

Plant Growth and the Circulation of a Mineral Nutrient

IGOR LEILER

Department of Biophysics, Faculty of Science, Kyoto University
Sakyo-ku, Kyoto, 606, Japan

(Received August 25, 1987)

Abstract The dependence of growth of a plant population on the circulation of a mineral nutrient is analyzed by means of a mathematical model which consists of four first order nonlinear differential equations. Three of them describe the nutrient flow between the nutrient pool, the plant population itself, and its litter. The remaining equation describes the plant growth. Michaelis-Menten kinetics is used to represent the material flow from the nutrient pool to the plant population, and the growth of the plant is described by a generalized logistic equation. A comprehensive analysis of the plant growth and its dependency on the system parameters is given.

INTRODUCTION

The material circulation in ecosystems, along with the energy flow, is a principal problem of systems ecology and environmental sciences, and various theoretical investigations have been developed. Waide et al. (1974) studied the calcium circulation in a forested watershed ecosystem by means of a linear system analysis. They analyzed the response of the system to a calcium input as well as the stability of circulation. Further, the nutrient uptake and the growth response of plants have been widely investigated as fundamental problems of plant production (e.g. Nye et al., 1975). It is clear that these two problems are closely related, and specifically the nonlinear response of plant growth is thought to play an important role in regulating nutrient cycle. The main objective of this paper is the interplay between plant growth and nutrient cycle with focus on the effects of nonlinear response of the former on the latter by using a simple model ecosystem.

We consider the cyclic flow of a mineral nutrient in a closed ecosystem consisting of three compartments: an available nutrient pool, a population of a single plant species and organic materials in the litter including decomposer organisms (Fig. 1). In the

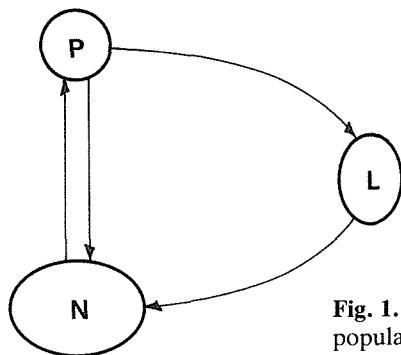


Fig. 1. Nutrient circulation. N—nutrient pool; P—plant population; L—litter and decomposers.

present model, input and output flow rates are assumed to be negligible compared with the internal flow rates of the nutrient. The nonlinear response of plant growth is taken into account by introducing the carrying capacity of the plant population, which depends on the concentration of the incorporated nutrient. Connecting this plant growth response with the cyclic flow of nutrient, we analyze the stability condition of nutrient cycle in the three compartment system.

THE MODEL

The mechanism of nutrient cycle is highly intricate even in a simple ecosystem (see for example Epstein, 1972), and we cannot give here a sweeping description of the circulation processes.

The plant takes up nutrients from the soil mainly through its roots and the absorbed nutrients cooperate with other factors in the process of plant growth. When a part of a plant such as withered leaves and branches, or a whole plant falls on the ground, the incorporated nutrients are released from the plant and become a part of the litter. There may also be a small contribution due to secretions and excretions. The mineral nutrients contained in organic materials of the litter are decomposed by the decomposers in the litter or leached by the physical environmental conditions, and released into the nutrient pool. Thus, the system repeats this cyclic process.

The above simplified picture serves as the basis of a model that deals with a mineral nutrient and a single plant species in a closed ecosystem. To specify a model we make further assumptions as follows:

- (1) Environmental conditions of the plant such as temperature, humidity and light intensity are optimal.
- (2) The nutrient is supposed to affect the growth rate of the plant only after it is absorbed.
- (3) The response of the plant to the incorporated nutrient is immediate and has no time delay in the time scale of our dynamical model.
- (4) The available nutrient pool and the litter are homogeneous.
- (5) All the plants are of the same genotype.

Suppose the following four variables:

x , y and z : the total amounts of the nutrient contained at time t in the available nutrient pool, in the plants and the litter, respectively,

w : the pure dry weight of the plant at time t , where we define
(pure dry weight) = (total dry weight) - (mineral nutrients)

Then, a dynamical model of the nutrient cycle can be given by the set of differential equations:

$$\frac{dx}{dt} = -\frac{Axw}{x+K} + Ly + Dz \quad (1.1.a)$$

$$\frac{dy}{dt} = -Ly - My + \frac{Axw}{x+K} \quad (1.1.b)$$

$$\frac{dz}{dt} = -Dz + My \quad (1.1.c)$$

$$\frac{dw}{dt} = R[F(c) - w]w \quad (1.1.d)$$

where c is the concentration of the nutrient in the dry matter of the plant:

$$c = \frac{y}{w + y}$$

Note that the nutrient cycle given by (1.1.a)–(1.1.c) is coupled with the growth equation of the plant governed by (1.1.d) through the term of uptake rate which appears in (1.1.a) and (1.1.b), and the function $F(c)$.

The first term of (1.1.a) represents the uptake rate of a plant, which is assumed to follow a Michaelis-Menten type kinetics. The constant A gives the maximum uptake rate. The absorption capacity of the plant, K , is a half-saturation constant, which corresponds to the amount of available nutrient x at which the uptake rate becomes a half of the maximum, and it is related to absorbing ability of the plant at a low concentration nutrient pool. It is also assumed as a first approximation that the uptake rate is proportional to the plant size, which is, in turn, proportional to the pure dry weight w . The second term Ly expresses a loss of the nutrient from the plant through leaching, secretions and excretions. These processes are physiologically important in the plant growth process, but in many cases the rates are relatively small (Parker, 1983). The third term Dz stands for the inflow from the litter, which ought to be the decomposition rate of organic matter in the litter, and the amount of the decomposers is assumed to be proportional to that of the nutrient contained in the litter. This assumption is made here for the sake of model simplicity, but it may be applicable to some cases (Heath et al., 1966).

The second term My of equation (1.1.b) stands for the loss of the incorporated nutrient from the plant due to the death and withering processes.

The last equation (1.1.d) represents the growth rate of plant in terms of the pure dry weight, where the carrying capacity $F(c)$ of plant biomass (pure dry weight) is assumed to depend on the concentration of the absorbed nutrient. It is known that per capita dry matter production of plant, $RF(c)$, generally depends on the concentration of nutrient in plant as shown in Fig. 2 (Larcher, 1980). This figure shows that there are basically three nutrient states in terms of $F(c)$: deficiency, adequate supply and toxic excess. It can be

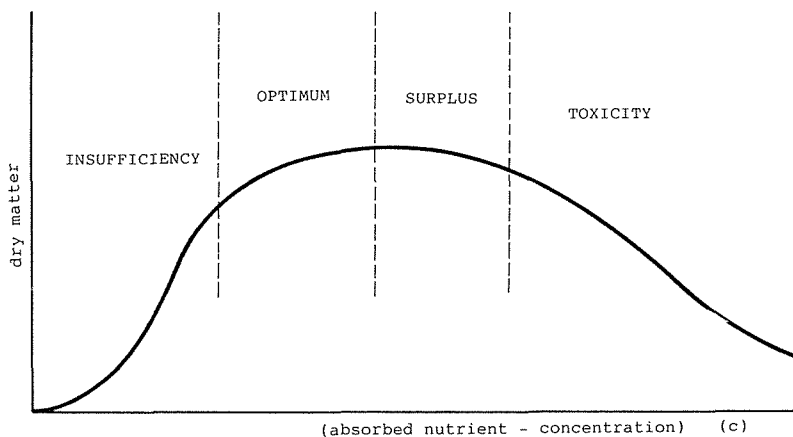


Fig. 2. Dry matter as a function of the absorbed nutrient (After Larcher, 1980).

seen that both, nutrient shortage and overabundance give the same suppressive effect on the plant production.

STATIONARY STATES

In the system (1.1) all the parameters are assumed to be nonnegative, i.e., $A, D, K, R > 0$, $L, M \geq 0$ and $L + M > 0$. Since we consider a closed system, the total amount of nutrient $x + y + z = m$ is conserved and only three of the equations (1.1) are independent. Therefore, we can obtain stationary points by solving the equations.

$$\frac{dx}{dt} = -\frac{Axw}{x+K} + Ly + D(m-x-y) = 0 \quad (3.1.a)$$

$$\frac{dy}{dt} = -By + \frac{Axw}{x+K} = 0 \quad (3.1.b)$$

$$\frac{dw}{dt} = R[F(c) - w]w = 0 \quad (3.1.c)$$

$$z = m - x - y \quad (3.1.d)$$

where $B = L + M$ and

$$c = \frac{y}{w+y} \quad \text{or} \quad y = \frac{c}{1-c}w \quad (3.2.a)$$

From (3.1.a) and (3.1.b), we have

$$x = m - \frac{M+D}{D}y \quad (3.2.b)$$

and also from (3.1.b), (3.2.a) and (3.2.b)

$$x = \frac{BKc}{A - (A+B)c} \quad (3.2.c)$$

$$y = \frac{D}{D+M} \left[m - \frac{BKc}{A - (A+B)c} \right] \quad (3.2.d)$$

Equation (3.2.d), combined with (3.2.a) and $F(c) = w$ gives the relation

$$\frac{c}{1-c}F(c) = \frac{D}{M+D} \left[m - \frac{BKc}{A - (A+B)c} \right] \quad (3.3)$$

When (3.3) has a solution c^* we have, from Eqs. (3.1.c), (3.1.d), (3.2.a) and (3.2.c) the following stationary point:

$$\begin{aligned} x^* &= \frac{BKc^*}{A - (A+B)c^*}, & y^* &= \frac{c^*}{1-c^*}F(c^*) \\ z^* &= \frac{M}{D} \frac{c^*}{1-c^*}F(c^*), & w^* &= F(c^*). \end{aligned} \quad (3.4)$$

The condition for this stationary point to be positive is

$$0 < c^* < \frac{A}{A+B}$$

Equation (3.1.c) involves another case, $w=0$, which generates out of Eqs. (3.1.a) and (3.1.b) another stationary point:

$$x^*=m, \quad y^*=z^*=w^*=0. \tag{3.5}$$

We now investigate equation (3.3) which determines the stationary value c^* . The right hand side of (3.3)

$$h(c) = \frac{D}{M+D} \left[m - \frac{BKc}{A-(A+B)c} \right] \tag{3.6}$$

is decreasing as the function of c in the range $0 < c < A/(A+B)$ with an asymptote at its boundary $c=A/(A+B)$, as shown in Fig. 3.a. The other branch of the hyperbola for $c > A/(A+B)$ is irrelevant to the present discussion. The left hand side of (3.3) (see Fig. 3.b)

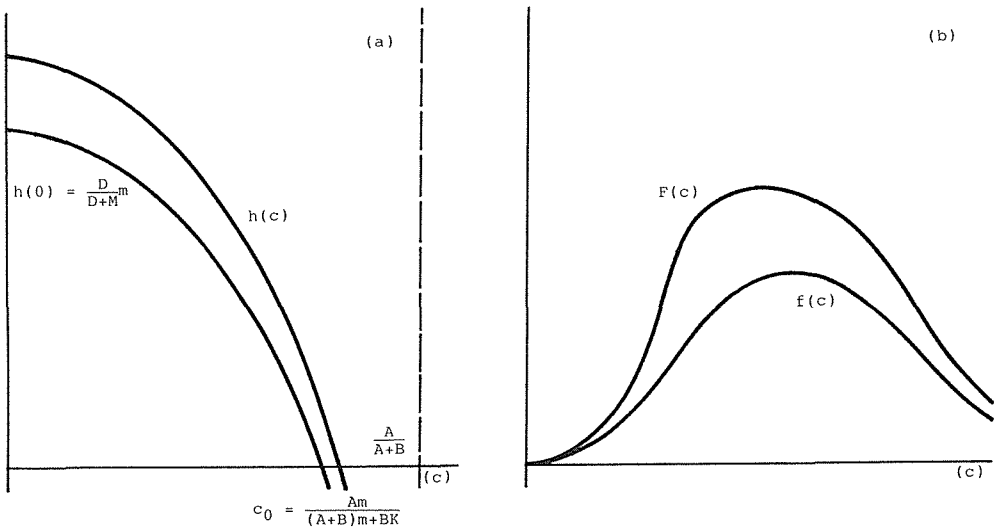


Fig. 3. A graph of function $h(c)$ and $f(c)$.

$$f(c) = \frac{c}{1-c} F(c) \tag{3.7}$$

is a function $F(c)$ of the type shown in Fig. 2 reduced by the factor $c/(1-c)$; note that $c/(1-c) < 1$ because nutrient concentration c is smaller than $1/2$ in any real system.

As typical situations, we can consider two cases depending upon the parameter values of the system (3.1) and the functional form of $F(c)$.

(i) Single intersection (Fig. 4)

In this case, the curve $h(c)$ has a single intersection with the curve $f(c)$ in the range $0 < c < A/(A+B)$, and it is the single solution c^* of the equation (3.3) which gives a positive stationary point (3.4). This situation will be expected to appear when the value of parameter K , B/A or m is large, provided that the curve $f(c)$ does not drop down very rapidly in this range.

(ii) Triple intersections (Fig. 5)

On the contrary, when the value of parameter K or A/B is relatively small, the

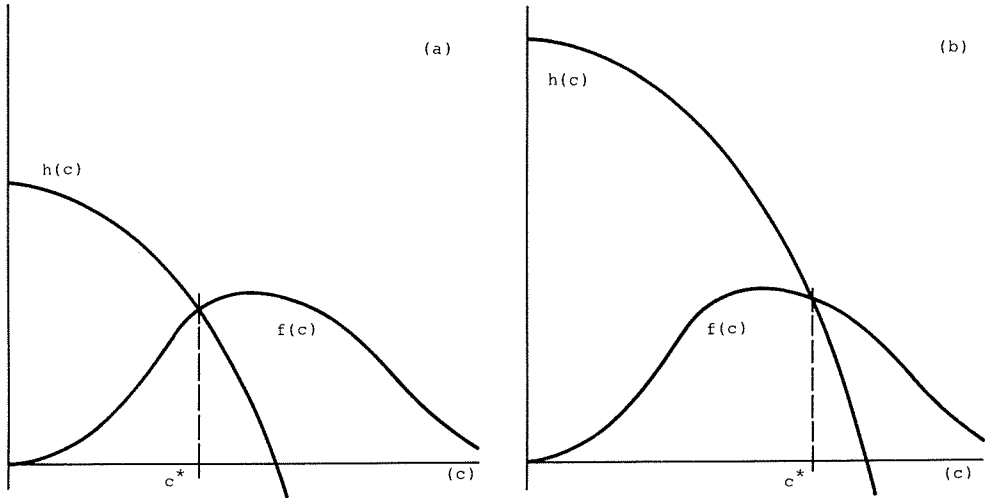


Fig. 4. Single intersection-one stationary point. (a) the point determined by c^* is asymptotically stable; (b) the point determined by c^* is asymptotically stable if R is sufficiently small, otherwise unstable.

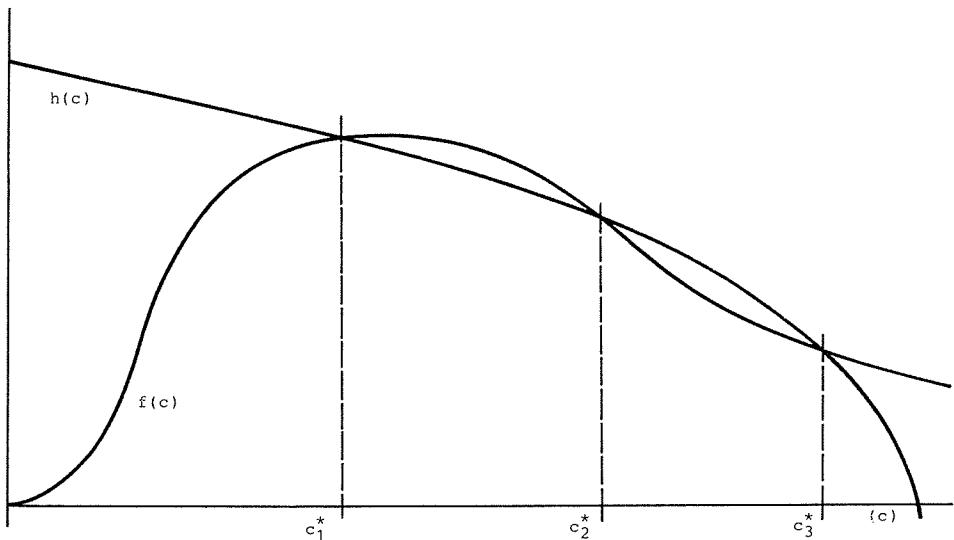


Fig. 5. Triple intersections-three stationary points. c_1^* determines an asymptotically stable stationary point; c_2^* determines an unstable stationary point; c_3^* determines a point whose stability character depends on R : the point is asymptotically stable for any sufficiently small R , otherwise unstable.

curve $h(c)$ has possibly three intersections with the curve $f(c)$ at c_1^* , c_2^* and c_3^* as shown in Fig. 5. Thus, in this case we have three positive stationary points.

STABILITY ANALYSIS

In the present model, the total amount of nutrient $m=x+y+z$ is conserved and the

growth of plant is also limited. Therefore, it can be seen that all trajectories of system (1.1) are bounded in the nonnegative domain of a four dimensional space (x, y, z, w) . In order to study asymptotical behavior of the system, we summarize in this section the results of stability analysis of the stationary points, which have been obtained in the previous section. The mathematical details of calculation are given in Appendix.

(i) When there is only one intersection of the two curves, $h(c)$ and $f(c)$, the system asymptotically approaches either this stationary point or a limit cycle.

First, it can be proved that if the value c^* of intersection lies in such a region that

$$\frac{df}{dc} = \frac{d}{dc} \left[\frac{c}{1-c} F(c) \right] \geq 0 \quad (4.1)$$

the stationary point given by (3.4) is stable and the system asymptotically approaches this stationary state.

Even if $df/dc < 0$ at c^* , as long as its absolute value $|df/dc|$ is smaller than some critical value, the stability can be secured; otherwise the stationary point given by c^* becomes unstable and the system approaches a limit cycle surrounding this unstable stationary point. It can also be seen that a larger value of the parameter R reduces this critical value and the instability of the stationary point occurs at rather small values of $|df/dc|$. This instability may possibly occur in a part of the descending region of the curve $f(c)$, and generally, c^* gives a stable stationary state on both sides of this region.

When $F(c)$ gives such severe condition that $F(c)=0$ in some part of the deficiency or toxic regions of the nutrient concentration (Fig. 2) and if c^* lies on that region, i.e., $F(c^*)=0$, the system approaches the state $x^*=m, y^*=z^*=w^*=0$, and hence the plants completely die out.

(ii) We next consider the case in which the two curves $h(c)$ and $f(c)$ have three intersections at c_1^*, c_2^* and c_3^* as shown in Fig. 5. In most cases the condition (4.1) holds at the point c_1^* and even if c_1^* lies in the region such that $df/dc < 0$, we can expect the value c_1^* to give a stable stationary point. At the value c_2^* the relation $|df/dc| > |dh/dc|$ always holds, which implies that the stationary point given by c_2^* is always unstable. The point c_3^* , which appears in the region $df/dc < 0$, mostly gives a stable stationary point provided that $|df/dc|$ does not exceed the critical value; otherwise a limit cycle takes place.

Therefore, in this case, depending upon an initial condition, the system asymptotically approaches either of the stable stationary states given by c_1^* and c_3^* , including a possibility of a limit cycle.

PARAMETER DEPENDENCE

Since the behavior of the present model depends on many parameter values, it would appear difficult to get a concise grasp of the characteristic properties of the system from the mathematical results obtained in the last section. However, assuming that the carrying capacity of plant $F(c)$ has the nutrient concentration dependence of the type given by Fig. 2, it is possible to develop a perspective on the properties of stationary states by paying attention to the two intercepts of the curve $y=h(c)$ (see Fig. 3):

$$h(0) = \frac{D}{D+M} m \quad \text{and} \quad c_0 = \frac{Am}{(A+B)m+KB} < \frac{A}{A+B}$$

As we have already discussed in the previous sections, the stationary states of our system are given by intersections of two curves $h(c)$ and $f(c)$. The parameter dependence of curve $h(c)$ is schematically shown in Fig. 3.a.

The following is a summary of the parameters that characterize the properties of the system.

(i) $B/A=(L+M)/A$. This is the ratio of the coefficients of the loss and uptake rates of the plant and it determines the position of asymptote $c=A/(A+B)$ of curve $h(c)$. If the value B/A becomes larger, the range of curve $h(c)$ is compressed, which shifts c_0 to a smaller value of c , and thus the value c^* for the stationary point, at which the curve $h(c)$ intersects with $f(c)$ also moves from the adequate nutrient region to the deficiency region where the plants are stunted. On the contrary, a smaller value of B/A moves the stationary point to the right and in the toxic region the plant may possibly be damaged by poisonous effects of the nutrient.

(ii) K . Half saturation constant K is a measure of the absorbing ability of the plant. The plant with a smaller half saturation constant has a higher uptake rate especially at low concentration of the available nutrient pool. A small value of K possibly shifts the stationary point from the deficiency region to the adequate one.

iii) M/D and m . A high decomposition rate raises the value of $h(0)$ (see Fig. 3.a). The total amount of nutrient, m , also lifts up the entire curve $h(c)$.

(iv) R . Although the stationary points are determined independently of the value of growth rate factor R , the stability condition of the stationary point is sensitively affected by R . A high growth rate of the plant destabilizes the stationary point in the range of a surplus nutrient, which corresponds to the descending part of the curve $f(c)$, and the system approaches a limit cycle.

Appendix

Stability

Consider system (3.1) and let

$$X(x, y, w) = -\frac{Axw}{x+K} + Ly + D(m-x-y)$$

$$Y(x, y, w) = -By + \frac{Axw}{x+K}$$

$$W(x, y, w) = R[F(c) - w]w.$$

Then we have

$$\frac{\partial X}{\partial x} = -\frac{AKw}{(x+K)^2} - D, \quad \frac{\partial X}{\partial y} = L - D, \quad \frac{\partial X}{\partial w} = -\frac{Ax}{x+K}$$

$$\frac{\partial X}{\partial x} = \frac{AKw}{(x+K)^2}, \quad \frac{\partial X}{\partial y} = -B, \quad \frac{\partial X}{\partial w} = \frac{Ax}{x+K}$$

$$\frac{\partial W}{\partial x} = 0, \quad \frac{\partial W}{\partial y} = R \frac{dF(c)}{dc} \frac{\partial c}{\partial y} w$$

$$\frac{\partial W}{\partial w} = R[F(c) - w] + R \left[\frac{dF(c)}{dc} \frac{\partial c}{\partial w} - 1 \right] w$$

Thus the matrix of linearized system at the stationary point (3.4) is given as

$$\begin{vmatrix} -\alpha(c)F(c)-D & L-D & -\frac{Bc}{1-c} \\ \alpha(c)F(c) & -B & \frac{Bc}{1-c} \\ 0 & R(1-c)^2\frac{dF(c)}{dc} & -R[c(1-c)\frac{dF(c)}{dc}+F(c)] \end{vmatrix}$$

where

$$\alpha(c) = \frac{[A-(A+B)c]^2}{AK(1-c)^2}$$

The characteristic equation of this matrix is given by

$$\begin{aligned} \lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 &= 0 \quad \text{with} \\ a_1 &= B + D + \alpha(c)F(c) + R(1-c)^2\frac{df(c)}{dc} \\ a_2 &= BD + [RB + (M+D)\alpha(c)]F(c) \\ &\quad + R[D + \alpha(c)F(c)](1-c)^2\frac{df(c)}{dc} \\ a_3 &= RBDF(c) + R(M+D)(1-c)^2\alpha(c)F(c)\frac{df(c)}{dc} \\ &= R(M+D)(1-c)^2\alpha(c)F(c)\left[\frac{df(c)}{dc} - \frac{dh(c)}{dc}\right], \end{aligned}$$

where

$$f(c) = \frac{c}{1-c}F(c) \quad \text{and} \quad h(c) = \frac{D}{M+D}\left[m - \frac{KBc}{A-(A+B)c}\right]$$

Therefore the stability conditions (Routh-Hurwitz)

$$a_1 > 0, \quad a_3 > 0$$

and

$$\begin{aligned} a_1a_2 - a_3 &= \left\{ B + D + \alpha(c)F(c) + R(1-c)^2\frac{df(c)}{dc} \right\} \\ &\quad \left\{ BD + R[D + \alpha(c)F(c)](1-c)^2\frac{df(c)}{dc} \right\} \\ &\quad + \left\{ B + \alpha(c)F(c) \right\} \left\{ RBF(c) + (M+D)\alpha(c)F(c) \right\} \\ &\quad + D(D+M)\alpha(c)F(c) + BF(c)R^2(1-c)^2\frac{df(c)}{dc} > 0 \end{aligned}$$

are satisfied when $df/dc > 0$.

Acknowledgments

Among all the members of Kyoto University Biophysycal Laboratory whose critical remarks

helped me to avoid the major blunders and make the ideas clearer (and I remain the sole responsible for all the remaining mistakes), I specially thank two: prof. Ei Teramoto, for without his encouragement and gentle criticism this paper wouldn't see the light of the day, and prof. Nanako Shigesada for all her invaluable comments.

References

- Epstein Emanuel (1972) *Mineral Nutrition of Plants: Principles and Perspectives*. Wiley, New York. 412 pp.
- Heath, G. W., Arnold K. Margaret and C. A. Edwards (1966) Studies in Leaf Litter Breakdown I. Breakdown Rates of Leaves of Different Species. *Pedobiologia* Bd. 6: 1-12.
- Larcher, W. (1980) *Physiological Plant Ecology* (2nd. ed.), (transl. M. A. Biederman-Thorson). Springer-Verlag, Berlin. 303 pp.
- Nye, P. H., J. L. Brewster, and K. K. S. Bhat, (1975) The Possibility of Predicting Solute Uptake and Plant Growth Response from Independently Measured Soil and Plant Characteristics: I. The Theoretical Basis of the Experiments. *Plant and Soil* 42: 161-170.
- Parker, G. G. (1983) Throughfall and Stemflow in the Forest Nutrient Cycle. *Adv. Ecol. Res.* 13: 57-133.
- Waide, J. B., J. E. Krebs, S. A. Clarkson and M. E. Setzler (1974) A Linear System Analysis of the Calcium Cycle in a Forested Watershed Ecosystem. *Prog. Theor. Biol.* 3: 261-345.

著者：イゴール・ライラ，〒606 京都市左京区北白川追分町 京都大学理学部生物物理学教室。