Plant Growth as a Function of a Single
Mineral Nutrient: An Open Model

IGOR LEILER

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

Abstract   Growth of a plant species as a function of a single mineral nutrient is described by a nonlinear response model. The model consists of four nonlinear differential equations; three of them describe the nutrient flow; the remaining equation describes the growth of plant species. The nutrient circulates between three compartments: the plant species, litter, and the nutrient pool compartment. The input and output of nutrient in respect to the system are considered as well; the nutrient pool and litter compartment are open, whereas the plant species is not assumed either to absorb or lose any nutrient in its contact with the environment. The uptake of nutrient is described by a general function, which takes saturation effect into account. The growth rate of plant species is described by a generalized logistic equation which depends on the concentration of absorbed nutrient.

   The stationary states of the model are studied and their local stability thoroughly investigated. The model's dependency on its own parameters is given an extensive consideration, which, in turn, leads to a theoretical answer on what kind of environment is best, in terms of survival, for a given plant species.

1. INTRODUCTION

   Recently, a number of papers on growth of plants as a function of the circulating materials have been published (e.g. Hallam & de Luna, 1984) and narrowed the gap between the experimental and theoretical studies on plant growth. There exists vast literature (e.g. Waide et al., 1974) which assumes linear response of the species to the nutrient concentration. However, this assumption may not suffice when a more detailed picture of the ecosystem's response to varying material levels is required.

   This paper, though it contains a similar idea as Hallam and de Luna's paper (generalization of the linear approach models on material circulation), attacks the problem in a different way. Whereas Hallam and de Luna take the material concentration (in their case a pollutant) as the crucial system variable, the present model deals instead with the total amounts of the circulating nutrient, and leads to theoretical results that are in complete agreement with biological facts as reviewed by Chapin (1980).

   This paper emphasizes the importance of material input and output. The roles of the other parameters are fully investigated elsewhere (Leiler, 1986); their roles are the same for both models, the closed, as well as the open variant.

   The analysis of the model will show that, both, insufficient and excessive inputs negatively affect the plant species. The same result holds for either too small or too large an output. The number of parameters that govern the system, though large, is

brought to the essential limit, and each parameter, as it will become clear through the analysis, plays its own role in the system.

The system (see Fig. 1.) is assumed to consist of three compartments: a nutrient pool, a plant species, and a litter compartment and each of these compartments is assumed to be homogeneous, responding immediately to the nutrient level contained in itself. Two of these compartments, the nutrient pool and litter compartment, are assumed open to the environment; i.e., the nutrient can be both, lost and absorbed, by either of the two compartments. The absorption can be due to atmospheric input, as well as due to the weathering of the basic rock. The loss of nutrient can be due to leaching and logging. Consumers are not considered a part of the system. The circulation of nutrient, together with its input and output, forms the base of the model, and this base is described by three nonlinear differential equations. The plant species is assumed to respond to different nutrient levels by its growth. An insufficient nutrient level results in stunted growth; the same effect follows from an excess of the nutrient. This response is described by a general logistic equation.
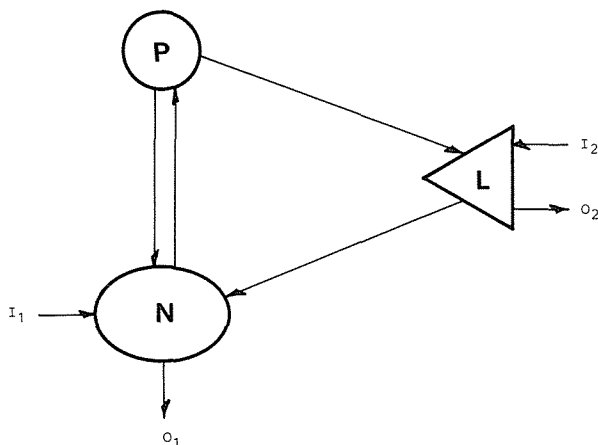
Fig. 1. Nutrient circulation. N: nutrient pool; P: plant population; L: litter and decomposers; I_k, O_k: inputs and outputs of the material.

The model and its explanation are given in section two. Section three deals with local stability of critical points. The biological analysis of the model is given in the fourth section, and the mathematical proofs form the last, fifth, section.

2. THE MODEL

The model is schematically shown in Figure 1. Let x, y, and z denote the total amounts of a mineral nutrient in the nutrient pool, plant species, and litter compartment, respectively, at time t. Further, let w represent the population biomass in pure dry weight (=dry weight−nutrients) of the plant population.

The system dynamics is given by the set of differential equations:

$$x' = -AS(x)w + Ly + Dz - P_1(x) + Q_1$$
$$y' = -Ly - My + AS(x)w$$
$$z' = -Dz + My - P_2(z) + Q_2 \qquad (2.1)$$
$$w' = R[F(c) - w]w$$

with an appropriate set of initial conditions, and

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

The constants A, D, Q_1, Q_2, and R are positive, whereas L and M are nonnegative and do not vanish simultaneously.

The uptake rate, $AS(x)w$, depends on the nutrient availability and the plant biomass. Generally accepted Michaelis-Menten kinetics is replaced by a general function form $AS(x)$, with S strictly increasing, differentiable, and

$$S(0) = 0, \quad \lim_{x \to \infty} S(x) = 1$$

Further, the uptake rate is assumed proportional to the plant biomass, which is, in turn, proportional to its pure dry weight w.

The leaching of nutrient from the plant to the nutrient pool is proportional to the total amount of nutrient contained in the plant population; L is the leaching constant; it can be zero for some nutrients and plants.

The decomposition rate, Dz, is linearly dependent on the amount of nutrient contained in the litter compartment; D is the decomposition constant.

The loss of nutrient from the system is given by $P_1(x)$ and $P_2(z)$. Both functions are strictly increasing: the more nutrient is there, the more is lost. On the one hand, the nutrient pool is not assumed to bind the nutrient; therefore $P_1(x)$ is unbounded. On the other hand, the litter can hold the nutrient, rendering it largely inaccessible to leaching; therefore, $P_2(z)$ can have an upper limit. Both functions are differentiable and

$$P_1(0) = P_2(0) = 0$$

The input of nutrient (from the environment) is constant; Q_1, Q_2 are the input rate constants.

The loss of nutrient due to the death process (fallen leaves and branches, dead roots) of the plant is proportional to the amount of nutrient in the plant; M is the mortality constant: it can be zero for some nutrients and plants.

The growth of the plant species, described by a general logistic equation (see Larcher, 1980), depends on the parameter R and function $F(c)$ (Fig. 2). The parameter R is the maximum growth rate; i. e., the growth rate when the amount of nutrient is optimal. The function $F(c)$ represents the relative growth rate which depends on the nutrient concentration, c, in the plant species. Either too high or too low nutrient concentration causes stunted growth (Austin & Austin, 1980) of the plant population. Thus, $F(c)$ has a functional form similar to the one in Figure 2. For a given $F(c)$ it seems reasonable to introduce a constant, w_m, with the following properties (see Fig. 2):

w_m is a critical value that separates the lower level from the upper level of the growth rate: it
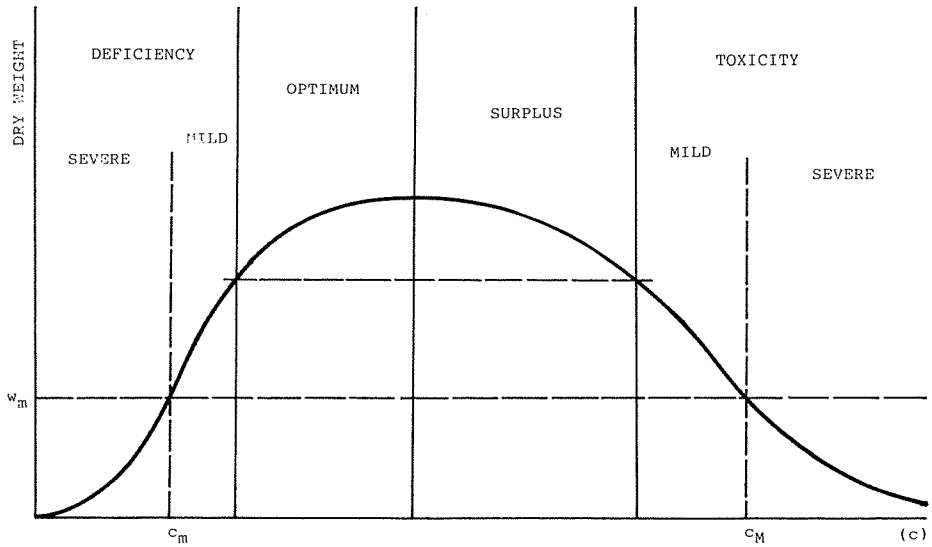
Fig. 2. Dry weight v.s. nutrient concentration. Response of a plant to various nutrient levels. w_m: minimum growth constant; c_m: deficiency constant; c_M: toxicity constant. (After Larcher, 1980)

serves as a measure of the plant's stuntedness. If $w \leq w_m$ then the plant is said to be stunted.

The introduction of this growth constant w_m (which, of course, depends on the plant species) induces the following two constants:

c_m is a deficiency constant: if $c \leq c_m$ then the plant growth will be stunted ($w \leq w_m$) due to the deficiency of the nutrient.

c_M is a toxicity constant: if $c \geq c_M$ then the plant growth will be stunted ($w \leq w_m$) due to the nutrient toxicity.

3. RESULTS

A. CRITICAL POINTS and THEIR STABILITY

A brief look at the system (2.1) clearly shows that its every solution (x, y, z, w) is nonnegative and bounded, $0 \leq (x, y, z, w) < \infty$, if such are the initial conditions.

In the rest of the paper, the following functions whose character will become clear through the subsequent analysis are extensively used:

$$f(c) = \frac{c}{1-c} F(c) \tag{3.0.a}$$

$$h(c) = Q_1 + Q_2 - P_1[S^{-1}(\frac{B}{A} \frac{c}{1-c})] \tag{3.0.b}$$

$$g(c) = P_2[P_2^{*-1}(Mf(c) + Q_2)] \tag{3.0.c}$$

$$P_2^*(z) = Dz + P_2(z) \tag{3.0.d}$$

where $B = L + M$. S^{-1} and P_2^{*-1} are the inverse functions of S and P_2^* respectively. Clearly, $h(c)$ is a strictly decreasing function, whereas the functional form of $g(c)$ depends on the functional form of $f(c)$, which, in turn depends on $F(c)$. A graphical representation of these functions is given in Figure 3., where it is assumed that $F(c)$ is a one humped curve, the most probable form the function $F(c)$ would take on in real situations.
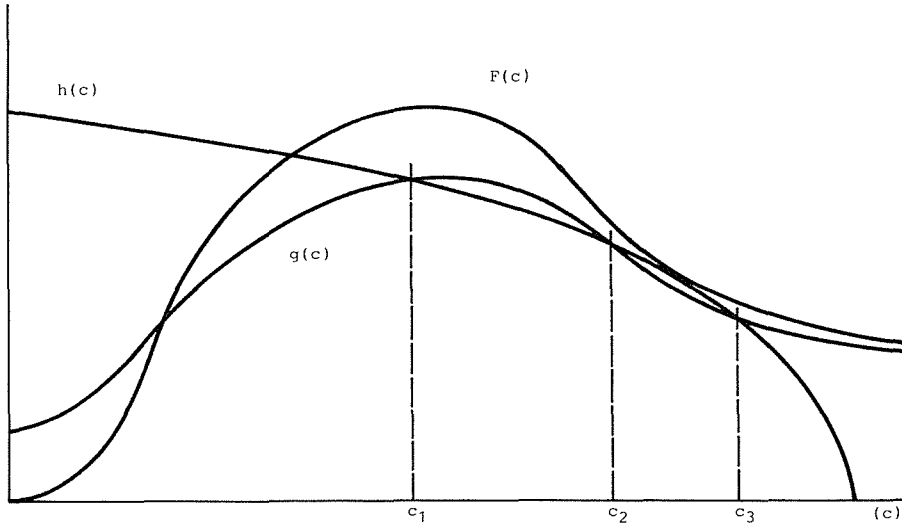
Fig. 3. Critical points of the system. A point given by c_1 is asimptotically stable; A point given by c_2 is unstable; A point given by c_3 can be either stable or unstable—its character depends mainly on R.

The critical points of the system will be derived first.

Statement 1 All the nontrivial $(w \neq 0)$ critical points, (x_c, y_c, z_c, w_c), of the system are given by

$$x_c = S^{-1}\left(\frac{B}{A} \frac{c^*}{1-c^*}\right)$$

$$y_c = f(c^*)$$

$$z_c = P_2^{*-1}(Mf(c^*) + Q_2) \tag{3.1}$$

$$w_c = F(c^*)$$

where c^* is a solution of the equation

$$h(c) = g(c) \tag{3.2}$$

Note that $y_c/(w_c + y_c) = f(c^*)/(F(c^*) + f(c^*)) = c^*$; that is, c^* represents the nutrient concentration in the plant. Note also that these critical points do not depend on the initial conditions.

The stability properties of the critical points are summarized in the following statements (see section 5 for the proofs).

Statement 2 Every critical point, given by Eqs. (3.1) and (3.2), is asymptotically stable if

$$\frac{df(c)}{dc}\Big|_{c=c^*}\geq 0 \quad \text{and} \quad F(c)>0$$

Statement 3 If the conditions

$$\frac{df(c)}{dc}<0$$

and

$$\frac{dg(c)}{dc}>\frac{dh(c)}{dc}$$

are satisfied at a critical point given by Eqs. (3.1) and (3.2) then the critical point will be asymptotically stable for any sufficiently small R.

Further, the critical point will be unstable if

$$\frac{dg(c)}{dc}<\frac{dh(c)}{dc}$$

The global stability of the model is still an open problem; however, all the numerical studies thus far conducted suggest that the model is globally stable at least when there exists exactly one critical point which is, in addition, asymptotically stable.

B. Critical Points and System Parameters

In this paragraph, the dependency of critical points on the parameters and functions involved in the model is studied. The parameters and functions in the model can be divided into several groups, according to their specific roles in the model:

 i)   uptake rate—maximum uptake rate A and function $S(x)$
 ii) loss rate—leaching constant L and mortality constant M
 iii) nutrient availability—decomposition constant D, inputs Q_1 and Q_2, outputs $P_1(x)$ and $P_2(z)$
 iv) growth—response function $F(c)$, deficiency constant c_m and toxicity constant c_m, and the maximum growth rate R

As it has been said already, this paper emphasizes the roles of input and output; therefore, only the parameters and functions concerned with input and output will be discussed.

All the subsequent propositions are concerned with the effects of the model parameters and functions on the model's critical points in terms of *nutrient deficiency* and *nutrient toxicity*. The term "nutrient deficiency" states that all the solutions of the equation $h(c)=g(c)$; i. e., the nutrient concentrations in the plant, lie in the deficiency interval $[0, c_m]$. Likewise, nutrient toxicity means that they all lie in the toxicity interval $[c_M, 1)$.

Proposition 1 A small input Q_1 (Q_2) tends to cause deficiency. A large input Q_1 (Q_2) may cause toxicity.

Proposition 2 A fast increasing output $P_1(x)$ causes the deficiency. A slowly increasing output $P_1(x)$ may cause the toxicity.

Proposition 3 A fast increasing output $P_2(z)$ may cause the deficiency. A slowly increasing output $P_2(z)$ may cause the toxicity.

All these propositions, which may appear to the reader heuristic, are such only because the number of parameters and functions which govern the system is rather large. The subsequent analysis of model and especially Eq. (3.2) will show that explicit formulations are by all means possible; however, various possibilities make the explicit formulations rather awkward—the essential information, mathematical as well as biological, becomes blurred.

4. BIOLOGICAL ANALYSIS

A closed variant $(P_1(x)=P_2(z)=Q_1=Q_2=0)$ of the present model, discussed in Leiler (1986), has led to a number of hypotheses on the evolutionary adaptation of plant species. A comparison of the closed model to the present model would show that both models display in essence the same features and lead to the same hypotheses. Those hypotheses have been based on the interplay between the intrinsic properties of the plant and the environmental conditions.

In this section I shall give an interpretation for the results of the model analysis in terms of evolution. This interpretation will form the answer to the following question:

Given an environment $(P_1(x)$, $P_2(z)$, Q_1, Q_2, and sometimes $D)$, what plant species can survive in it?

The following two cases may be considered:

Case a). Nutrient-poor environment: the case when the inputs Q_1 and Q_2 are relatively small, whereas the outputs $P_1(x)$ and $P_2(z)$ are relatively fast increasing functions. There are many ecosystems with a nutrient-poor environment, and yet, the plant species are surviving. This fact can be explained in terms of the model if the plant has the following properties:

i) The deficiency constant, c_m, has to be sufficiently small. In other words, a plant species has to be highly tolerant to low levels of the available nutrient.
ii) The uptake rate $AS(x)$ should be sufficiently large, i. e., a plant species should be sufficiently effective in taking up the nutrient at its low concentrations.
iii) The loss of nutrient through leaching (L) and death process (M) should not be too large, i. e., both, the leaching constant L and death constant M should be sufficiently small.
iv) The plant biomass, $w=F(c)$, should not be too large.

Case b). Nutrient-rich environment: the case where the inputs Q_1 and Q_2 are relatively large, whereas the outputs $P_1(x)$ and $P_2(z)$ are relatively slowly increasing

functions. A nutrient-rich environment may not be too good a host of a plant species with a low tolerance for high nutrient concentrations. Thus, a nutrient-rich environment can support only those species that can successfully tolerate and avoid toxicity. The following conclusions are based on the analysis of the model:

i') The toxicity constant, c_M, has to be sufficiently large, i. e., the plant species has to be highly tolerant to the toxic nutrient levels.
ii') The maximum uptake rate, A, should not be too large.
iii') The loss of nutrient through leaching (L) and death process (M) should be sufficiently large.
iv') The plant species's size, $w=F(c)$, should not be too small.

The above conclusions help explain certain facts on the adaptation of plants to different environmental conditions; moreover, the theoretical explanation is in complete agreement with known biological facts as reviewed by Chapin (1980).

5. MATHEMATICAL ANALYSIS AND PROOFS

Proof of Statement 1   First, Eqs. (3.1), together with Eq. (3.2), will be derived, and then the existence of at least one solution of Eq. (3.2) proved.

Every critical point satisfies the following equations:

$$x'=y'=z'=w'=0$$

and the first three equations give:

$$Q_1+Q_2-P_1(x)-P_2(z)=0 \qquad \text{(input=output)} \qquad (5.1)$$

A trivial critical point is obtained by setting $w=0$. Thus, a trivial critical point, (x_c, y_c, z_c, w_c), is given by

$$x_c=P_1^{-1}[DP_2^{*-1}(Q_2)+Q_1], \qquad y_c=0$$
$$z_c=P_2^{*-1}(Q_2), \qquad w_c=0$$

The function P_2^*, as well as P_1, is strictly increasing; therefore, its inverse P_2^{*-1} (P_1^{-1}) always exists.

A nontrivial critical point is obtained by setting

$$w=F(c)$$

From $z'=0$ follows that

$$z=P_2^{*-1}(My+Q_2)$$

and Eq. (5.1) changes into

$$P_2[P_2^{*-1}(My+Q_2)]=Q_1+Q_2-P_1(x) \qquad (5.2)$$

Further, from $y'=0$ follows that

$$x=S^{-1}(\frac{B}{A}\frac{c}{1-c}) \qquad (5.3)$$

It is also obvious that

$$y = f(c) \tag{5.4}$$

Combining (5.2), (5.3), and (5.4) gives

$$P_2[P_2^{*-1}(Mf(c) + Q_2)] = Q_1 + Q_2 - P_1[S^{-1}(\frac{B}{A}\frac{c}{1-c})] \tag{5.5}$$

which is equivalent to Eq. (3.2); Eqs. (3.1) are an obvious consequence of the above calculation. A graphical representation of Eq. (5.5), i.e., (3.2), together with the function $F(c)$, is given in Figure 3.

Eq. (5.5), i.e., (3.2), consists of only continuous functions. Clearly (see also Fig. 3)

$$h(0) = Q_1 + Q_2 > 0 \tag{5.6.a}$$

$$g(0) = P_2[P_2^{*-1}(Q_2)] > 0 \tag{5.6.b}$$

From (5.6.b) follows that

$$g(0) = P_2[P_2^{*-1}(Q_2)] < P_2^*[P_2^{*-1}(Q_2)] = Q_2$$

Thus;

$$0 < g(0) \leq h(0) \tag{5.7}$$

It is obvious from (3.0.b) that the function $h(c)$ is strictly decreasing, and $h(c) = 0$ at

$$c = \frac{AS(u)}{AS(u) + B} < \frac{A}{A + B} < 1 \qquad u = P^{-1}(Q_1 + Q_2) \tag{5.8}$$

The function $g(c)$ is continuous, nonnegative and $g(0) \leq h(0)$; therefore, there exists c, such that $h(c) = g(c)$. This completes the proof of Statement 1. Q. E. D.

Proof of Statement 2 Let $F(c) > 0$; then the matrix of the linearized system is

$$A = \begin{bmatrix} -AS'F - P_1' & L & D & -AS \\ AS'F & -B & 0 & AS \\ 0 & M & -D - P_2' & 0 \\ 0 & R^*F' & 0 & -R^*f' \end{bmatrix}$$

where

$$S' = \frac{dS(x)}{dx}\Big|_{x=x_c} \qquad F = F(c) \qquad P_1' = \frac{dP_1(x)}{dx}\Big|_{x=x_c}$$

$$S = S(x_c) \qquad P_2' = \frac{dP_2(z)}{dz}\Big|_{z=z_c} \qquad R^* = (1-c)^2 R$$

$$F' = \frac{dF(c)}{dc} \qquad f' = \frac{df(c)}{dc}$$

A critical point is asymptotically stable if and only if all the roots of the characteristic polynomial

$$det(A-\lambda I)=\lambda^4+a_1\lambda^3+a_2\lambda^2+a_3\lambda+a_4 \qquad (5.9)$$
(I is the unit matrix)

have nonnegative real parts.
Here

$$a_1=AS'F+P_1'+B+D+P_2'+R^*f'$$

$$a_2=BP_1'+MAS'F+B(D+P_2')+BRF+(D+P_2')AS'F$$

$$\quad +P_1'(D+P_2')+(D+P_2')R^*f' \qquad (5.10)$$

$$\quad +AS'FR^*f'+P_1'R^*f'$$

$$a_3=P_1'B(D+P_2')+P_2'MAS'F+P_1'BRF+MAS'FR^*f'$$

$$\quad +B(D+P_2')RF+(D+P_2')AS'FR^*f'+P_1'(D+P_2')R^*f'$$

$$a_4=P_1'B(D+P_2')RF+P_2'MAS'FR^*f'$$

In order to see that all the roots of (5.9) have nonnegative real parts, the following inequalities must be proved (Routh-Hurwitz condition):

$$a_1>0$$

$$a_1a_2-a_3>0$$

$$(a_1a_2-a_3)a_3-a_1^2a_4>0$$

$$a_4>0$$

The proof of these inequalities is quite lengthy, yet elementary, and as such omitted. Q. E. D.

Proof of Statement 3   In order to prove this proposition, the coefficients a_i of Eq. (5.9) are rewritten as:

$$a_i=A_i+B_iRf' \qquad i=1, 2, 3, 4$$

Comparison of these with (5.10) shows that

$$A_i, \ B_i>0 \qquad i=1, 2, 3, 4$$

Further, a_4 can be transformed into

$$a_4=ARS'F(D+P_2')(1-c)^2[\frac{dg(c)}{dc}-\frac{dh(c)}{dc}]$$

and the condition

$$\frac{dg(c)}{dc}>\frac{dh(c)}{dc}$$

assures that $a_4>0$ which is a necessary condition for the asymptotic stability of the critical point.
If, on the other hand

$$\frac{dg(c)}{dc} < \frac{dh(c)}{dc}$$

which can happen only if

$$\frac{df(c)}{dc} < 0$$

then the point in question will be unstable. This proves the second part of Statement 3. The first part assumes

$$\frac{df(c)}{dc} < 0$$

and

$$\frac{dg(c)}{dc} > \frac{dh(c)}{dc}$$

which assures that $a_4 > 0$ as mentioned above. Further, if R is sufficiently small then

$$a_i = A_i + B_i R f' \approx A_i > 0 \qquad i = 1, 2, 3$$

and it can be easily seen that

$$a_1 a_2 - a_3 > 0$$

$$(a_1 a_2 - a_3) a_3 - a_1^2 a_4 > 0$$

Thus, the point in question is asymptotically stable. This completes the proof of Statement 3. Q.E.D.

Proof of Proposition 1 In order to prove this proposition, as well as all the others, the analysis of Eq. (3.2), i.e.,

$$h(c) = g(c) \tag{5.11}$$

is necessary.

The function $h(c)$ (see Fig. 3 and (3.0.b), (3.0.c)) is strictly decreasing, and $g(c)$ is a strictly increasing function at least at those points where $F(c)$ is not decreasing. Further, it has been shown (Eq. (5.7) and (5.8)) that

$$h(0) \geq g(0) > 0$$

and $h(c_z) = 0$ at

$$c_z = \frac{AS(u)}{AS(u) + B} \qquad u = P_1^{-1}(Q_1 + Q_2)$$

Let c^* be a solution of Eq. (5.11); then

$$c^* \leq c_z < \frac{A}{A+B} \tag{5.12}$$

It can easily be seen that Eq. (5.11) possesses at most one solution in an interval in

which $F(c)$ is not decreasing; for in such an interval $g(c)$ is strictly increasing, whereas $h(c)$ is strictly decreasing.

Proposition 1 is a consequence of the following consideration: the function $g(c)$ is independent of Q_1, and

$$h(c, Q_1^*) < h(c, Q_1^{**}) \qquad \text{if} \qquad Q_1^* < Q_1^{**}$$

This means that $h(c)$ decreases together with Q_1. So does also c^*. Note that the present analysis is concerned only with the stable critical points which lie in the range where $g(c)$ is increasing. Thus, the deficiency may follow. On the other hand, a sufficiently large Q_1 will cause the toxicity provided that

$$c_M < \frac{A}{A+B}$$

for if this is not the case then the toxicity range cannot be attained (see (5.12)).

The same is true for Q_2, which can be shown by the following: Function $g(c)$ can be rewritten with the help of (3.0.b) and (3.0.d) as

$$g(c) = Mf(c) + Q_2 - DP_2^{*-1}[Mf(c) + Q_2]$$

Thus, the Eq. (5.11) becomes

$$Q_1 - P_1[S^{-1}(\frac{B}{A} \frac{c}{1-c})] = Mf(c) - DP_2^{*-1}(Mf(c) + Q_2)$$

By denoting the left side of this equation by $H(c)$ and its right side by $G(c)$ the following can be easily seen: The function $H(c)$ is independent of Q_2 and strictly decreasing in c. The function $G(c)$ depends on Q_2 and

$$G(c, Q_2^*) \geq G(c, Q_2^{**})$$

if

$$Q_2^* < Q_2^{**}$$

because P_2^{*-1} is an increasing function. Therefore, the function $G(c)$ decreases as Q_2 increases, which means that c^* decreases together with Q_2; the deficiency may follow. On the other hand, a sufficiently large Q_2 will cause the toxicity provided that

$$c_M < \frac{A}{A+B}$$

and given that D is large enough; however, a small D can prevent the toxicity. Q.E.D.

Proposition 2 is obvious. From Eq. (3.0.b) it can be easily seen that a fast increasing P_1 means that $h(c)$ decreases fast; therefore, c_z, together with c^*, will be small; hence, the deficiency is unavoidable. A slowly increasing P_1 leads to a relatively large c_z; however, that need not cause the toxicity; e.g., a small enough Q_1 will prevent it. Q.E.D.

Similar reasoning proves Proposition 3. A fast increasing output P_2 causes function $g(c)$ to increase fast; thus, c^* will be small, and the deficiency may follow. On the other hand, a slowly increasing P_2 leads to a relatively large c^*, which may cause the toxicity. Q.E.D.

References

Austin, M. P. & B. O. Austin (1980) Behaviour of experimental plant communities along a nutrient gradient. *Journal of Ecology* 68: 891–918.

Chapin, F. S. III (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11: 233–260.

Hallam, T. G. & J. T. de Luna (1984) Effects of toxicants on populations: A qualitative approach III. Environmental and food chain pathways. *Journal of Theoretical Biology* 109: 411–429.

Larcher, W. (1980) *Physiological plant ecology*. (transl. M. A. Biederman-Thorson), 2nd ed. Springer-Verlag, Berlin. 303 pp.

Leiler, I. (1986) Material circulation and growth-with special reference to pollution problems. *Ecological Modelling* 31: 125–131.

Waide, J. B., J. E. Krebs, S. P. Clarkson, and E. M. Setzler, (1974) A linear system analysis of the calcium cycle in a forested watershed ecosystem. *Progress in Theoretical Biology* 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.