f(\nu)\,d\nu\,;\ \int_0^s f(s-\nu)\,g(\nu)\,d\nu\,,\ s \in \mathbb{R}_{+0}$$

have the same $\mathcal{L}$.T. as $F(\lambda)G(\lambda)$.

<u>Hence, the integrodifferential system</u>

$$\begin{cases} \dot{y} = -\delta y + \delta\varepsilon x - \int_0^{+\infty} f_1(s)\,x(t-s)\,ds + \int_0^{+\infty} f_2(s)\,x(t-s)\,ds \\ \dot{x} = y - \underline{\underline{\varepsilon x}} \end{cases} \qquad (41)$$

<u>where we define</u> "$f_1(s)$", "$f_2(s)$" <u>as</u>

$$\Rightarrow \quad f_1(s) := B\,g(s)\quad,\ f_2(s) := C\int_0^s g(s-\nu)f(\nu)\,d\nu\,,\ s \in \mathbb{R}_{+0}$$

<u>has the same characteristic equation as the lin. system (38).</u>

We denote by

$$\beta_1 = \int_0^{+\infty} s\, f_1(s)\,ds = B\,T_g \quad ; \quad \beta_0 = \int_0^{+\infty} f_1(s)\,ds = B$$

$$\alpha_1 = C\int_0^{+\infty} s\, f_2(s)\,ds = C\,(T_f + T_g)\,;\ \alpha_0 = \int_0^{+\infty} f_2(s)\,ds = C$$

<u>where</u> $\beta_0 - \alpha_0 = B - C = c\,N_2^* U'(N_1^*)\,(aU^* - b\gamma) > 0$

We study the asymptotic stability of the trivial solution of the linearized system (32) by the method of Liapunov functionals:

Denote by $\omega_i(r)$, $r \geq 0$, some scalar, continuous, increasing function such that:

$$\omega_i(0) = 0 \quad , \quad \omega_i(r) > 0 \quad \text{for } r > 0 \, , \quad \lim_{r \to +\infty} \omega_i(r) = +\infty .$$

The following theorem holds:

<u>Theorem 2.</u> Let $V(\underline{x}_t)$ be a continuous scalar functional $: X_H(t) \to \mathbb{R}$ such that:

$$V(\underline{0}) = 0$$

$$V(\underline{x}_t) \geq \omega_1(|\underline{x}(t)|)$$

$$\dot{V}(\underline{x}_t)_{(32)} \leq -\omega_2(|\underline{x}(t)|)$$

for $t \geq t_0$, then $\underline{x} = \underline{0}$ is asymptotically stable.

(In $\omega_2$ we can omit the assumption: $\lim_{r \to +\infty} \omega_2(r) = +\infty$)

(See, e.g.: J.K. Hale. Theory of functional differential Equations. Springer Verlag, 1977).

$$\begin{cases} \dot{y} = -\delta y + \delta \varepsilon x - \int_0^{+\infty} f_1(s)\, x(t-s)\, ds + \int_0^{+\infty} f_2(s)\, x(t-s)\, ds \\ \dot{x} = y - \varepsilon x \end{cases} \qquad (41)$$

Hence, it is sufficient to prove asymptotic stability for the trivial solution $y(t) = x(t) = 0 \quad \forall t \in \mathbb{R}$ of (41) to ensure the asymptotic stability of the positive equilibrium $\underline{X}^* = (N_1^*, N_2^*)^T$ of the original system (1).

According to Theor. 2, we can try to prove asymptotic stability by the functional:

$$V(\underline{x}_t) = y^2 + \varpi x^2 + V_0^2(\underline{x}_t) + + \int_0^{+\infty} (f_1(s) + f_2(s)) \int_{t-s}^{t} dt_1 \int_{t_1}^{t} \left( y^2(u) + (\varepsilon + \beta_0 - \alpha_0) x^2(u) \right) du\, ds, \qquad (42)$$

$\varpi \in \mathbb{R}_+$, where

$$V_0(\underline{x}_t) = y + \delta x - \int_0^{+\infty} f_1(s) \int_{t-s}^{t} x(t_1)\, dt_1\, ds + \int_0^{+\infty} f_2(s) \int_{t-s}^{t} x(t_1)\, dt_1\, ds .$$

By choosing in $\mathbb{R}^2$ the Euclidean norm, once defined $k = \min\{1, \varpi\}$, it follows that:

i) $\quad V(\underline{x}_t) \geq k\, |\underline{x}(t)|^2 \quad, \forall t \geq t_0 \qquad (43)$

ii) Concerning the time derivative of $V(\underline{x}_t)$ along the solutions of (41):

- $$\frac{d}{dt}(\varpi x^2(t)) = 2\varpi\, x(t)\, (y(t) - \varepsilon x(t)) = = 2\varpi x y - 2\varpi \varepsilon x^2 \qquad (44\text{-}a)$$

$$\frac{d}{dt}y^2(t) = 2y(t)\left(-\delta y + \delta\varepsilon x - \int_0^{+\infty} f_1(s)x(t-s)ds + \int_0^{+\infty} f_2(s)x(t-s)ds\right)$$

$$= -2\delta y^2 + 2\delta\varepsilon xy \underbrace{- 2y\int_0^{+\infty} f_1(s)x(t-s)ds}_{} +$$

$$\underbrace{+2y\int_0^{+\infty} f_2(s)x(t-s)ds}_{}.$$

Now observe that:

$$\int_0^{+\infty} f_1(s)\int_{t-s}^{t} x'(u)du\,ds = x\beta_0 - \int_0^{+\infty} f_1(s)x(t-s)ds$$

Thus:

$$\int_0^{+\infty} f_1(s)x(t-s)ds = \beta_0 x - \int_0^{+\infty} f_1(s)\int_{t-s}^{t}(y(u)-\varepsilon x(u))du\,ds$$

and analogously

$$\int_0^{+\infty} f_2(s)x(t-s)ds = \alpha_0 x - \int_0^{+\infty} f_2(s)\int_{t-s}^{t}(y(u)-\varepsilon x(u))du\,ds.$$

Therefore:

$$\underbrace{-2y\int_0^{+\infty} f_1(s)x(t-s)ds}_{} + \underbrace{2y\int_0^{+\infty} f_2(s)x(t-s)ds}_{} =$$

$$-2(\beta_0-\alpha_0)xy + 2y\int_0^{+\infty} f_1(s)\int_{t-s}^{t}(y(u)-\varepsilon x(u))du\,ds$$

$$-2y\int_0^{+\infty} f_2(s)\int_{t-s}^{t}(y(u)-\varepsilon x(u))du\,ds \leq$$

$$\leq -2(\beta_0-\alpha_0)xy + y^2\beta_1 + \varepsilon y^2\beta_1 + \int_0^{+\infty} f_1(s)\int_{t-s}^{t}(y^2(u)+\varepsilon x^2(u))du\,ds$$

$$+ y^2\alpha_1 + \varepsilon y^2\alpha_1 + \int_0^{+\infty} f_2(s)\int_{t-s}^{t}(y^2(u)+\varepsilon x^2(u))du\,ds$$

Finally, we obtain:

$$\frac{d}{dt}y^2(t) \leq -2\delta y^2 + 2\delta\varepsilon xy - 2(\beta_0-\alpha_0)xy +$$

$$+(1+\varepsilon)(\alpha_1+\beta_1)y^2 + \int_0^{+\infty}(f_1(s)+f_2(s))\int_{t-s}^{t}(y^2(u)+\varepsilon x^2(u))du\,ds \quad (44\text{-b})$$

Consider now the contributions due to $V_0^2(\underline{x}_t)$:

$$\frac{d}{dt}V_0(\underline{x}_t) = \frac{d}{dt}\left(y+\delta x - \int_0^{+\infty} f_1(s)\int_{t-s}^{t} x(t_1)\,dt_1\,ds + \int_0^{+\infty} f_2(s)\int_{t-s}^{t} x(t_1)\,dt_1\,ds\right)$$

$$= \dot{y} + \delta\dot{x} - (\beta_0-\alpha_0)x + \int_0^{+\infty} f_1(s)x(t-s)\,ds - \int_0^{+\infty} f_2(s)x(t-s)\,ds =$$

$$= \cancel{-\delta y + \delta\varepsilon x} \cancel{+\delta y - \delta\varepsilon x} - \int_0^{+\infty} f_1(s)\cancel{x(t-s)}\,ds + \int_0^{+\infty} f_2(s)\cancel{x(t-s)}\,ds$$

$$- (\beta_0-\alpha_0)x + \int_0^{+\infty} f_1(s)\cancel{x(t-s)}\,ds - \int_0^{+\infty} f_2(s)\cancel{x(t-s)}\,ds =$$

$$= -(\beta_0-\alpha_0)x \quad , \quad \beta_0-\alpha_0>0.$$

Hence:

$$\frac{d\,V_0^2(\underline{x}_t)}{dt} = -2(\beta_0-\alpha_0)x\,V_0(\underline{x}_t) =$$

$$= -2(\beta_0-\alpha_0)xy - 2(\beta_0-\alpha_0)\delta x^2 + 2(\beta_0-\alpha_0)x\int_0^{+\infty} f_1(s)\int_{t-s}^{t} x(t_1)\,dt_1\,ds$$

$$- 2(\beta_0-\alpha_0)x\int_0^{+\infty} f_2(s)\int_{t-s}^{t} x(t_1)\,dt_1\,ds \leqslant$$

$$\leqslant -2(\beta_0-\alpha_0)xy - 2(\beta_0-\alpha_0)\delta x^2 + (\beta_0-\alpha_0)(\beta_1+\alpha_1)x^2 +$$

$$+ (\beta_0-\alpha_0)\int_0^{+\infty}(f_1(s)+f_2(s))\int_{t-s}^{t} x^2(t_1)\,dt_1\,ds. \qquad (44c)$$

The integral term in (44-c) jointly with the one in (44-b) give rise to:

$$\int_0^{+\infty}(f_1(s)+f_2(s))\int_{t-s}^{t}\left(y^2(u)+(\varepsilon+\beta_0-\alpha_0)x^2(u)\right)du\,ds. \qquad (44\text{-}d)$$

Now, observe that the time derivative of the integral term in the functional (42), i.e.

$$\frac{d}{dt}\left\{\int_0^{+\infty}(f_1(s)+f_2(s))\int_{t-s}^{t} dt_1\int_{t_1}^{t}\left(y^2(u)+(\varepsilon+\beta_0-\alpha_0)x^2(u)\right)du\,ds\right\} =$$

$$= (\beta_1+\alpha_1)\left(y^2+(\varepsilon+\beta_0-\alpha_0)x^2\right)$$

$$- \int_0^{+\infty}(f_1(s)+f_2(s))\int_{t-s}^{t}\left(y^2(u)+(\varepsilon+\beta_0-\alpha_0)x^2(u)\right)du\,ds \qquad (44\text{-}e)$$

is such that the 2nd term in (44-e) cancels (44-d).

Now, taking jointly (44-a)-(44-e), we finally obtain:

$$\left.\frac{dV(\underline{x}_t)}{dt}\right|_{(41)} \leq -\left\{2(\beta_0-\alpha_0)\delta + 2\varpi\varepsilon - (2(\beta_0-\alpha_0)+\varepsilon)(\alpha_1+\beta_1)\right\}x^2 + \overbrace{2\left\{\varpi - 2(\beta_0-\alpha_0)+\delta\varepsilon\right\}xy}^{=0} + - \left\{2\delta - (2+\varepsilon)(\alpha_1+\beta_1)\right\}y^2 \qquad (45)$$

It is possible to choose nonnegative "$\delta$" and "$\varepsilon$" satisfying $\delta+\varepsilon = A$ and a positive "$\varpi$" such that:

$$\varpi = 2(\beta_0-\alpha_0) - \delta\varepsilon \qquad (46)$$

By this choice the 2nd term in (45) equals zero.

If it is possible to choose $\delta, \varepsilon, \varpi$ such that:

i) $\delta+\varepsilon = A$

ii) $\varpi = 2(\beta_0-\alpha_0) - \delta\varepsilon > 0$

iii) $\alpha_1+\beta_1 < \dfrac{2(\beta_0-\alpha_0)\delta + 2\varpi\varepsilon}{2(\beta_0-\alpha_0)+\varepsilon}$

iv) $\alpha_1+\beta_1 < \dfrac{2\delta}{2+\varepsilon}$

then $\left.\dfrac{dV(\underline{x}_t)}{dt}\right|_{(41)} \leq -\omega_3(|\underline{x}(t)|)$ and the asymptotic stability follows.

Observe that, if we choose

$$\delta = A, \quad \varepsilon = 0, \quad \varpi = 2(\beta_0-\alpha_0) > 0 \qquad (47)$$

the conditions iii), iv) become identical and are

$$\boxed{\alpha_1+\beta_1 < A} \qquad (48).$$

The choice (47) (i.e. $\delta = A$, $\varepsilon = 0$, $W = 2(\beta_0 - \alpha_0)$) is the <u>best</u> in the sense that it gives the <u>maximum</u> upper bound on $\alpha_1 + \beta_1$.
Note that (48) (i.e. $\alpha_1 + \beta_1 < A$) is necessary since $\alpha_1 + \beta_1 < \frac{2\delta}{2+\varepsilon}$, $\delta + \varepsilon = A$ and $\varepsilon \geq 0$ imply (48).

Therefore, we can prove the following theorem:

<u>Theorem 3.</u> The positive equilibrium of (1) is asymptotically stable if

$$\alpha_1 + \beta_1 < A \tag{48}$$

<u>Proof</u>. The choice $\delta = A$, $\varepsilon = 0$ implies that system (41) becomes

$$\begin{cases} \dot{y} = -Ay - \int_0^{+\infty} f_1(s)x(t-s)\,ds + \int_0^{+\infty} f_2(s)x(t-s)\,ds \\ \dot{x} = y \end{cases} \tag{49}$$

and the functional $V(\underline{x}_t)$ in (42), with the further choice $W = 2(\beta_0 - \alpha_0)$, has a time derivative that along the solutions of (49) results (c.f.(45)):

$$\dot{V}(\underline{x}_t)\big|_{(49)} \leq -2\,(A - (\alpha_1 + \beta_1))\,(y^2 + (\beta_0 - \alpha_0)x^2) \leq$$
$$\leq -2k\,(A - (\alpha_1 + \beta_1))\,|\underline{x}|^2 \tag{50}$$

where $k = \min\{1, \beta_0 - \alpha_0\}$ and $|\underline{x}|$ is the usual Euclidean norm in $\mathbb{R}^2$.
This completes the proof. ■

<u>REMARK</u>: for $\varepsilon = 0$, without $V_0^2(\underline{x}_t)$, <u>fails</u> <u>to</u> <u>be</u> <u>true</u> 25
<u>negative</u> <u>definiteness</u> <u>of</u> $\underline{\dot{V}}$ (*is absent any term in "$-x^2$"*)

## Some Remarks on Theor. 3.

The sufficient condition for asymptotic stability of the positive equilibrium of (1) reads:

$$(B+C)\,T_g + C\,T_r < A$$

where

$T_r$ average time delay in recycling process
$T_g$ " " " in growth response to nutrient uptake.

$$A = D + a N_2^* U'(N_1^*) \qquad U^* = \frac{\gamma + D}{c} < 1 \qquad U^* = U(N_1^*)$$

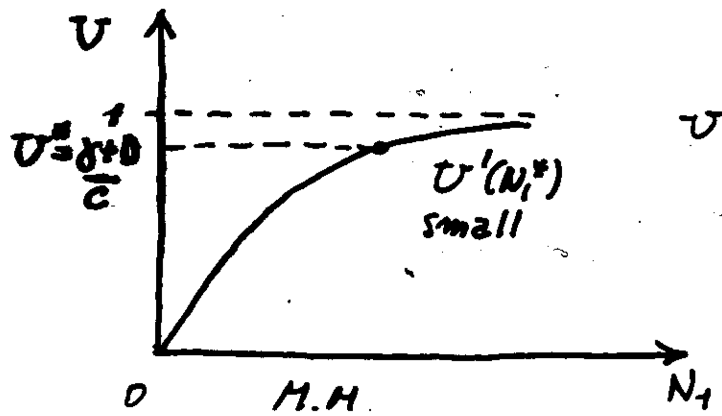
$$B = ac\, N_2^* U^* U'(N_1^*) \qquad N_2^* = \frac{D(N_1^0 - N_1^*)}{aU^* - b\gamma}$$

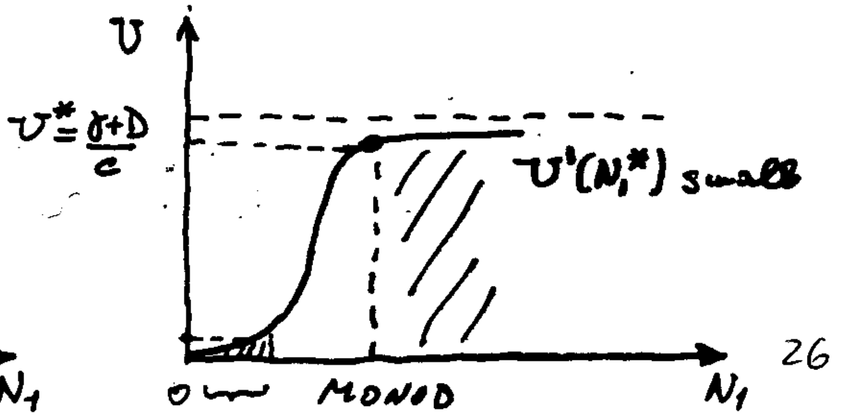
$$C = b\gamma c\, N_2^* U'(N_1^*)$$

By this nomenclature, the sufficient condition for asymptotic stability of the positive equilibrium becomes:

$$(aU^* + b\gamma)T_g + b\gamma \frac{D(N_1^0 - N_1^*)}{aU^* - b\gamma}\, T_r < \frac{aU^* - b\gamma}{c(N_1^0 - N_1^*)\,\underline{U'(N_1^*)}} + \frac{a}{c}$$

where the parameters which can be controlled are
"$D$" the "wash-out" constant; $\left(D : U^* = \frac{\gamma+D}{c} \Leftrightarrow U'(N_1^*) \text{ small}\right)$
"$N_1^0$" the input nutrient concentration. $(N_1^0 \gtrsim N_1^*)$



## Chemostat equations with only the delayed recycling.

In this section we consider the chemostat equations without delayed response in the growth of the biotic species, i.e. assuming for $g(s) = \delta(s)$, where $\delta(s)$ is the delta Dirac function, and thus obtaining:

$$
\begin{aligned}
\dot{N}_1 &= D(N_1^0 - N_1) - a\,U(N_1)N_2 + b\gamma \int_0^{+\infty} f(s)\, N_2(t-s)\, ds \\
\dot{N}_2 &= -(\gamma + D)\, N_2 + c\,U(N_1)\, N_2
\end{aligned}
\qquad (2.1)
$$

supplemented with the same i.c. as system (1), and where all the parameters are defined as in Section 1.

With the same kind of proof as for Theorem 1 in Section 1, the following holds:

Theorem 2.1. All the solutions $\underline{X}(t) = \underline{X}(t, \underline{\Phi})$, $\underline{\phi} \in Q_H$, of (1.1) are uniform bounded in $\mathbb{R}^2_{+0}$.

REMARKS

The proof can be performed by the functional:

$$W(\underline{X}_t) = N_1 + \frac{a}{c} N_2 + b\gamma \int_0^{+\infty} f(s) \int_{t-s}^{t} N_2(u)\, du\, ds \qquad (2.2)$$

Defined

$$\eta = \frac{a}{c} + b\gamma T_r \qquad (2.3)$$

and $\beta = 2\eta H$, one obtains that in $\mathbb{R}^2_{+0}$

$$N_1(t) + N_2(t) \leq N_1^0 \quad \forall\, t \geq t_0 \qquad (2.4)$$

if $\underline{\beta \leq N_1^0}$, otherwise

$$N_1(t) + N_2(t) \leqslant \beta \qquad \forall\, t \geqslant t_0. \tag{2.5}$$

Hence, defined

$$K = \max\left\{ N_1^0 \,,\; 2\eta H \right\} \quad , \eta = \frac{a}{c} + b\gamma T_r \tag{2.6}$$

the solutions of (2.1) with *i.c.* $\underline{\phi} \in Q_H$ are <u>uniform</u> <u>bounded</u> in:

$$\Omega_1 = \left\{ \underline{X} \in \mathbb{R}^2_{+0} \mid N_1 + N_2 \leqslant K \right\} \tag{2.7}$$

Furthermore, an <u>attractive</u> <u>domain</u> (as $t \to +\infty$) for all the solutions of (2.1) with i.c. in $Q_H$ is:

$$\Omega = \left\{ \underline{X} \in \mathbb{R}^2_{+0} \mid N_1 + N_2 \leqslant N_1^0 \right\} \quad . \tag{2.8}$$

- Therefore, whenever be $T_r > 0$, we can choose the uniform bound $H$ on the i.c. $\underline{\phi}$ in order that $2\eta H \leqslant N_1^0$, *i.e.* $\Omega_1 \equiv \Omega$.
- Observe that system (2.1) has the same positive equilibrium $\underline{X}^* = (N_1^*, N_2^*)^T$ of system (1):

$$N_1^* = U^{-1}\left(\frac{\gamma + D}{c}\right) \;,\quad N_2^* = \frac{D(N_1^0 - N_1^*)}{aU^* - b\gamma} \tag{2.9}$$

which exists provided that

$$\frac{\gamma + D}{c} < 1 \quad , \quad N_1^0 > N_1^* \tag{2.10}$$

- Of course $\underline{X}^* \in \Omega$.

It is suitable to perform the variables changes:

$$x_i = N_i - N_i^* \quad , -N_i^* \le x_i < +\infty \quad , \quad i=1,2 \qquad (2.11)$$

and

$$\xi(x_1) = U(N_1) - U^* \quad , -U^* \le \xi(x_1) < 1 - U^* \qquad (2.12)$$

observing that $\xi(x_1)x_1 \geq 0$ and $\xi(x_1)x_1 = 0$ iff $x_1 = 0$.

System (2.1) becomes:

$$\begin{cases} \dot{x}_1 = -Dx_1 - aN_2\xi(x_1) - aU^*x_2 + b\gamma \int_0^{+\infty} f(s)x_2(t-s)ds \\ \dot{x}_2 = c N_2 \xi(x_1) \end{cases} \qquad (2.13)$$

with i.c. $\underline{\varphi} = \underline{\phi} - \underline{X}^*$ , $\underline{\phi} \in \Omega_H$, and the positive equilibrium transformed into the trivial solution:

$$x_1(t) = x_2(t) = 0 \quad \text{for all } t \in \mathbb{R}. \qquad (2.14).$$

We study its stability by the <u>Liapunov functional</u>:

$$V(\underline{x}_t) = w_1 N_1^* \int_0^{x_1} \xi(v)\,dv + w_2\left(x_2 - N_2^* \log \frac{x_2 + N_2^*}{N_2^*}\right) +$$

$$+ \frac{1}{2} b\gamma c \int_0^{+\infty} f(s) \int_{t-s}^{t} dt_1 \int_{t_1}^{t} N_2^2(u)\xi^2(x_1(u))\,du\,ds \,, \qquad (2.15)$$

where $w_i \in \mathbb{R}_+$, $i = 1,2$ are arbitrary constants.

Furthermore, we assume a <u>Michelis-Menten saturation law for $U(N_1)$</u>: $U(N_1) = \frac{N_1}{L+N_1}$ <u>which provides</u>:

$$\xi^2(x_1) \leq \frac{1}{L+N_1^*} x_1 \xi(x_1) \qquad \forall x_1 \,. \qquad (2.16)$$

We can prove the following

Theorem 2.2. If the average time delay $T_r$ satisfies

$$T_r^2 < \frac{4aD}{(b\gamma c)^2 U^*} \cdot \frac{N_1^*}{K} , \qquad (2.17)$$

$K = \max\{N_1^0, 2(\frac{a}{c} + b\gamma T_r)H\}$, then all the solutions of (2.13) with i.c. $\underline{\varphi} \in \Gamma_\ell$, $\Gamma_\ell = \{\underline{\varphi} \mid V(\underline{\varphi}) < \ell\}$, approach $x_1 = x_2 = 0$ as $t \to +\infty$.

Proof.

$$\dot{V}(\underline{x}_t)_{(2.13)} = -w_1 D N_1^* x_1 \xi(x_1) - w_1 a N_1^* N_2 \xi^2(x_1) +$$

$$-\overline{w}_1 a N_1^* U^* \xi(x_1) x_2 + \overline{w}_2 c\, \xi(x_1) x_2 + \frac{1}{2} b\gamma c N_2^2 T_r \xi^2(x_1)$$

$$- \frac{1}{2} b\gamma c \int_0^{+\infty} f(s) \int_{t-s}^{t} N_2^2(u) \xi^2(x_1(u))\, du\, ds +$$

$$+ \overline{w}_1 N_1^* b\gamma\, \xi(x_1) \int_0^{+\infty} f(s) x_2(t-s) ds \qquad (2.18).$$

Concerning the last term in (2.18):

$$\int_0^{+\infty} f(s) \int_{t-s}^{t} x_2'(u)\, du\, ds = x_2 - \int_0^{+\infty} f(s) x_2(t-s) ds$$

Thanks to the 2nd of (2.13):

$$\int_0^{+\infty} f(s) x_2(t-s) ds = x_2 - c \int_0^{+\infty} f(s) \int_{t-s}^{t} N_2(u) \xi(x_1(u))\, du\, ds$$

Hence

$$\overline{w}_1 N_1^* b\gamma\, \xi(x_1) \int_0^{+\infty} f(s) x_2(t-s) ds = \overline{w}_1 N_1^* b\gamma\, \xi(x_1) x_2 +$$

$$- b\gamma c N_1^* \overline{w}_1 \xi(x_1) \int_0^{+\infty} f(s) \int_{t-s}^{t} N_2(u) \xi(x_1(u))\, du\, ds \qquad (2.19)$$

The last term in (2.19) provides the inequality:

$$-b\gamma c\,\varpi_1 N_1^* \xi(x_1)\int_0^{+\infty} f(s)\int_{t-s}^{t} N_2(u)\,\xi(x_1(u))\,du\,ds \le$$

$$\le \frac{1}{2}\, b\gamma c \int_0^{+\infty} f(s)\int_{t-s}^{t}\left[\left(\varpi_1 N_1^* \xi(x_1(t))\right)^2 + N_2^2(u)\,\xi^2(x_1(u))\right]du\,ds =$$

$$= \frac{1}{2}\,\varpi_1^2 N_1^{*2}\, b\gamma c\, T_r\, \xi^2(x_1) + \frac{1}{2} b\gamma c \int_0^{+\infty} f(s)\int_{t-s}^{t} N_2^2(u)\,\xi^2(x_1(u))\,du\,ds$$

By inserting this inequality in (2.19) and then the resulting one in (2.18) we obtain:

$$\dot V(\underline{x}_t)_{(2.13)} \le -\varpi_1 N_1^*\left[D x_1 \xi(x_1) - \varpi_1 \frac{b\gamma c}{2} T_r N_1^* \xi^2(x_1)\right] +$$

$$- N_2\left[\varpi_1 a N_1^* - \frac{b\gamma c}{2} N_2 T_r\right]\xi^2(x_1) - \overbrace{\left[\varpi_1 N_1^*(aU^* - b\gamma) - \varpi_2 c\right]}^{=0}\xi(x_1)\,x_2 .$$

Since $aU^* - b\gamma > 0$ we choose

$$\varpi_2 = \frac{N_1^*(aU^* - b\gamma)}{c}\,\varpi_1 , \quad \forall \varpi_1 \in \mathbb{R}_+ .$$

Furthermore, observe that:

- $N_1^*\, \xi^2(x_1) \le \dfrac{N_1^*}{L+N_1^*}\,\xi(x_1)\,x_1 = U^*\,\xi(x_1)\,x_1$
- $0 < N_2(t) \le K \quad \forall\, t \ge t_0$. Then

$$\dot V(\underline{x}_t)_{(2.13)} \le -\varpi_1 N_1^*\left[D - \varpi_1 \frac{b\gamma c}{2} U^* T_r\right]\xi(x_1)\,x_1 +$$

$$- N_2\left[\varpi_1 a N_1^* - \frac{b\gamma c}{2} K T_r\right]\xi^2(x_1) \qquad (2.20)$$

(2.20) is negative semi-definite if we choose $\varpi_1$:

$$\frac{b\gamma c K T_r}{2aN^*} < \varpi_1 < \frac{2D}{b\gamma c U^*}\,\frac{1}{T_r} \qquad (2.21)$$

The inequality (2.17) assures that the choice (2.21) for $\varpi_1$ exists.

Let E be the set in $\Gamma_\ell = \{\underline{\varphi} \mid V(\underline{\varphi}) < \ell\}$ where $\dot{V}(\underline{\varphi})_{(2.13)} = 0$.

From (2.20) it follows that $E \subseteq E' = \{\underline{\varphi} \in \Gamma_\ell \mid \varphi_1 = 0\}$.

If $\underline{x}_t \in E$, then $x_{1t} = 0 \quad \forall t \in \mathbb{R}$. Hence from (2.13):

$$\begin{aligned} \dot{x}_1\big|_E &= -aU^* x_2 + b\gamma \int_0^{+\infty} f(s)\, x_2(t-s)\, ds \\ \dot{x}_2\big|_E &= 0 \end{aligned} \tag{2.22}$$

Any invariant solution of (2.22) must have $x_{2t} = \bar{x}_2$, $\bar{x}_2$ constant $\forall t \in \mathbb{R}$, i.e.

$$\dot{x}_1\big|_E = -(aU^* - b\gamma)\,\bar{x}_2 \,.$$

Since $aU^* - b\gamma > 0$, then $\bar{x}_2 = 0$. Therefore, the only invariant subset $M$ of E is the trivial solution: $M = \{\underline{x}_t = \underline{0} \,, \forall t \in \mathbb{R}\}$. ■

## REMARKS

a) A slight modification of the proof gives rise to a different sufficient condition on $T_r$:

$$T_r < \min\left\{ \frac{2D}{b\gamma c\, U^*} \,,\, \frac{2a}{b\gamma c}\,\frac{N_1^*}{K} \right\} \tag{2.23}$$

Of course, the "best" condition on $T_r$ remains (2.17).

REMARKS

b) If we choose the i.c. $\underline{\varphi} = \underline{\phi} - \underline{X}^*$ with $\underline{\phi} \in Q_H$ where H is sufficiently small so that

$$H \leq \frac{N_1^0}{2\left(\frac{a}{c} + b\gamma T_r\right)}, \quad \text{then}$$

condition (2.17) reads:

$$T_r^2 < \frac{4aD}{(b\gamma c)^2 U^*} \frac{N_1^*}{N_1^0}.$$

c) If we set "$T_g = 0$" into the sufficient condition obtained by Liapunov functionals on the chemostat linearized equations (Theorem 3, previous section) we obtain:

$$T_r < \frac{D + aN_2^* U'(N_1^*)}{b\gamma c\, N_2^* U'(N_1^*)}$$

d) An analysis performed on the characteristic equation

$$\lambda^2 + \lambda A - C\mathcal{L}(\lambda) + B = 0$$

where $\mathcal{L}(\lambda) = \int_0^{+\infty} f(s) e^{-\lambda s} ds$ and

$$A = D + aN_2^* U'(N_1^*),\ B = ac\,U^* N_2^* U'(N_1^*),\ C = b\gamma c N_2^* U'(N_1^*)$$

shows that

i) for a general delay Kernel "$f(s)$" the positive equilibrium is locally asymptotically stable if

$$\gamma \leq \frac{D^2 + a^2 N_2^{*2} U'(N_1^*)^2}{2a N_1^* U'(N_1^*)}$$

## REMARKS

d) *ii)* If "$f(s)$" is one of the $\gamma$-distributions

$$f(s) = \frac{\alpha^p}{(p-1)!}\, s^{p-1} \exp(-\alpha s), \quad s \in \mathbb{R}_{+0}$$

$p \in \mathbb{N} = \{1, 2, \dots\}$, $\alpha \in \mathbb{R}_+$, then for any order "$p$" the positive equilibrium is locally asymptotically stable. $\left(T_r = \frac{p}{\alpha}\right)$

e) If "$f(s) = \delta(s)$" (instantaneous recycling) the positive equilibrium is globally asymptotically stable.

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## DEFINITIONS.

$$(1) \quad \dot{\underline{X}} = \underline{F}(t, \underline{X}_t) \quad , \quad \underline{F}(t, \underline{0}) = \underline{0}$$

i.c. $\underline{X}_{t_0} = \underline{\phi} \in \mathcal{C}_H$

<u>Definition 1</u>. The solutions of (1) are <u>equi-bounded</u> if for any $H>0$ and $t_0 \in \mathbb{R}$, there exists a constant $\beta(t_0,H)>0$ such that if $\underline{\phi} \in \mathcal{C}_H$,

$$|\underline{X}(t;t_0,\underline{\phi})| < \beta(t_0,H) \quad \text{for all } t \geq t_0 .$$

<u>Def. 2.</u> The solutions of (1) are <u>uniform-bounded</u> if the $\beta$ in Def. 1 is independent of $t_0$.

<u>Def. 3</u>. The trivial solution of (1) is <u>stable</u> if for any $0<\varepsilon<H$ there exists a $\delta=\delta(\varepsilon,t_0)>0$ such that for any $\underline{\phi} \in \mathcal{C}_\delta$

$$|\underline{X}(t;t_0,\underline{\phi})| \leq \varepsilon \quad \text{for all } t \geq t_0 .$$

<u>Def. 4</u> The stability is <u>uniform</u> if the "$\delta$" in Def. 3 is independent of $t_0$.

<u>Def. 5</u>. The trivial solution of (1) is <u>asymptotically stable</u> if: (i) it is stable, (ii) for any $t_0$, $\exists\ \Delta=\Delta(t_0)>0$ such that

$$\lim_{t\to+\infty} \underline{X}(t;t_0,\underline{\phi}) = \underline{0} \quad , \quad \underline{\phi} \in \mathcal{C}_\Delta$$

Def. 6. The trivial solution of (1) is Exponentially Stable if any solution $\underline{X}(t; t_0, \underline{\phi})$ satisfies the inequality

$$\left|\underline{X}(t; t_0, \underline{\phi})\right| \leqslant B \|\underline{\phi}\| \exp(-\alpha(t-t_0)) \quad t \geqslant t_0$$

$$B > 0, \quad \alpha > 0, \quad \|\underline{\phi}\| \leqslant H_1 \leqslant H.$$